Opinion TRENDS in Cognitive Sciences Vol.9 No.12 December 2005

Towards a neural basis of music perception

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Music perception involves complex brain functions underlying acoustic analysis, auditory memory, auditory scene analysis, and processing of musical syntax and semantics. Moreover, music perception potentially affects emotion, influences the autonomic nervous system, the hormonal and immune systems, and activates (pre)motor representations. During the past few years, research activities on different aspects of music processing and their neural correlates have rapidly progressed. This article provides an overview of recent developments and a framework for the perceptual side of music processing. This framework lays out a model of the cognitive modules involved in music perception, and incorporates information about the time course of activity of some of these modules, as well as research findings about where in the brain these modules might be located.

Introduction

During the past few years, music has increasingly been used as a tool for the investigation of human cognition and its underlying brain mechanisms. Music is one of the oldest and most basic socio-cognitive domains of the human species. It is assumed by some that human musical abilities played a key phylogenetical role in the evolution of language, and that music-making behaviour covered important evolutionary functions such as communication, cooperation, social cohesion and group coordination (for reviews, see [1]). Likewise, it has been shown that, ontogenetically, infants' first steps into language are based considerably on prosodic information [2], and musical communication in early childhood (such as maternal music) might play a major role in the emotional, cognitive and social development of children [3]. Music is a ubiquitous phenomenon: throughout human history, in every human culture, people have played and enjoyed music. Only humans learn to play musical instruments, and only humans play instruments cooperatively together in groups. Making music in a group is a tremendously demanding task for the human brain that engages virtually all cognitive processes that we know about, including perception, action, cognition, social cognition, emotion, learning and memory. This richness makes music an ideal tool to investigate the workings of the human brain.

When we listen to music, the auditory information passes through different processing stages until bodily reactions are possibly elicited, and until a musical percept becomes conscious. This article presents a model in which the different stages of music perception are assigned to different modules (see Figure 1; for investigations related to music production, see, e.g. [4,5]). The current model is based on previous modular approaches to music perception [6,7], but extends them by: (i) relating operations of different modules to ERP components (thus being able to provide information about the time course of their activity); (ii) adding modules that have become important in the literature on music perception in the past 5 years or so; and (iii) integrating recent research about where in the brain some of these modules might be located.

Early processing stages

Acoustic information is translated into neural activity in the cochlea, and progressively transformed in the auditory brainstem, as indicated by different neural response properties for pitch, timbre, roughness, intensity and interaural disparities in the superior olivary complex and the inferior colliculus [8,9]. This pre-processing enables the registration of auditory signals of danger as early as at the level of the superior colliculus and the thalamus. From the thalamus, information is projected mainly into the (primary) auditory cortex [10]. The thalamus is also directly connected with the amygdala [11] and medial orbitofrontal cortex [12], structures implicated in emotion and control of emotional behaviour. In the auditory cortex (most probably in primary and adjacent secondary auditory fields), more specific information about acoustic features, such as pitch height, pitch chroma, timbre, intensity and roughness is extracted [10,13–17]. These operations appear to be reflected in electrophysiological recordings in ERP components that have latencies of up to 100 ms (e.g. the P1 and N1; for effects of musical training on feature extraction see, e.g. [18]). The details about how and where in the auditory cortex these features are extracted are still not well understood. With respect to the meaning of sounds it is interesting that just a short single tone can sound, for example, 'bright', 'rough', or 'dull'; that is, single tones are already capable of conveying meaning information.

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Available online 3 November 2005

www.sciencedirect.com 1364-6613/$ - see front matter doi:10.1016/j.tics.2005.10.001

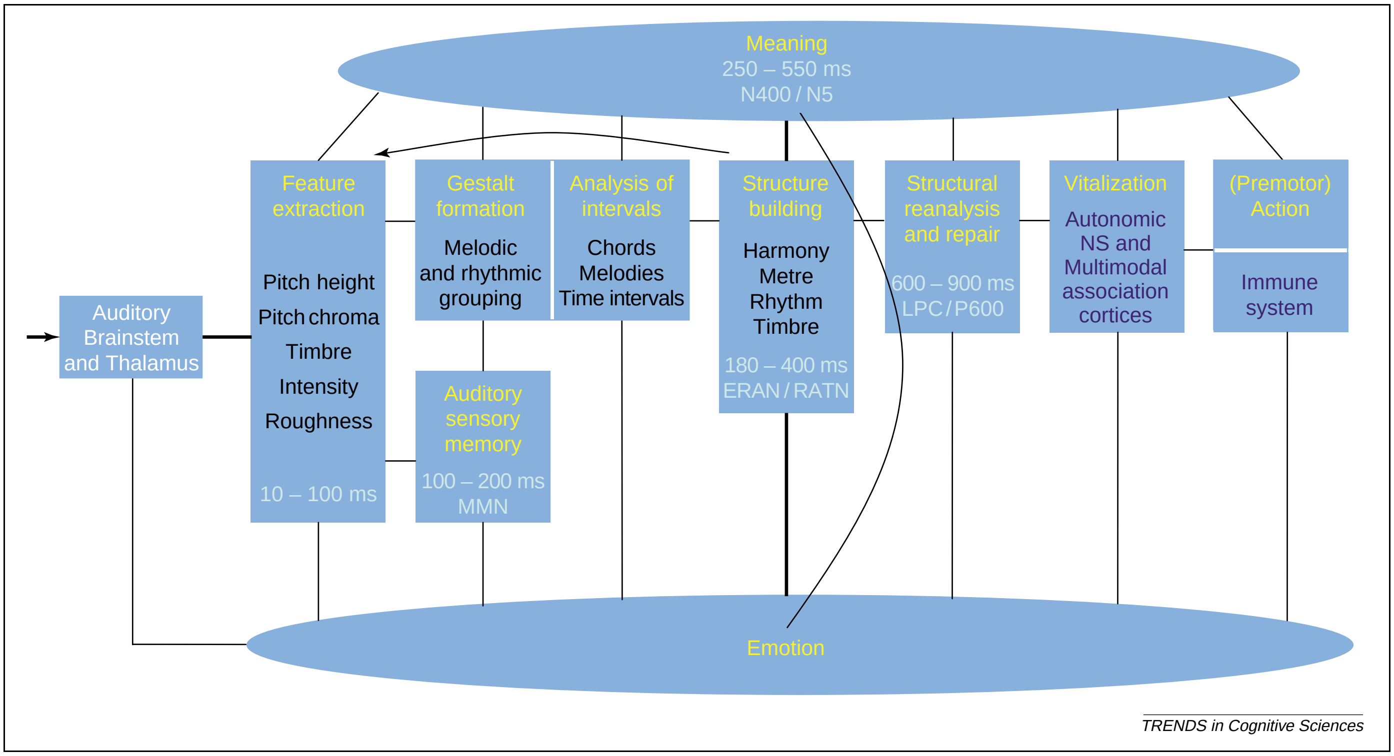

Figure 1. Neurocognitive model of music perception, showing the modules to which different aspects of music perception can be assigned (see text for details).

After auditory features have been extracted, the acoustic information enters the auditory sensory memory, and a stage in which auditory *Gestalten* (e.g. represenatations comprising several perceptual elements) are formed (Figure 1). Operations of auditory sensory memory are at least partly reflected in the mismatch negativity (MMN) [19]. The MMN has been used to investigate effects of musical training on the processing of pitch [20], melodic encoding [21,22], grouping of sequential sounds [23], and spatial attention [24]. Similar training effects have also been shown for the processing of phonemes [19]. The MMN usually has latencies of about 100–200 ms, and the main generators of the MMN are located in the auditory cortex (within, and in the close vicinity of the primary auditory cortex), but neural populations located in the frontal cortex – presumably in the inferior frontolateral cortex, particularly Brodmann's areas (BA) 44 and 45, and in the dorsolateral prefrontal cortex near and within the inferior frontal sulcus – appear to be crucially involved in the MMN mechanism [19,25]. The formation of auditory Gestalten entails processes of melodic, rhythmic, timbral and spatial grouping, that is, a considerable part of the auditory scene analysis and auditory stream segregation [26,27]. Grouping of acoustic events follows Gestalt principles such as similarity, proximity and continuity. In everyday life, such operations are not only important for music processing, but also, for instance, for separating a speaker's voice during a conversation from other sound sources in the environment. That is, these operations are important because their function is to recognize and to follow acoustic objects, and to establish a cognitive representation of the acoustic environment.

Presumably closely linked to the stage of auditory Gestalt formation is a stage of a more fine-grained analysis of intervals, which might include: (i) a more detailed processing of the pitch relations between the tones of a melody, or between the tones of a chord (required to determine whether the chord is a major or minor chord, played in root position, inversion, etc.); and possibly (ii) a more detailed processing of temporal intervals. Melodic and temporal intervals appear to be processed independently, as suggested by the observation that brain damage can interfere with the discrimination of pitch relations but spare the accurate interpretation of time relations, and vice versa [28,29]. However, these different types of interval processing have so far not been dissociated in functional imaging studies [30].

It has been suggested that the analysis of the contour of a melody (which is part of the auditory Gestalt formation) relies particularly on the posterior part of the right superior temporal gyrus (STG), whereas the processing of more detailed interval information appears to involve both posterior and anterior areas of the supratemporal cortex bilaterally [28,31,32]. The planum temporale has been particularly implicated in the processing of pitch intervals and sound sequences [32,33], and it has been argued that the planum temporale is a crucial structure for auditory scene analysis and stream segregation [34]. However, details about the neural correlates of both auditory Gestalt formation and interval analysis still need to be specified.

When intelligence comes into play

In contrast to previous models, the present one also includes modules of syntactic processing (see Figure 1 and

Box 1. Processing structure in music

A central module of the model presented in Figure 1 (main text) refers to syntactic structure building. In major/minor tonal music, certain regularities govern the combination of chord functions into harmonic sequences (see Fig. Ia,b). Harmonic regularities build only part of a musical syntax, other structural aspects comprise melodic, rhythmic, metric, (and possibly timbral) structure. Neurophysiological studies using EEG and MEG have shown that music-syntactic violations elicit anterior brain responses with negative polarity over frontal regions, which emerge around 180–350 ms after the onset of an irregular chord (Fig. Ic). In experiments with isochronous, repetitive stimulation, this effect is maximal at around 180–200 ms over right anterior electrodes (denoted as 'early right anterior negativity', or ERAN) [37,39,65]. In experiments in which the occurrence of irregular chords is unpredictable, the negativity has a longer latency, and a more anterior-temporal distribution (denoted as 'right anterior-temporal negativity', or RATN) [71,72].

Functional imaging studies using chord sequence paradigms [63, 73–75] and melodies [76] suggest that music-syntactic processing activates the pars opercularis of the inferior frontolateral cortex (corresponding to BA44) bilaterally, but with right-hemispheric weighting (Fig. Id). However, it appears that BA44 is not the only structure involved in music-syntactic processing: additional activations have been reported for the anterior portion of the STG [63,74], and for ventrolateral premotor cortex (vlPMC) [53,63,74,77]. The anterior portion of the STG appears to be interconnected with fronto-opercular cortex [78], and has been implicated in syntactic processing during language comprehension [79]. Activations of inferior frontolateral cortex (BA44), often along with vlPMC, have been reported in a variety of functional imaging studies on auditory processing using musical stimuli, linguistic stimuli, auditory oddball paradigms, pitch discrimination tasks and serial prediction tasks, underlining the importance of these structures for the sequencing of structural information, the recognition of structure, and the prediction of sequential information [80].

The processing of structural properties and the detection of structural irregularities requires the computation of structural relations between sequential events. In the above-mentioned experiments that used chord sequence paradigms to investigate the processing of harmonic structure, the music-structural analysis of the chord functions required a computation of the harmonic relation between a chord and the preceding harmonic context. Such a computation is more difficult for irregular than for regular chord functions, mainly because the computation of the harmonic relation will be less common for irregular than for regular chords. This increased difficulty is reflected in a stronger activation of BA44 (presumably along with anterior STG and vlPMC) in repsonse to irregular chords, and the stronger activation of BA44 appears to correlate with the perception of a music-syntactically irregular chord as unexpected.

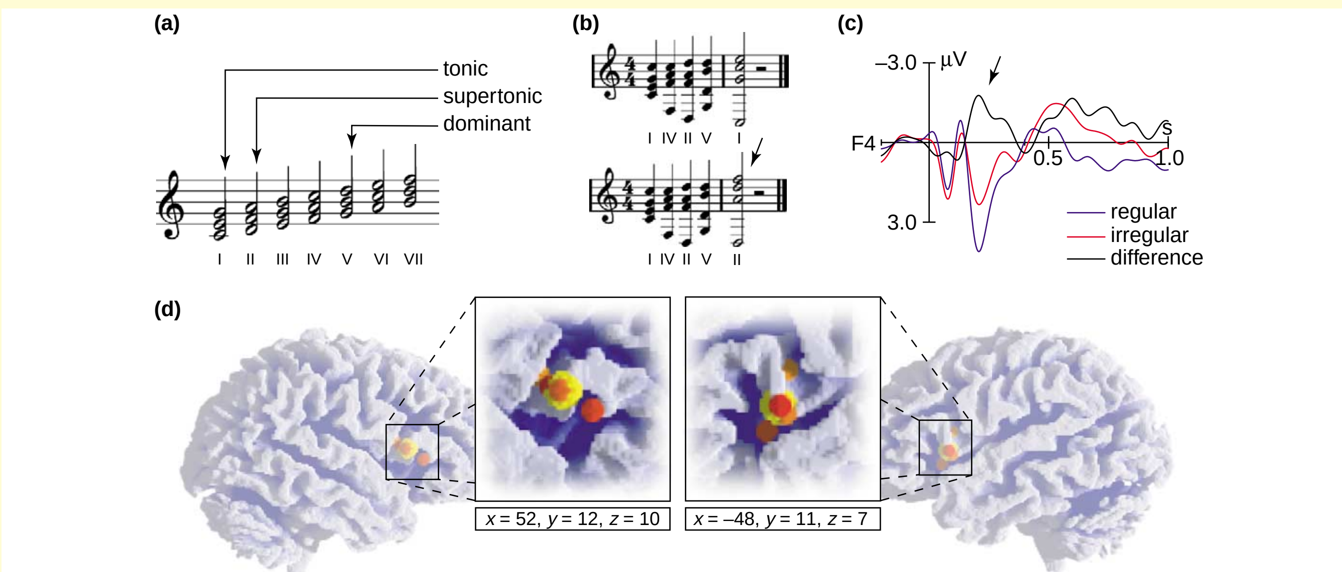

Figure I. (a) Examples of chord functions: the chord built on the first tone of a scale is denoted as the 'tonic', the chord on the second tone as the 'supertonic', and the chord on the fifth tone as the 'dominant'. **(b)** The dominant–tonic progression represents a regular ending of a harmonic sequence (top), the dominant–supertonic progression is less regular and unacceptable as a marker of the end of a harmonic progression (bottom sequence; the arrow indicates the less regular chord). **(c)** ERPs elicited in a passive listening condition by the final chords of the two sequence types shown in (b). Both sequence types were presented in pseudorandom order equiprobably in all twelve major keys. Brain responses to irregular (red waveform) chords clearly differ from those to regular (blue) chords (best seen in the black difference wave = regular subtracted from irregular). The first significant difference between the two waveforms (indicated by the arrow) is maximal around 200 ms after the onset of the final chord in the sequence and taken to reflect processes of music-syntactic analysis. **(d)** Activation foci (small red spheres) reported by functional imaging studies on music-syntactic processing using chord sequence paradigms [63,73–75] and melodies [76]. Large yellow spheres show the mean coordinates of foci (averaged for each hemisphere across studies; coordinates refer to standard stereotaxic space).

below). All types of music show an organization of perceptually discrete elements (such as tones, intervals and chords) into sequences that are structured according to syntactic regularities [35–37]. The analysis of musical structure requires the computation of structural relations between these elements, for example that of the relation between a chord function and a preceding harmonic context (the neural correlates underlying music-syntactic processing are discussed in Box 1). Similar operations presumably exist for the processing of rhythm and metre (for investigations on the detection of musical phrase boundaries see [38]). The processing of musical syntax appears to be quite automatic: electrophysiological effects of music-syntactic processing have been observed in passive listening paradigms (e.g. while participants play a video game, or read a book) [39], and harmonic priming effects can be observed when the harmonic dimension of musical information is task-irrelevant and participants have to make phonemic judgements on sung chords [40].

Box 2. Processing meaning in music

The model outlined in this article assumes musical meaning to be closely related to a variety of aspects of music perception. Music is a means of communication, although usually used differently from language when conveying meaning information (but see also [81]). Aspects of musical meaning might comprise: (i) meaning that emerges from common patterns or forms (e.g. musical sound patterns that resemble gestures, prosodic features, sounds of objects, or qualities of objects); (ii) meaning that arises from the suggestion of a particular mood (e.g. happy, sad); (iii) meaning arising from extra-musical associations (e.g. any national anthem); and (iv) meaning arising from combinations of formal structures that create tension (e.g. when perceiving an unexpected chord) and resolution [42]. Numerous musical sounds and forms are associated with a fixed semantic meaning, for example, sounds associated with concepts like 'rough', 'warm', 'bright' or 'soft', and musical phrases that sound 'friendly', 'angry' or 'gigantic'. Because some musical forms mimic prosodic and other gestures, their meaning is possibly universal across cultures. Other musical forms have culturally determined meanings, for example a church anthem and the word devotion.

A recent EEG study [42] investigated processing of musical semantics with a semantic priming paradigm in which short musical excerpts were followed by the presentation of a target word that was semantically either related or unrelated to the musical excerpt. As a control condition, the same target words were also presented after a sentence that was semantically either related or unrelated to the target word. The pool of target words included both concrete (e.g. *cellar*, *river*, *needle*) and abstract words (e.g. *devotion*, *illusion*, *arrival*). In the language condition (in which target words followed the presentation of sentences), semantically unrelated target words elicited an N400 (compared with related target words; Fig. Ia). The N400 is a classic electrophysiological marker of semantic processing, here reflecting processes related to linguistic analysis that were dependent on the degree of fit between the semantic content of prime sentences and target words. In the music condition (when target words followed musical excerpts), the same N400 effect was elicited by target words that were semantically unrelated to the preceding musical prime stimulus (compared with related target words; Fig. Ib).

These results demonstrate that musical information can prime representations of meaningful concepts, and that music can have a systematic influence on the semantic processing of words. This indicates that music is capable of conveying meaning information, and that the priming effects on the semantic processing of words can be identical for music and language. Notably, the musical pieces used were unfamiliar to the subjects, so the results cannot be attributed to semantic priming via a suggestive title or other prior knowledge of the semantic connotations of the piece. Moreover, N400 effects were the same for target words with and without emotional content, showing that meaning in music is not restricted to its emotive properties.

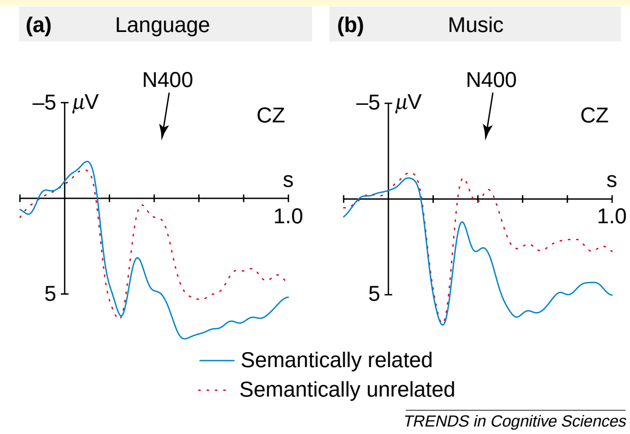

Figure I. ERPs elicited by target words that were semantically related (solid blue line) and unrelated (red dashed line) to **(a)** sentences and **(b)** musical excerpts. In both the language and the music condition, target words that were semantically unrelated to a prime stimulus elicited an N400 compared with semantically related target words, indicating that both linguistic and musical primes had an influence on the semantic processing of words. Data redrawn from [42].

Numerous studies have shown that even non-musicians (i.e. individuals who have not received formal musical training) have a highly sophisticated (implicit) knowledge about musical syntax [35], knowledge which is presumably acquired during listening experiences in everyday life. Note that music-syntactic processing requires processing of long-distance dependencies at a level of complexity that is termed phrase-structure grammar [41]. The ability to process phrase-structure grammar is available to all humans (as evidenced by the use of language), whereas non-human primates are not able to master such grammars [41]. Thus, it is highly likely that only humans can adequately process music-syntactic information at the phrase-structure level.

The music-psychological literature suggests that the outcome of syntactic processing is important for processing meaning and emotion in music [42]. For example, structurally irregular musical events, such as irregular chord functions, can elicit emotional (or affective) responses such as surprise, and these events can have a musical meaning, a fact that is used by composers as a means of expression (see Box 2 for additional information about musical meaning).

Subsequent stages of syntactic processing can occur when structural reanalysis and repair is required. It appears that these processes are reflected in the ERP as positive potentials that are maximal around 600–900 ms, in particular the P600/LPC (late positive component) [37,43].

How the body reacts to music

The present model of music perception also takes the potential 'vitalization' of an individual into account: vitalization entails activity of the autonomic nervous system (i.e. regulation of sympathetic and parasympathetic activity) along with the cognitive integration of musical and non-musical information. Non-musical information comprises associations evoked by the music, as well as emotional (e.g. happy) and bodily reactions (e.g. tensioned or relaxed). The integration of musical and non-musical information requires multimodal association cortices, presumably parietal association cortices in the region of BA7 (where the musical percept might also become conscious [44]). Effects of music perception on activity of the autonomic nervous system have mainly been investigated by measuring electrodermal activity and heart rate, as well as the number and intensity of reported 'shivers' and 'chills' [45–48].

Vitalizing processes can, in turn, have an influence on processes within the immune system. Effects of music processing on the immune system have been assessed by measuring variations of (salivary) immunoglobulin A concentrations [49–51]. Interestingly, effects on the immune system have been suggested to be closely tied to motor activity [51] (see also Figure 1, rightmost box). With respect to music perception, it is important to note that there might be overlap between neural activities of the late stages of perception and those related to the early stages of action (such as premotor functions related to action planning) [52,53]. Recently, it has been shown that music perception can interfere with action planning in musicians [54,55], and listening to piano pieces appears to activate (pre)motor activity in pianists [56]. Movement induction by music perception in the way of tapping, dancing or singing along with music is a very common experience [47], and also has social functions such as bonding between individuals of the same, as well as different, groups [57]. These evolutionarily advantageous social aspects of music-making behaviour are presumably accompanied by positive effects on the immune system, and such positive effects might represent one origin for the evolution of cooperative music-making behaviour in humans.

Action induction by music perception is accompanied by neural impulses in the reticular formation (in the brainstem; for example, for the release of energy to move during joyful excitement). It is highly likely that connections also exist between the reticular formation and structures of the auditory brainstem (as well as between reticular formation and the auditory cortex) [58], and that the neural activity of the reticular formation therefore also influences the processing of (new) incoming acoustic information.

Music perception and memory

The modules presented in Figure 1 are associated with a variety of memory functions. For example, the auditory sensory memory (presumably along with Gestalt formation) is connected with both working memory [59] and long-term memory [19] (see above for information about brain structures implicated in auditory sensory memory). Structure building requires working memory as well as a long-term store for syntactic regularities, and processing of meaning information is presumably tied to a mental lexicon (containing lexical-semantic knowledge), as well as to a musical lexicon containing knowledge about timbres, melodic contours, phrases and musical pieces [6]. However, the details about interconnections between the different modules and different memory functions remain to be worked out.

Neuroimaging studies suggest that working memory for pitch mainly involves the inferior frontal gyrus (BA 44,45, 46), premotor cortex (BA 6), as well as inferior and superior parietal areas (BA40, BA7) and the cerebellum [33,53,60]. PET data suggest that access to musical semantic memory involves the (left) middle temporal gyrus, and that musical semantic representations (that is, parts of a probable musical lexicon) are stored in (left) anterior temporal areas [61]. Further research in these areas is needed to clearly differentiate memory operations from operations of the modules described in Figure 1; it is important to bear in mind that, especially in functional imaging experiments, both types of operations usually co-occur.

Music and language

One of the most intriguing findings in music psychology research is that even individuals without formal musical training show sophisticated abilities to acquire knowledge about musical syntax, and to understand (and enjoy) music. This finding strongly supports the notion that musicality is a natural ability of the human brain. Interestingly, it appears that human musical abilities are important for the acquisition and the processing of language: infants acquire much information about word and phrase boundaries (possibly even about word meaning) through different types of prosodic cues (i.e. the musical cues of language, such as speech melody, metre, rhythm and timbre) [2]. Moreover, tonal languages rely on a meticulous decoding of pitch relations between phonemes, and non-tonal languages also require an accurate analysis of speech prosody to decode structure and meaning of speech. The assumption of an intimate connection between music and speech is corroborated by the findings of overlapping and shared neural resources for music and language processing in both adults and children [36,62–65] (see also Boxes 1 and 2). In this respect it appears that the human brain, at least at an early age, does not treat language and music as strictly separate domains, but rather treats language as a special case of music.

Perspectives and future directions

The model provided in this review helps to identify aspects of music perception that need future research (see also Box 3). For example, with respect to the processing of musical meaning, further research is needed to discern the physical properties that determine the meaning of short acoustic signals, as well as of more complex musical information. This line of research could also investigate which of such properties have a universal meaning, and which are culturally determined.

Another field for future research is the investigation of emotion with music. Music is particularly suitable for the study of human emotion (especially for the investigation of positive emotion) but surprisingly few functional imaging studies have so far addressed this issue [46,66–68].

Box 3. Questions for future research

- How are acoustic features decoded at the cortical level?
- What is the neural basis of auditory scene analysis and stream segregation?
- How does the brain recognize musical Gestalts?
- What are the physical properties that determine the meaning of short acoustic signals, as well as of more complex musical information? Which of such properties have a universal meaning, and which are culturally determined?
- What are the cognitive influences and the underlying neural correlates of the effects that music perception (and production) has on the autonomic nervous system, hormonal and immune systems, and, thus, on human health? How are such effects on these systems influenced by social aspects of music-making behaviour? How can music therapy benefit from these effects?
- What are the shared mechanisms and shared representations underlying music perception and production?
- How do the different modules of music processing interact with each other, and interact with different auditory memories?

Related to this field are studies on effects of music perception and production on the autonomic nervous system (and consequently on the hormonal [69]), as well as on the immune system. Despite the effects of music on the immune system and human health, very little is known about both the cognitive influences and the underlying neural correlates of these effects. Research in this area could also provide explanations for physiological effects of music therapy.

Recently, music has also been used in the investigation of human action [5,54,55]. Future studies could further take advantage of music to investigate the planning and control of highly complex actions, acquisition of motor skills, and influences of emotion on action [70]. The strong impact of music, especially rhythm, on motor actions makes music a valuable tool to investigate the shared mechanisms and shared representations underlying music perception and production.

Another interesting perspective is the investigation of social cognition and music. Making music in a group is always a social situation that requires cooperation and communication. Music allows us to investigate influences of social situations on both perception and production in ecologically valid situations, and research on social cognition with music could shed light on how individuals understand others' intentions and emotions when making music together in a group. Investigations in this area would ideally also consider effects that social aspects of music-making behaviour might have on the autonomic nervous system and the immune system, and, thus, on human health. In conclusion, the present article presents a new model of music perception that incorporates modules of music-syntactic and music-semantic processing, and that emphasizes the effects of music perception on vitalization, premotor processes and the immune system. The purpose of this model is to support and stimulate future research and, thus, to lead to a better understanding of the neural basis of music perception.

Acknowledgements
The authors thank A.F. Friederici, B. Poulin, D. Sammler, S. Jentschke, T. Fritz, K. Schulze, and N. Steinbeis for their contributions to the development of the model.

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