Musical syntax is processed in Broca's area: an MEG study

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The present experiment was designed to localize the neural substrates that process music-syntactic incongruities, using magnetoencephalography (MEG). Electrically, such processing has been proposed to be indicated by early right-anterior negativity (ERAN), which is elicited by harmonically inappropriate chords occurring within a major-minor tonal context. In the present experiment, such chords elicited an early effect, taken as the magnetic equivalent of the ERAN (termed mERAN). The source of mERAN activity was localized in Broca's area and its right-hemisphere homologue, areas involved in syntactic analysis during auditory language comprehension. We find that these areas are also responsible for an analysis of incoming harmonic sequences, indicating that these regions process syntactic information that is less language-specific than previously believed.

It seems plausible that music, like language, has a syntax: both have a structure based on complex rules. However, how a musical syntax may be described has remained a matter of debate[1–4]. To investigate the processing of musical syntax, EEG studies[5,6] have taken advantage of the listener's ability to expect specific musical events according to a preceding musical context, and to detect violations of harmonic expectancies within a musical sequence. This ability may be an indication that a musical syntax exists, mainly because the specificity of harmonic expectancy corresponds to the degree of harmonic relatedness as described by music theory[1,7–9]. That is, subjects expect to hear in sequence harmonically related but not harmonically unrelated chords.

Event-related brain potentials (ERPs) elicited by syntactic incongruities in language and music were compared in a previous study[5]. In that study, harmonic incongruities were interpreted as grammatical incongruity in music. It was shown that both musical and linguistic structural incongruities elicit positivities with a latency of about 600 ms (the so-called P600) that are statistically indistinguishable. The P600 reflects more general knowledge-based structural integration during the perception of rule-governed sequences. Additionally, a negative music-specific ERP component with a latency of around 350 ms and an anterior right-hemisphere lateralization was observed. This right anterio temporal negativity (RATN) was elicited by out-of-key chords, and taken to reflect the application of music-syntactic rules.

In another EEG study[6], harmonically unrelated and functionally inappropriate chords occurred within sequences of in-key chords. Sequences consisting of in-key chords were composed to build up a musical context, which correlates in listeners with the buildup of strong expectancies to hear harmonically appropriate chords in sequence[7,8]. The principles that form the basis of these expectancies have been described as a 'hierarchy of harmonic stability'[8], and correspond to the theory of harmony[7,8]. Harmonically appropriate chords are tonally related chords or chord functions that fit well at certain positions in a musical context (for example, a tonic chord at the end of a sequence)[8]. Inappropriate chords elicited an early right-anterior negativity (ERAN). Notably, such chords were consonant major chords; it was only the musical context that made them sound unexpected. Within the musical context, they could only be differentiated from the in-key chords by the application of (implicit) musical knowledge about the principles of harmonic relatedness described by music theory. These principles or rules of music theory may be thought of as musical syntax[4–8].

Here we used the same experimental protocol as the preceding EEG study[6]. Participants (all 'non-musicians') were presented with directly succeeding chord sequences, each consisting of five chords (Fig. 1). Sequences consisting exclusively of in-key chords (cadences) established a musical context toward the end of each sequence (Fig. 1a). Due to the buildup of musical context, harmonic expectancies that were most specific at the end of each sequence were generated in listeners. Besides the in-key chord sequences, however, some sequences contained harmonically unexpected chords: a 'Neapolitan sixth chord' occurred at the third position in 25%, and at the fifth position in another 25% of all sequences (Fig. 1b and c). This chord is a variation of the subdominant, and contains two out-of-key notes, although the chord itself is major and consonant.

Compared to in-key chords, chords containing out-of-key ('non-diatonic') notes are, in music-theoretical terms, more distant from the tonal center, and therefore perceived as unexpected[6,8,9,11,12]. As noted before, the ability of listeners to expect chords according to their harmonic relatedness to a preceding harmonic context has been proposed to reflect the existence of a musical syntax. Because the Neapolitan chords violated the expectancy for tonally related chords to follow, effects elicited by the Neapolitan chords were thus proposed to reflect music-syntactic processing. Because of the musical context buildup, the harmonic expectancies of listeners were violated to a higher degree at the fifth position (where the expectancies were most specific) compared to the third position of a sequence. Therefore, the effects of Neapolitan chords were proposed to be larger at the fifth compared to the third position. In addition, from a music-theoretical perspective, Neapolitan chords function harmonically as a subdominant

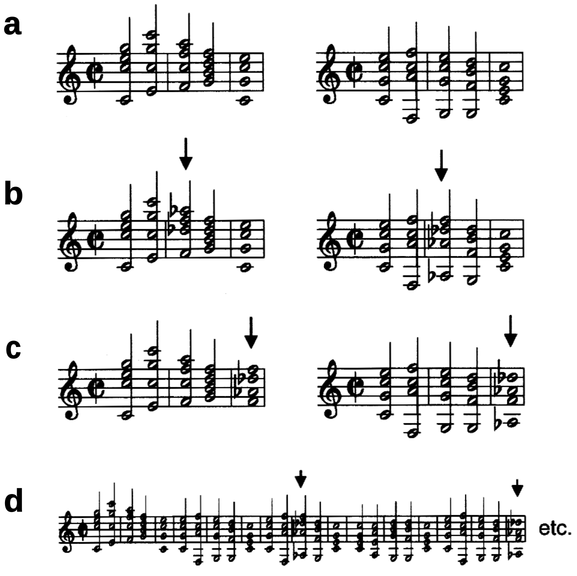

Fig. 1. Examples of chord sequences. (**a**) Cadences consisting exclusively of in-key chords. (**b**) Chord sequences containing a Neapolitan sixth chord at the third position. (**c**) Chord sequences containing a Neapolitan at the fifth position; Neapolitan chords are indicated by arrows. (**d**) Example of directly succeeding chord sequences as presented in the experiment.

variation; a Neapolitan chord at the third position of the sequence was, functionally, fairly suitable (because a subdominant in that position was appropriate), whereas a Neapolitan at the fifth position was functionally inappropriate (because only a tonic chord would be appropriate in that position).

Thus, a Neapolitan chord as presented here may be taken as ‘music-syntactically’ incongruous on the basis of both music-psychological (with respect to harmonic expectations) and music-theoretical reasoning (with respect to harmonic chord functions and rules). From both perspectives, the degree of music-syntactic incongruity is higher for Neapolitans at the fifth compared to the third position. In the present study, we show that the magnetic effect elicited by the Neapolitans was stronger at the fifth compared to the third position, indicating that this effect reflects music-syntactic processing. This effect was generated in both hemispheres in the inferior pars opercularis, known in the left hemisphere as Broca’s area.

RESULTS

In-key chords elicited a large mean global field power (MGFP, a measure of the strength of an evoked field), present in all subjects at around 200 ms (relative to stimulus onset, Fig. 2a). (This magnetic effect will henceforth be referred to as the P2m.) Brain responses elicited from Neapolitan and in-key chords in the fifth position clearly differed (Fig. 2b). Neapolitan chords elicited a particular early magnetic field effect, which was, at any sensor, nearly uni-modal over time, and was largest around 200 ms (like the P2m). This effect (henceforth referred to as the mERAN) can best be seen in the difference waves of Fig. 2b. Virtually no magnetic effects were observable after around 350 ms, for Neapolitans or for in-key chords.

The field maps of both P2m and mERAN reveal a dipolar pattern over each hemisphere (Fig. 3a and b). In all subjects, the fields of the mERAN had virtually an inversed ‘polarity’ compared to the fields of the P2m. Moreover, the steepest field gradients of the mERAN are anterior to those of the P2m, indicating that the neural generators of the mERAN are anterior to those of the P2m.

Effects elicited by Neapolitan chords at the third and fifth position were very similar in distribution and time course; however, the third-position effects were distinctly smaller (about half of the strength of fifth-position effects, Figs. 2c and 3c). The MGFP of the mERAN (in-key chord signals subtracted from Neapolitan chord signals, Fig. 4) elicited at the third position differed significantly from the MGFP of the mERAN elicited at the fifth position (paired t-test; $t = 5.69$, $p = 0.005$). (MGFP was calculated for third and fifth position for each subject separately in the time window from 170–210 ms.)

Dipole solutions

Dipole solutions for the P2m and the mERAN elicited at the fifth position were obtained from each subject. (The signal-to-noise ratio (SNR) of the effects elicited by Neapolitan chords at the third position was too low to calculate reliable dipole solutions; see Methods.) Then, locations of dipoles were transformed into a Talairach-sized standard brain, and averaged across subjects. For the P2m, one dipole was located in each hemisphere within the middle part of Heschl’s gyrus (in the superior temporal

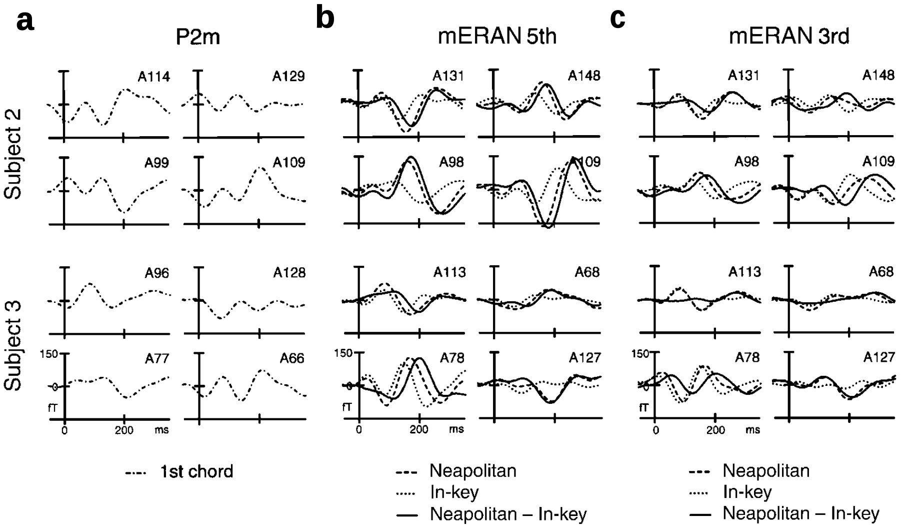

Fig. 2. Time courses of magnetic field strength. Data were chosen from two representative subjects at four sensors located in the magnetic field maxima. (**a**) P2m time course elicited by in-key chords. (**b**) Signals evoked by chords at the fifth position, plotted separately for Neapolitan (dashed lines) and in-key chords (dotted lines). The effect elicited by Neapolitan chords (mERAN) is indicated by the solid lines (difference wave, Neapolitan chord signals subtracted from in-key chord signals); this effect was maximal around 200 ms. (**c**) Signals evoked by chords at the third position (line designations as in **b**).

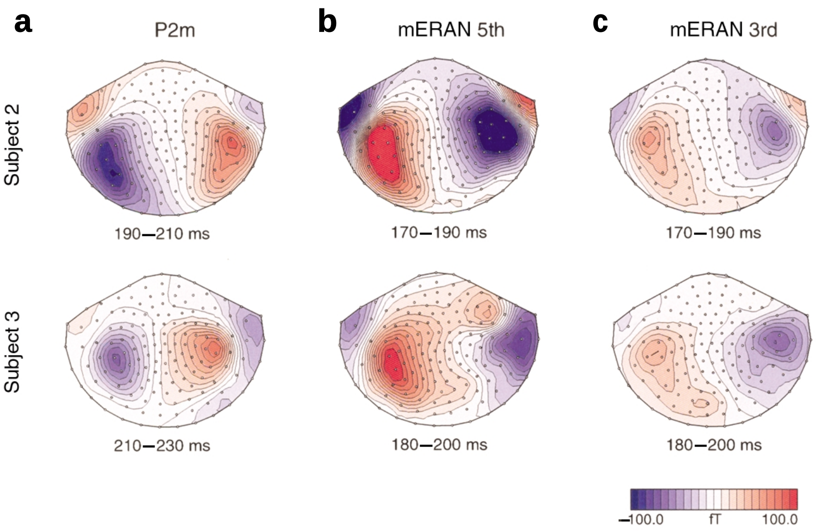

Fig. 3. P2m and mERAN, magnetic field maps. The maps of the mERAN were calculated by subtracting the event-related magnetic fields (ERFs) elicited by in-key chords from the ERFs of Neapolitan chords.

gyrus), which corresponds to Brodmann's area (BA) 41 (Fig. 5). The dipole solution for the mERAN indicated, in each hemisphere, one dipole located in the inferior part of the pars opercularis (in the inferior frontal gyrus, part of BA 44; Fig. 5). The residual normalized variance of dipole solutions was, on average, 5% for the mERAN and 4% for the P2m.

The generators of the mERAN were located approximately 2.5 cm anteriorly, and 1.0 cm superiorly with respect to the generators of the P2m (Table 1). The generators of both the P2m and the mERAN appear to have a stronger dipole moment in the right than in the left hemisphere; a right-hemispheric predominance of the mERAN was present in four of six subjects. However, statistical analysis did not reveal a hemispheric difference of effects.

To test whether the dipole locations of mERAN and P2m differed significantly, *y*- and *z*-coordinates of dipoles were analyzed separately using ANOVAs with condition (P2m × mERAN) and hemisphere (left × right dipoles) as factors. Both ANOVAs for *y*- and *z*-coordinates yielded an effect of condition (*y*-coordinates, $F_{1,5} = 37.2$, $p < 0.005$; *z*-coordinates, $F_{1,5} = 21.5$, $p < 0.01$), indicating that the mERAN is generated anteriorly and superiorly to the P2m.

Only very small P1 and N1 were elicited by all chords. This is presumably a consequence of the continuous stimulus presentation, in which one chord directly followed the other; the onset of each chord was not an abrupt change in loudness. Particularly, the N1 is thought to correspond to transient detection, because the N1 is evoked by sudden changes in the level of energy impinging on the sensory receptors[13,14].

Discussion

In-key chords elicited a distinct magnetic field effect, which was maximal around 200 ms (P2m). The P2m is suggested here as the magnetic equivalent of the electrical P2, because of its time course, its 'polarity,' and the location and orientation of its generators. (The generators would produce a positive electrical potential over fronto-central scalp regions.) The average of the transformed individual dipole solutions yielded two generators of the P2m, one located in each hemisphere in the middle of Heschl's gyrus (that is, within or near the primary auditory cortex, near the generators of the P1m[15–17] and the N1m[18–20]). The dipole of the P2m tended to have a stronger dipole moment in the right compared to the left hemisphere. This finding might reflect a preference of the right hemisphere for the processing of tones and chords[21–24].

Neapolitan chords at the fifth position of the chord sequences elicited magnetic fields that differed distinctly from those elicited by in-key chords at the same position (although participants were instructed to ignore the harmonies; see Methods). Neapolitan chords elicited an early magnetic field effect that was maximal around 200 ms, the mERAN. The mERAN is regarded here as the magnetic equivalent of the (electrical) ERAN. Four findings support this assumption. First, the mERAN was sensitive to harmonically inappropriate chords. Second, the time course of the mERAN was virtually identical to the time course of the ERAN[6]. Third, in all subjects, the fields of the mERAN had an inversed polarity compared to the fields of the P2m (corresponding to the ERAN and the P2). Fourth, the mERAN is, like the ERAN, considerably smaller (about 50%) when elicited by Neapolitan chords at the third versus the fifth position (see below).

In contrast to the P2m, the generators of the mERAN were not located within the temporal lobe. The mERAN was generated approximately 2.5 cm anterior to and 1.0 cm superior to the P2m in both hemispheres, namely, in each hemisphere within the inferior part of BA 44 (inferior part of the pars opercularis). In the left hemisphere, this is known as Broca's area.

The mERAN, like the ERAN, is suggested to reflect the brain's response to a harmonic context violation. Chords preceding the Neapolitan chords at the fifth position strongly established a tonal key. During such a sequence, listeners build up a 'hierarchy of harmonic stability'[8], which induces strong harmonic expectations for harmonically appropriate chords to follow. At the fifth position of the chord sequences, a tonic chord was harmonically most appropriate. Instead of a tonic, a Neapolitan chord occurred, which contained out-of-key notes and therefore sounded unexpected in the established tonal environment[6–9,12,25–27]. Moreover, the remaining in-key note of the Neapolitan chords (in *C* major, *f*) was also unexpected, because it does not belong to the tonic chord. The ability to perceive distances between chords (and keys, respectively) and to expect certain harmonies (and harmonic functions) to a higher or lower degree can only rely on a representation of the principles of harmonic relatedness described by music

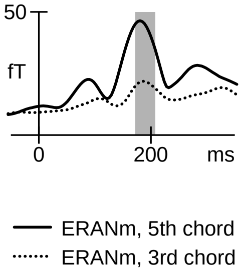

Fig. 4. Mean global field power signals of the mERAN (MGFP averaged over all MEG channels and all subjects). The MGFP was significantly stronger (shaded area) at the fifth position versus the third position.

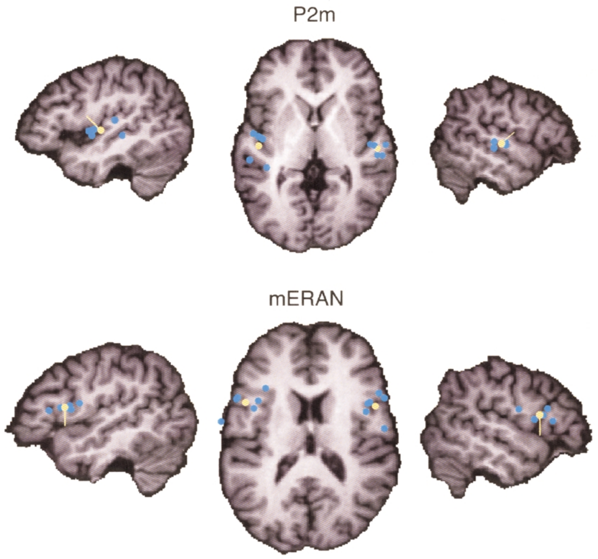

Fig. 5. Grand average dipole solutions for P2m and mERAN. Grand average dipole solutions, yellow; P2m, top; mERAN, bottom. Each panel shows left and right sagittal and axial (parallel to AC-PC line) view. Dipole solutions for both the P2m and the mERAN refer to two-dipole configurations (one dipole in each hemisphere). Blue discs, single subject solutions.

theory. These principles, or rules, were reflected in the harmonic expectancies of listeners and may be interpreted as musical syntax (see Introduction).

The mERAN was distinctly larger when elicited at the fifth compared to the third position. This finding supports the hypothesis that the mERAN reflects music-syntactic processing, because the degree of music-syntactic incongruity was higher at the fifth compared to the third position. Because of the musical context buildup, which was more specific at the end of the sequence, and because of the inappropriate chord function of a Neapolitan at the fifth position (subdominant-variation instead of tonic), the musical syntax was violated to a higher degree at the fifth compared to the third position.

mERAN and MMNm

The mERAN is generated more anteriorly than the mismatch negativity (MMN) or its magnetic equivalent (MMNm). Whereas the MMN receives its main contributions from generators located in temporal areas[28], we found that the mERAN was generated in the frontal lobe. Frontal contributions to the MMN have been reported for the frequency-MMN and EEG, but not for MEG[29], Broca's area or its homologue[30–32]. Moreover, Neapolitan chords were not physical oddballs (no physical regularity preceded the Neapolitan chords); thus no frequency- or spectral-MMN could be elicited. Therefore, results support the hypothesis that the mERAN is not an MMN, at least not the 'classical' MMN[6,14,42].

The Neapolitan chords at the third and fifth position were physically identical. Therefore, it could only be the degree of music-syntactic incongruity, referring only to music-theoretical terms, that modulated the amplitude of the mERAN. That is, the finding that the mERAN is larger when elicited at the fifth position again strongly supports the hypothesis that the mERAN is not an MMN. Rather, the results indicate that the mERAN is specifically correlated with the processing of auditory information within a complex rule-based context.

Inferior BA 44 and syntax processing in language

Broca's area and its right homologue, particularly the inferior part of BA 44, are involved in the processing of syntactic aspects during language comprehension[33–40], and are specialized for fast and automatic syntactic parsing processes[10]. The early left anterior negativity (ELAN) reflecting these processes[10,41] is also generated, at least partially, in Broca's area and its right-hemisphere homologue[38]. The dipole solution for the magnetic ELAN reveals dipoles in the left and the right inferior frontal cortex (with very similar locations as the mERAN) in addition to bilateral temporal dipoles[38]. As described in the Introduction, the ERAN highly resembles the ELAN, though with a different hemispheric weighting.

The present results indicate that Broca's area and its right-hemisphere homologue might also be involved in the processing of musical syntax, suggesting that these brain areas process considerably less domain-specific syntactic information than previously believed. Like syntactic information of language, which is fast and automatically processed in Broca's area and its right-hemisphere homologue, music-syntactic information processed in the same brain structures also seems to be processed automatically[42]. The magnetic fields of the mERAN were, in four of six subjects (but not in the grand average), stronger over the right than over the left hemisphere. This finding is consistent with the ELAN, which is prevalently (although not consistently) stronger over the left hemisphere. It is thus suggested here, as a working hypothesis, that the left pars opercularis is more involved in the processing of language syntax, and the right pars opercularis more in the processing of musical syntax. However, both hemispheres seem to be considerably activated in both domains.

In the present study, harmonically inappropriate chords activated Broca's area and its right-hemisphere homologue. This finding is important for several reasons. First, it demonstrates that complex rule-based information is processed in these areas with considerably less domain-specificity than previously believed[21,39,43]. This might suggest that these areas process syntax, that is, complex rule-based information, in a domain other than language. This finding might lead to new investigations of syntax processing in the musical, or even other auditory but non-linguistic domains. Second, it reveals from a functional-neuroanatomical view a strong relationship between the processing of language and music. This relationship might at least partly account for influences of musical training on verbal abilities[44,45]. Third, the present study introduced a new method of investigating music perception using

Table 1. Locations and strengths of P2m and mERAN dipoles (grand average of back-transformed dipole solutions).

	Dipole coordinates (x, y, z) and dipole moments (Q)			
	P2m left (mean ± s.e.m.)	P2m right (mean ± s.e.m.)	mERAN left (mean ± s.e.m.)	mERAN right (mean ± s.e.m.)
x (mm)	–45 ± 2	51 ± 2	–48 ± 5	50 ± 3
y (mm)	–16 ± 4	–19 ± 2	9 ± 4	6 ± 4
z (mm)	4 ± 2	4 ± 1	16 ± 1	14 ± 2
Q (nAm)	14 ± 5	22 ± 10	31 ± 15	35 ± 12

Values are given with respect to the Talairach coordinate system.

MEG. Effects were elicited in 'non-musicians' (even though Neapolitan chords were task-irrelevant), supporting the hypothesis of an (implicit) musical ability of the human brain, and enabling a broad generalization of the present findings.

METHODS

Subjects. Six right-handed and normal-hearing subjects (20 to 27 years old; mean, 22.5; 4 females) participated in the experiment. Subjects were non-musicians, that is, they had never learned singing or an instrument, and they did not have any special musical education besides normal school education.

Stimuli. The pool of stimuli consisted of 128 different chord sequences; each sequence consisted of five chords. The first chord was always the tonic of the following chord sequence; chords at the second position were tonic, mediant, submediant, subdominant, dominant of the dominant, secondary dominant of mediant, secondary dominant of submediant or secondary dominant of supertonic. The third position chord was subdominant, dominant, dominant six-four, Neapolitan sixth, or if preceded by a secondary dominant-mediant, the submediant or supertonic. The fourth position chord was the dominant seventh, and the fifth position chord was either the tonic or the Neapolitan sixth. Texture of chords followed the classical theory of harmony[46]. From the pool of 128 sequences, 1350 chord sequences were randomly chosen such that the secondary dominants, Neapolitan chords at the third position, and Neapolitan chords at the fifth position of a sequence occurred with a probability of 25% each. Presentation time for chords 1 to 4 was 600 ms, and for chord 5, 1200 ms. In 10% of the sequences, an in-key chord from position 2–5 was played by an instrument other than piano. Chord sequences were presented in direct succession. The same stimuli were used in experiment 1 of the preceding EEG study[6].

Procedure. Three experimental sessions were conducted (each comprising three blocks). Participants were only informed about the deviant instruments, not about the Neapolitan chords or their nature. Participants were instructed to ignore the harmonies.

MEG recording. The continuous raw MEG was recorded using the 4D-Neuroimaging Magnes WHS 2500 whole-head system (San Diego, California), which used 148 magnetometer channels, 11 magnetic reference channels and four EOG channels. Signals were digitized with a bandwidth of 0.1 Hz to 50 Hz and a sampling rate of 254.31 Hz. The continuous MEG data were filtered off-line with a 2–10 Hz band-pass filter (1001 points, FIR). All subjects' averaged data were transformed onto a sensor-position representative for all blocks of this subject using ASA (ANT Software, Enschede, The Netherlands) and were accumulated per subject across all blocks and sessions.

Data analysis. For each participant, a realistically shaped volume conductor was constructed, scaled to the subject's real head size. This was achieved by adjusting the size of the Curry-Warped brain (an average brain obtained from more than 100 subjects; Neuroscan Labs, Sterling, Virginia, B. Maess and U. Oertel, *Neuroimage*, **10**, A8, 1999) to each individual head shape. This method results in independent scaling factors for all three spatial dimensions. The adjustment procedure thus enabled source localization with an accuracy close that achieved with individual MR-based models. These scaling factors were also useful for the transformation of localization results into the Talairach-sized brain.

To achieve a higher signal-to-noise ratio, the ERFs evoked by all in-key chords were combined (The magnetic field maps of the P1, N1 and P2m virtually did not differ between in-key chords presented at different positions within the chord-sequences.) Dipole orientations were separated into tangential and radial contributions for each subject. The radial contributions were then eliminated. The criterion for an acceptable dipole solution was the explanation of at least 90% of normalized variance for each subject. The data of only two subjects fulfilled the criterion for the mERAN elicited at the third position, so no grand-average of dipole solutions was done in this case.

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Note: Examples of the stimuli are available on the Nature Neuroscience web site (http://www.neurosci.nature.com/web_specials).

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