

Music-syntactic Processing and Auditory Memory – Similarities and Differences between ERAN and MMN

Running head: Review of the ERAN and comparison to the MMN.

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Abstract

The ERAN is an ERP reflecting processing of music-syntactic information, i.e. of acoustic information structured according to abstract and complex regularities. The ERAN is usually maximal between 150-250 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 (also sometimes referred to as music-syntactic MMN) 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 inter-sound relationships that are extracted on-line 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.

Introduction

In 1992, a study from Saarinen et al. changed the concept of the mismatch negativity (MMN) dramatically (Saarinen et al., 1992). Whereas previous studies had inves-

tigated 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, i.e. to mismatches that do not necessarily have to be physical in nature (for other studies reporting abstract feature MMNs see, e.g., Paavilainen et al., 1998, 2001, 2003, 2007; Korzyukov et al., 2003; Schröger et al., 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 et al., 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 Loui et al., 2005; Leino et al., 2007). 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 (reminiscent of a musical piece, Figure 1b), with 50 percent of the stimuli being regular sequences, 25 percent containing an irregular chord at the third, and 25 percent an irregular chord at the final position of the sequence.

The irregular chords elicited an ERP effect which had a strong resemblance with 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 to 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 et al., 2002a, 2003a,b,c), 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 et al., 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 et al., 2007; Maess et al., 2001; Miranda & Ullman, in press; Maidhof & Koelsch, 2007). Note that similar conflicts exist for most (if not all) endogenous ERP components: E.g., 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 et al., 2000; van den Brink et al., 2001), and the MMN has sometimes positive polarity in infants (e.g., Winkler et al., 2003; Friederici et al., 2002).

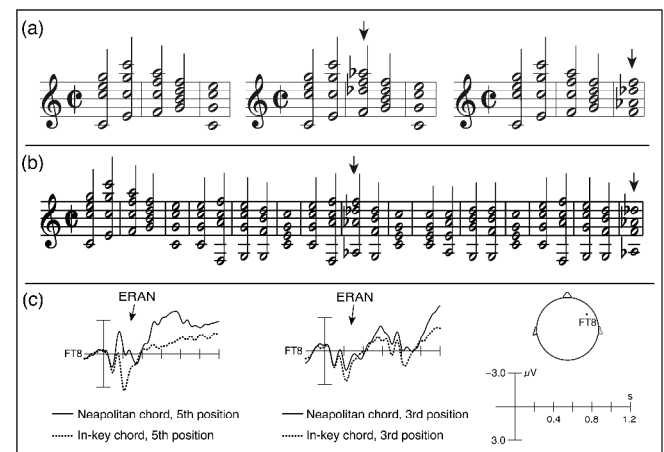


Figure 1. (a) Examples of chord sequences containing in-key chords only (left), a Neapolitan sixth chord at the third (middle), and at the fifth position (right). In the experiment, sequences were presented in direct succession (b). Compared to regular in-key chords, the music-syntactically irregular 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).

Functional Significance

The ERAN reflects music-syntactic processing, i.e. processing of abstract regularity-based auditory information. In major-minor tonal music (often simply referred to as “Western” music), musical syntax process-

ing 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) As a pre-requisite for the syntactic processing of harmonies, a tonal centre has to be extracted (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 (that is, as the tonal centre, 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 centre 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 centre in terms of harmonic distance from the tonal centre (see Figure 2a for explanation of chord functions). E.g., 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 centre 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 centre (e.g., to the dominant, that is 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 centre – the music might again move away from the tonal centre (e.g. to the dominant of *G* major), until it returns to the tonal centre of *G*, and then to the tonal centre of *C* major (for EEG and fMRI studies investigating neural correlates of the processing of changes in tonal key

see Koelsch et al., 2002c; Janata et al., 2002; Koelsch et al., 2003c; Koelsch et al., 2005b).

(4) The succession of chord functions follows statistical regularities, that is, probabilities of chord transitions (Riemann, 1877; Rohrmeier, 2005). For example, in a statistical study by Rohrmeier (2005) 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 regards 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 et al., 2000). While listeners familiar with (Western) tonal music perceive a sequence of chords, they automatically make 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 (e.g., Woolhouse & Cross, 2006), and it appears that many of these principles represent abstract, rather than physical (or acoustical) features (Woolhouse & Cross, 2006; 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., in press).

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 haven’t received formal musical training) are based on extensive musical experi-

ence (e.g., Lamont & Cross, 1994). Likewise, calculating subtle distances between chord functions and a tonal centre 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 learnt through early childhood (Lamont & Cross, 1994). That is, while it is conceivable that humans naive to Western music find the probabilities for chord transitions plausible (because they follow abstract mathematical principles which 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 differ-

ent 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 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; Loui et al., 2005; Leino et al., 2007) 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).

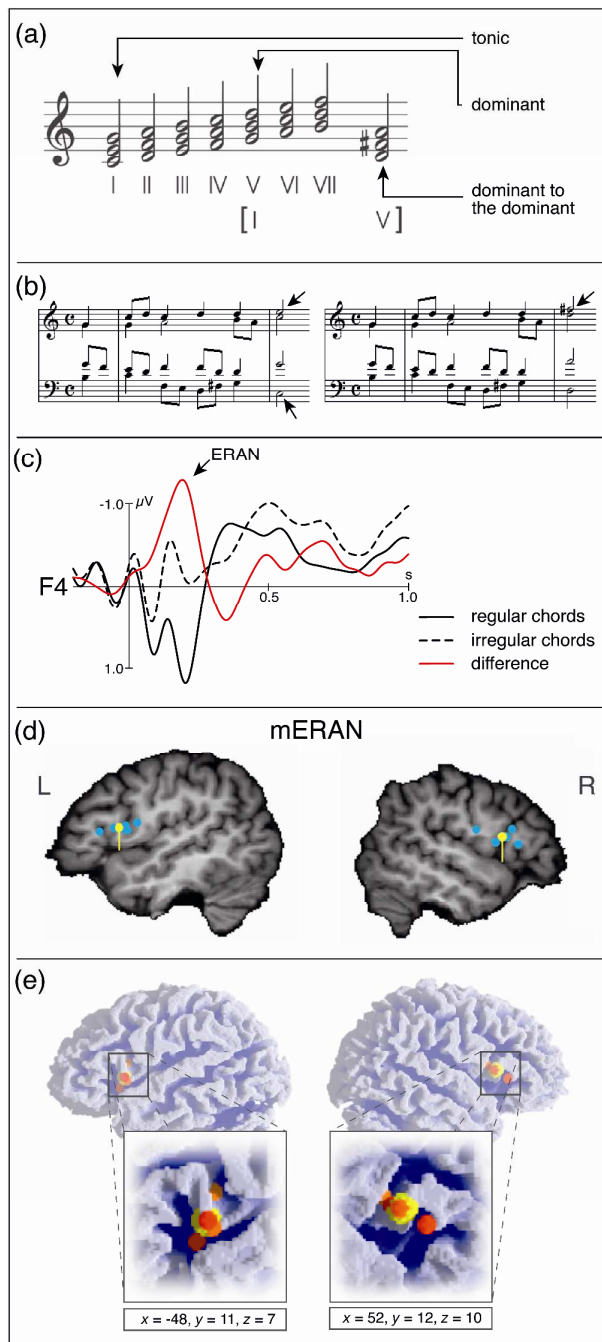


Figure 2. Chord functions are the chords built on the tones of a scale (a). The chord on the first scale tone, e.g., is denoted as the tonic, the chord on the second scale tone (in major) as supertonic, on the third scale tone as mediant, on the fourth scale tone as subdominant, and the chord on the 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 pro-

gression 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) shows the ERPs elicited by the final chords of these two sequence types (recorded from a right-frontal electrode site [F4] from twelve subjects, from Koelsch, 2005). Both sequence types were presented in pseudorandom order equiprobably in all twelve 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 (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) shows activation foci (small spheres) reported by functional imaging studies on music-syntactic processing using chord sequence paradigms (Koelsch et al., 2005; Maess et al., 2001; Tillmann et al., 2003; Koelsch et al., 2002c) 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 & Siebel, 2005.

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; Regnault et al., 2001; Poulin-Charronnat, Bigand & Koelsch, 2006; Koelsch 2005, Koelsch et al., 2007; Koelsch & Jentschke, in press), 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 et al., 2007; Koelsch & Jentschke, in press). 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 of Figure 2b) introduced two new pitches, whereas the irregular chords at the sequence ending (so-called double dominants, shown in the right panel of Figure 2b) introduced only one new pitch (the new pitches introduced by the final chords are indicated by the arrows of Figure 2b). 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 percent) 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 et al., 2007; Koelsch & Jentschke, in press).

The peak latency of the ERAN is often between 170 and 220 ms, with the exception of three studies: Koelsch & 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 non-musicians), and Patel et al. (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 non-repetitive 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 (Miranda & Ullmann, 2007; Brattico et al., 2006). Moreover, a study from Schön & 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 on-line establishment of regularities – that is, based on representations of regularities that are extracted on-line 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 on-line establishment of regularities with long-term experience or long-term representations that might influence the generation of the MMN: E.g., 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 et al., 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 et al., 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 on-line from the acoustic environment: For example, in the classical study from Näätänen et al. (1997), 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 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 on-line 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 (3), see *ibid.*, 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 Widmann et al., 2004; Schön & Besson, 2005).

(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 inter-sound relationship. These statements

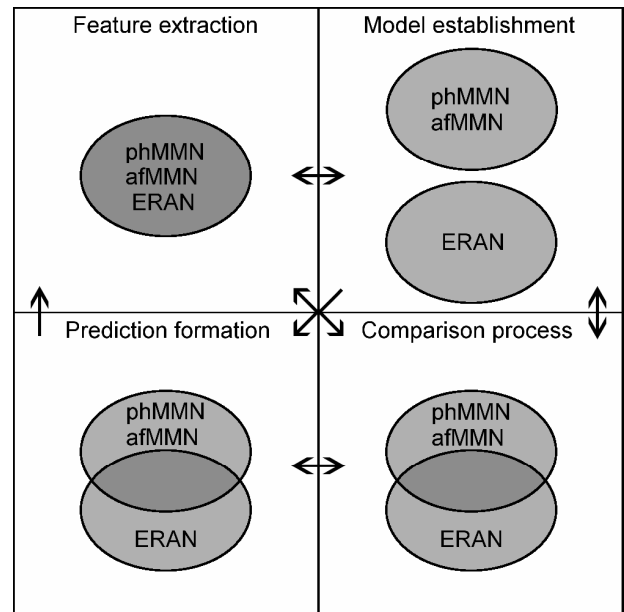


Figure 3. Systematic overview of processes required to elicit MMN and ERAN (see text for details). Whereas the extraction of acoustic features is identical for both MMN and ERAN (top left quadrant), MMN and ERAN differ with regard to the establishment of a model of intersound-relationships (top right quadrant): In the case of the MMN, a model of regularities is based on inter-sound relationships that are extracted on-line 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 inter-sound 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.

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 on-line, and they are, moreover, not necessarily based on the inter-sound 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 (2), however, in the case of the MMN the predictions are based on regularities that are established on-line based on the inter-sound relationships of the acoustic input, whereas in the case of the ERAN the predictions are based on representations (of music-syntactic regularities) that already exist in a long-term memory format. To date it is not known to which 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 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 (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 next section for further details).

In addition, Winkler (2007) states that the primary function of the MMN-generating process is to maintain neuronal models un-

derlying 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 which 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 inter-sound 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 et al., 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 behavioural methods (Slevc et al., 2007). In the study from Koelsch 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 (Alho et al., 1996; Alain, Woods, & Knight, 1998; Giard et al., 1990; Opitz et al., 2002; Liebenthal et al., 2003; Molholm et al., 2005; Rinne et al., 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 et al., 2002; Koelsch et al., 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 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 non-musicians (Koelsch et al., 2002), and in the fMRI study from Koelsch 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 Assessment of Alertness and Sedation Scale

level 2-3, mean Bispectral Index = 68), the ERAN is abolished during this level of sedation (Koelsch et al., 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 et al., 2004; Heinke & Koelsch, 2005).

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 et al., 2005; Steinbeis & Koelsch, 2008; Slevc et al., 2007).

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 et al., 2008), 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 et al., 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 et al., 2002b), 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 which deviated in their sound intensity from standard chords. These conditions enabled 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).

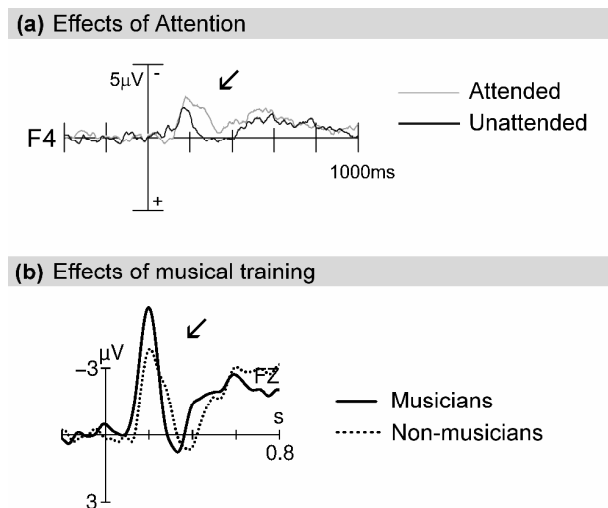


Figure 4. **A** shows difference ERPs (tonic subtracted from Neapolitan chords) elicited when attention was focussed on the musical stimulus (grey line), and when attention was focussed on a reading comprehension task (black line). The E(R)AN (indicated by the arrow) clearly differed between conditions, being smaller in the unattend-condition (figure adapted from Loui et al., 2005). **B** shows difference ERPs (tonic subtracted from Neapolitan chords) elicited in musicians (solid line) and non-musicians (dotted line). The ERAN (arrow) clearly differed between groups, being smaller in the group of non-musicians.

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 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 et al., 2004, Heinke & Koelsch, 2005).

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, 2001), the processing of abstract features such as interval and contour changes (Ter-vaniemi et al., 2001; Fujioka et al., 2004), 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 ("non-musicians"). 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 & Kansok, 2002), and in amateur musicians (Koelsch et al., 2007) compared to non-musicians. 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 non-musicians, Koelsch & Sammler, 2007) and amateur musicians (compared to non-musicians, Koelsch & Jentschke, in press), 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 et al., 2005b).

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 behavioural studies showing that musicians respond faster, and more accurately to music-structural irregularities than non-musicians (e.g., Bigand et al., 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 Schön et al., 2004; Magne et al., 2006; Moreno & Besson, 2006). 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 two hours (Koelsch & Jentschke, in press; 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 pre-

sent 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 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 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 supertonic and Neapolitan (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 has shown MMN-like discriminative responses in newborns (although sometimes with positive polarity; Ruusuvirta et al., 2003, 2004; Winkler et al., 2003; Maurer et al., 2003; Stefanics et al., 2007) to both physical deviants (e.g., Alho et al., 1990; Cheour et al., 2002a,b; 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 et al. (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., Maurer et al., 2003; Kushnerenko et al., 2007; Friederici, 2005, 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 inter-sound regularities that are extracted on-line 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, e.g., 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., 2008, in that study the ERAN was elicited by supertonic chords). Similar results were obtained in another study using Neapolitan chords 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 nine, 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 both children 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 to that of adults (with clear activations of inferior frontolateral cortex elicited by Neapolitan chords; Koelsch et al., 2005b). 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., 2005; irregular chords were Neapolitan chords). However, in another study with 5-year-olds (Jentschke et al., 2008; irregular chords were supertonic chords) 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, e.g. 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 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 build-up 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, i.e. of acoustic information structured according to abstract and complex regularities which 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 previ-

ously 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 which are extracted on-line from the acoustic environment. By contrast, music-syntactic processing (as reflected in the ERAN) is based on a structural model which 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 which 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, e.g. 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 MMN also represent the foundation for music-syntactic processing.

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