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Neural substrates of processing syntax and semantics in music

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Growing evidence indicates that syntax and semantics are basic aspects of music. After the onset of a chord, initial music-syntactic processing can be observed at about 150–400 ms and processing of musical semantics at about 300–500 ms. Processing of musical syntax activates inferior frontolateral cortex, ventrolateral premotor cortex and presumably the anterior part of the superior temporal gyrus. These brain structures have been implicated in sequencing of complex auditory information, identification of structural relationships, and serial prediction. Processing of musical semantics appears to activate posterior temporal regions. The processes and brain structures involved in the perception of syntax and semantics in music have considerable overlap with those involved in language perception, underlining intimate links between music and language in the human brain.

Addresses

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Introduction

Music is one of the oldest, and most basic, socio-cognitive domains of the human species. Primate vocalizations are mainly determined by music-like features (such as pitch, amplitude- and frequency- modulations, timbre and rhythm), and it is assumed that human musical abilities played a key phylogenetical part in the evolution of language [1•]. Likewise, it is assumed that, ontogenetically, infants' first steps into language are based on prosodic information, and that musical communication in early childhood (such as maternal music) has a major role for emotional, cognitive and social development of children [2]. The music faculty is in some respects unique to the human species; only humans compose music, learn to play musical instruments and play instruments cooperatively together in groups. Playing a musical instrument in a group is a tremendously demanding task for the human brain that potentially engages all cognitive pro-

cesses that we are aware of. It involves perception, action, learning, memory, emotion, etc., making music an ideal tool to investigate human cognition and the underlying brain mechanisms. The relatively young discipline of 'neurocognition of music' includes a wide field of biopsychological research, beginning with the investigation of psychoacoustics and the neural coding of sounds, and ending with brain functions underlying cognition and emotion during the perception and production of highly complex musical information [1•,3•]. This review focuses on two basic dimensions of music perception: the processing of syntax and of semantics in music.

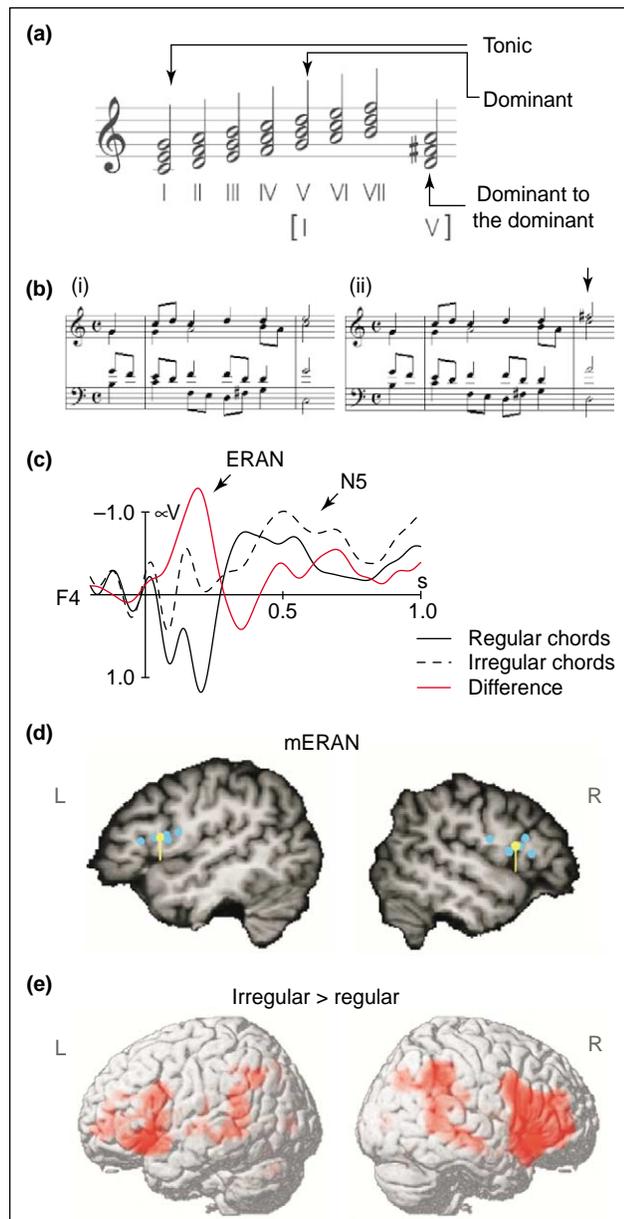
Processing syntax in music

All types of music are guided by certain regularities. These regularities constrain, for example, how individual tones, simultaneous tones (i.e. intervals and chords) and durations of tones are arranged to form meaningful musical phrases. Obviously, many regularities are culture-specific and differ between musical styles. To date, the processing of regularities has mainly been investigated with respect to major–minor tonal music; this music is formed on the basis of the major–minor tonal system that underlies the majority of Western music. Basic principles and regularities of this tonal system have been described in music theory. One aspect of these regularities pertains to the arrangement of chord functions within harmonic progressions (other regularities build melodic, rhythmic and metric structure). The regularity-based arrangement of chord functions builds a harmonic structure, and might be regarded as part of a major–minor tonal syntax (Figure 1a and b). Listeners who grew up in a Western culture are usually quite familiar with these regularities (even if they have not received formal musical training), presumably because of their listening experiences in everyday life. It is unknown if listeners who are completely unfamiliar with Western tonal music can also recognize basic syntactic irregularities of major–minor tonal music.

Brain indices of processing harmonic structure

Processing of chord functions has been investigated behaviorally [4], and with neurophysiological measures such as electroencephalography (EEG) [5–7], magnetoencephalography (MEG) [8] and functional magnetic resonance imaging (fMRI) [9–11]. These studies used chord sequence paradigms in which chords presented at particular positions within harmonic sequences are structurally more or less (ir)regular. Figure 1b shows musical sequences ending on music-syntactically regular and irregular chord functions (see the Figure 1 legend for details). Note that the final chord of the irregular

Figure 1



Neural correlates of music-syntactic processing. **(a)** In major-minor tonal music, chord functions are arranged within harmonic sequences according to certain regularities. Chord functions are the chords built on the tones of a scale. The chord on the first scale tone, for example, is denoted as the tonic 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). **(b)** 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. **(i)** The sequence shown ends on a regular dominant-*tonic* progression, **(ii)** the final chord of this sequence is a dominant to the dominant (arrow). This chord function is irregular, especially at the end of a harmonic progression (sound examples are available at www.stefan-koelsch.de/TC_DD). **(c)** Electric brain potentials (in μV) elicited by the final chords of the two sequence types presented in b (recorded from a right-frontal

sequence (right panel of Figure 1b) does not represent a physical irregularity. It is, thus, not possible to detect the irregular chords on the basis of the operations of cognitive modules that detect physical irregularities (such as the auditory sensory memory). It is only possible to detect the irregular chords on the basis of the operations of a cognitive module that serves the processing of musical structure.

The event-related brain potential (ERP) data of Figure 1c illustrate the time course of activity of this module. Music-syntactically irregular chords elicit an early right anterior negativity (ERAN): this ERP effect is often maximal at about 200 ms after the onset of the chord, and is strongest over right-frontal electrode leads (although the ERAN is also clearly present over the left hemisphere, and is sometimes bilateral). Interestingly, the ERAN can be elicited in participants without formal musical training. That is, even if participants are not familiar with concepts such as 'tonic', or 'dominant', their brains have a sophisticated (implicit) knowledge about major-minor tonal syntax, and process this musical information surprisingly rapidly and accurately according to this knowledge. These findings are in line with several studies indicating that the ability to acquire knowledge about musical regularities effortlessly, and the ability to process musical information skillfully according to this knowledge, is a general ability of the human brain (details have been reviewed elsewhere [3[•],4]). This general ability underscores the biological relevance of music. Musical abilities are important, for example, with regards to language perception: in tonal languages, changes in pitch lead to changes in word meaning, and in both tonal and non-tonal languages, prosody (i.e. the musical features of language such as melody, timbre, rhythm and metre) is of crucial importance for the coding of both the structure and the meaning of speech. Corroboratively, recent EEG studies revealed similarities for the processing of intonational phase boundaries in language and music [12,13] and showed that musical training can

electrode site [F4] from twelve subjects). Both sequence types were presented in pseudorandom order with equal probability in all twelve major keys. Brain responses to irregular chords clearly differ from those to regular chords. The first difference between the two black waveforms is maximal at about 0.2 s after the onset of the chord (this is best seen in the red difference wave, which represents regular subtracted from irregular chords) and has a right-frontal preponderance. This early right anterior negativity (ERAN) is usually followed by a later negativity, the N5 (short arrow). **(d)** With MEG, the magnetic equivalent of the ERAN was localized to the inferior frontolateral cortex (adapted from Maess *et al.* with permission of Nature Publishing Group [<http://www.nature.com/>] [8]; single-subject dipole solutions are indicated by blue disks, yellow dipoles indicate the grand-average of these source reconstructions). **(e)** fMRI data obtained from 20 subjects using a similar chord-sequence paradigm (the statistical parametric maps show areas that are more strongly activated during the processing of irregular than during the processing of regular chords). Corroborating the MEG data, the fMRI data indicate activations of IFLC. Additionally, the fMRI data indicate activations of the ventrolateral premotor cortex, the anterior portion of the STG, and posterior temporal lobe structures.

facilitate the processing of pitch contour in spoken (non-tonal) language [14].

The neural mechanisms underlying the generation of the ERAN can operate independently of attention (although the amplitude of the ERAN is influenced by attentional demands): the ERAN can be elicited when subjects read a book, play a video game or are lightly sedated with propofol [15^{*}]. The ERAN is sensitive to musical training [16], and can be elicited in children aged 5 years and older (and possibly in even younger children [17]).

Spatial aspects of music-syntactic processing

Using MEG, it was found that processing of music-syntactically irregular chords activates the inferior part of Brodmann's area (BA) 44, that is, the inferior fronto-lateral cortex (IFLC; [8], see Figure 1d). This area in the left hemisphere is often denoted as 'Broca's area', an area that has also been implicated in the processing of linguistic syntax. With fMRI, it has been demonstrated that the processing of unexpected chords does not only activate Broca's area (and the homotope area in the right hemisphere) [9–11] but also posterior temporal regions [10,11] (see also Figure 1e). Both Broca's area and posterior temporal regions are crucially involved in the processing of language [18]; the interplay between these structures has for a long time been thought to be language-specific. The data presented in Figure 1e demonstrate that the cortical 'language-network' is also involved in the processing of music. This network often shows a right-hemispheric weighting in the musical domain, and a left-hemispheric weighting in the language domain (specializations of the two hemispheres for different features of auditory information have been discussed elsewhere [19]).

The ERAN is reminiscent of early anterior negativities that correlate with the early detection of an error in the syntactic structure of a sentence (usually observed with a maximum over the left hemisphere). The early left anterior negativity (ELAN), for example, has been observed in response to words with unexpected syntactic properties in sentences (phrase structure violations) [18]. That is, both ERAN and ELAN are sensitive to violations of an expected structure. Moreover, the generation of the ELAN appears to rely on neuronal generators that overlap with those of the ERAN, in that both components receive contributions from the same brain region in the inferior frontolateral cortex (lower part of BA 44) [8], and possibly from the anterior superior temporal gyrus (aSTG; see also below). Taken together, these findings indicate a noticeable overlap of neural resources that are engaged for the (early) processing of syntax in music, and syntax in language.

Besides IFLC, two additional structures have been observed in relation to music-syntactic processing: the

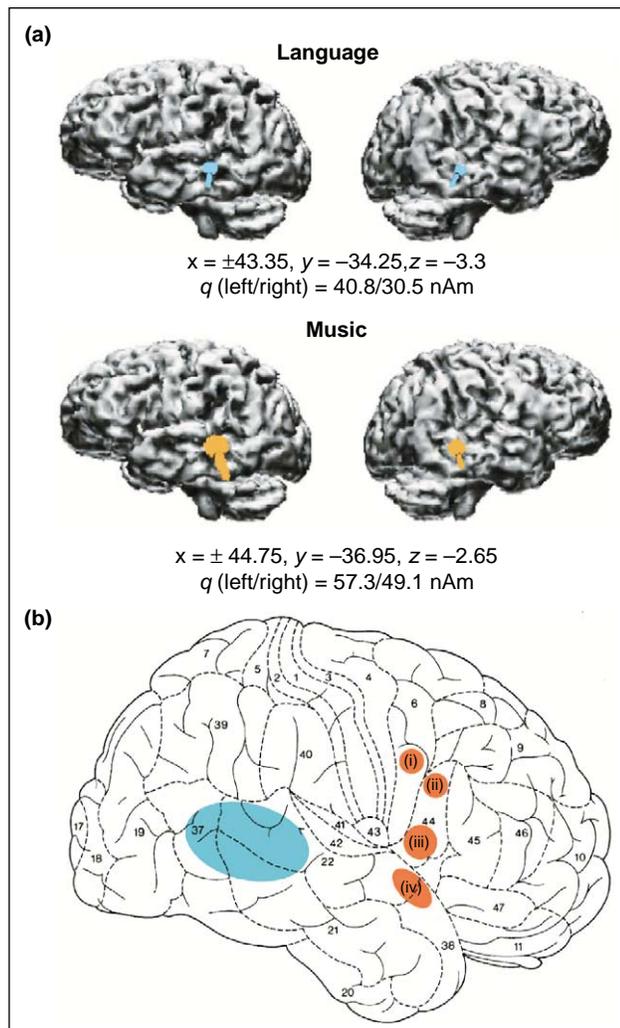
ventrolateral premotor cortex (vIPMC) and the aSTG (Figures 1 and 2 Figures 1e and 2b). Activations of IFLC along with the aSTG have been reported in previous functional imaging studies on syntactic processing using musical [10,11] and linguistic stimuli [18,20,21].

Activations of the IFLC (BA44), often along with the vIPMC, have been reported by a number of functional imaging studies using musical stimuli, linguistic stimuli, auditory oddball paradigms, pitch discrimination tasks, and serial prediction tasks [9–11,18,22–25]. On a more abstract level, the IFLC (BA44), and the vIPMC have been implicated in the analysis, recognition and prediction of sequential auditory information [25–28]. Fronto-opercular cortex (along with vIPMC) identifies structural relationships (rather than simple acoustic properties) among events occurring within auditory sequences, and these areas are involved in a fast short-term prediction of upcoming events; violations of predictions activate these areas [25]. The presentation of an irregular chord function violates the expectancies of listeners familiar with the regularities of tonal music. Unusual calculations of the relationship between the irregular chord function and the preceding harmonic context presumably activate a network comprising the pars opercularis in the IFLC, the vIPMC and presumably the anterior STG. These calculations are related to the sequencing of the chords, and the detection of a violation of a serial prediction. Whether or not neural substrates of these processes can functionally and anatomically be distinguished from each other remains to be specified. Likewise, it is not known if the representation of musical syntax is located in the same areas that are involved in the processing of musical syntax [29].

It has been suggested that there might be an immediate link between the prediction of upcoming events and the representation of corresponding motor schemas in the lateral premotor cortex (PMC) that enables an immediate mapping of perception onto action, that is, premotor programs for articulation, or 'vocal plans' [25]. Such a mapping is needed, for example, when singing along in a group, and is presumably also involved in the learning and understanding of musical syntax.

The ERAN is not the only electrophysiological index of music-syntactic processing, ERP studies investigating the processing of musical structure report a variety of ERP components such as P300 [5], RATN (right anterior temporal negativity) [6], and P600 [6,7,30]. The P600 (a positivity maximal at about 600 ms) appears to be related to processes of structural integration during the perception of music or language. Because the P600 can be observed in response to structural incongruities of both music and language [6], it has been suggested that resources for syntactic integration are shared between music and language [29]. The similarities between

Figure 2



Spatial aspects of processing syntax and semantics in music. **(a)** Neural generators of the N400 effect elicited by target words that were semantically (un)related to preceding sentences (top, blue dipoles), or musical excerpts (bottom, brown dipoles). The topology of the neural sources of the N400 did not differ between the language and the music condition (adapted from [34*]); x -, y -, and z -coordinates refer to standard stereotaxic space, dipole moments [q] are given in nanoampere-meters. **(b)** Spatial aspects of processing syntax and semantics in music. Orange areas represent activation foci described in previous imaging studies on music-syntactic processing: **(i)** vIPMC, IFLC **(ii)** superior and **(iii)** inferior pars opercularis and **(iv)** anterior STG. The blue oval represents an area that is assumed to be involved in the processing of musical semantics, and in the integration of semantic and syntactic information.

ERAN and ELAN suggest that not only neural resources for late but also for earlier syntactic processes are shared between music and language.

Processing meaning in music

Music can transfer meaningful information, and is an important means of communication. Most theorists dis-

tinguish between different aspects of musical meaning: first, meaning that emerges from common patterns or forms (e.g. musical sound patterns that resemble sounds of objects, or qualities of objects), second, meaning that arises from the suggestion of a particular mood (e.g. happy), third, meaning inferred by extramusical associations (e.g. any national anthem), and fourth, meaning that emerges from combinations of formal structures that create tension (e.g. when perceiving an unexpected chord) and resolution [31]. The emergence of meaning based on the processing of musical structure requires integration of both expected and unexpected events into a larger, meaningful musical context.

Such processes of musical integration appear to be reflected in a later negativity evoked by unexpected (irregular) chord functions (Figure 1b,c). This negativity usually reaches its maximal amplitude at about 500 ms after the onset of a chord and has been denoted as N5 [32; Figure 1c]. Note that processes of semantic integration during the perception of language are reflected in the N400 [33], a negativity peaking at about 400 ms after the onset of a word. Similarly to the N400 amplitude, which correlates with the amount of semantic integration required by a word, the N5 amplitude is related to the amount of harmonic integration required by a musical event [32].

Differences in scalp topography between N400 and N5 indicate that these two ERP components do not reflect identical cortical processes. However, because the N5 roughly resembles the N400, and because the cognitive processes following musical expectancy violations have theoretically been related to the processing of meaningful information, it appears likely that the N5 reflects neural operations that are at least partly related to the processing of musical meaning, and that the N5 entails processes that might also contribute to the generation of the N400 (note that irregular chord functions, and deceptive cadences, are prominent elements of major-minor tonal music that are used by composers as a means of expression). The N5 has not been localized to date, but it is possible that the N5 receives contributions from those posterior temporal lobe structures that have been shown with fMRI to be activated during the processing of unexpected chords. These structures are also known to be involved in the processing of lexical-semantic aspects, that is, meaning of language [18].

The N400 has recently been used to investigate processing of musical semantics in a semantic priming paradigm [34*]. In this study, sentences and musical excerpts were presented as prime stimuli. The prime stimuli were semantically either related or unrelated to a target word that followed the prime stimulus. For example, the sentence 'The gaze wandered into the distance' primes the word 'wideness' (semantically related), rather than the

word ‘narrowness’ (semantically unrelated). Analogously, certain musical passages, for example, those from Mozart’s symphonies, prime the word ‘angel’, rather than the word ‘scallywag’.

In the language condition (i.e. when target words followed the presentation of sentences), unrelated words elicited a clear N400 effect (this is a classical semantic priming effect). This semantic priming effect was also observed when target words followed musical excerpts. That is, target words that were semantically unrelated to a preceding musical excerpt also elicited a clear N400. The N400 effects did not differ between the language condition (in which the target words followed sentences) and the music condition (in which the target words followed musical excerpts), neither with respect to amplitude nor with respect to latency or scalp distribution. Figure 2a shows the results of a source analysis of the N400 effects. In both conditions, the main sources of these effects were localized bilaterally in the posterior part of the medial temporal gyrus (BA 21/37), in proximity to the superior temporal sulcus. As mentioned above, these regions have been implicated in the processing of semantic information during language processing [18,35].

The N400 effect in the music condition demonstrates that musical information can have a systematic influence on the semantic processing of words. The N400 effects did not differ between the music and the language condition, indicating that musical and linguistic priming can have the same effects on the semantic processing of words. That is, the data demonstrate that music can activate representations of meaningful concepts (and that, thus, music is capable of transferring considerably more meaningful information than previously believed), and that the cognitive operations that decode meaningful information while listening to music can be identical to those that serve semantic processing during language perception.

The N400 effect was observed for both abstract and concrete words, showing that music can convey both abstract and concrete semantic information. Moreover, effects were also observed when emotional relationships between prime and target words were balanced, indicating that music does not only transfer emotional information.

Conclusions

The present findings provide information about the processing of musical syntax and musical semantics. Results indicate that the human brain processes music and language with overlapping cognitive mechanisms, in overlapping cerebral structures. This view corresponds with the assumption that music and speech are intimately connected in early life, that musical elements pave the way to linguistic capacities earlier than phonetic ele-

ments, and that melodic aspects of adult speech to infants represent the infants’ earliest associations between sound patterns and meaning [36], and between sound patterns and syntactic structure [37]. Thus, despite the view of some linguists that music and language are strictly separate domains [38], the combined findings indicate that the human brain engages a variety of neural mechanisms for the processing of both music and language, underscoring the intimate relationship between music and language in the human brain.

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