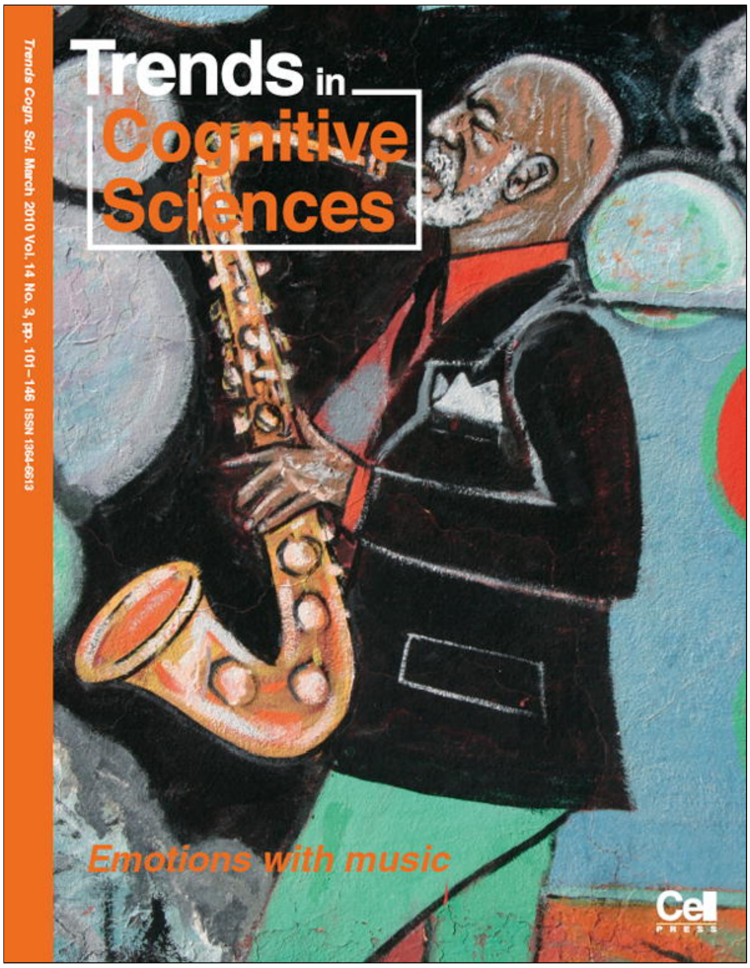
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Review

Towards a neural basis of music-evoked emotions

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Music is capable of evoking exceptionally strong emotions and of reliably affecting the mood of individuals. Functional neuroimaging and lesion studies show that music-evoked emotions can modulate activity in virtually all limbic and paralimbic brain structures. These structures are crucially involved in the initiation, generation, detection, maintenance, regulation and termination of emotions that have survival value for the individual and the species. Therefore, at least some music-evoked emotions involve the very core of evolutionarily adaptive neuroaffective mechanisms. Because dysfunctions in these structures are related to emotional disorders, a better understanding of music-evoked emotions and their neural correlates can lead to a more systematic and effective use of music in therapy.

The benefits of investigating emotion with music

In most humans, music can strongly affect emotion and mood, and such effects are among the main reasons to produce, and listen to, music [1,2]. However, a common misconception is that music-evoked emotions only involve aesthetic experiences, lacking motivational components and goal relevance (Box 1; for reviews see Refs. [2,3]). This view implies that music is not capable of evoking "everyday emotions", and therefore is not well suited to investigate the neural basis of real emotions. Challenging that view, this article provides an overview of neuroscience studies on music and emotion, showing that activity in each and every so-called limbic and paralimbic brain structures can be modulated by listening to music, in both musically trained and untrained individuals. Therefore, music is a well-suited tool to investigate the neural correlates of emotion. A particular advantage of music is that it enables researchers to study a range of positive emotions (such as fun, joy and "chills"), some of which are otherwise difficult to evoke in experimental settings. Moreover, studying the neural correlates of emotions with music also has direct relevance for music-therapeutic applications (Box 2).

The following sections outline how neuroscience studies on music and emotion have advanced our understanding of the functional significance of different limbic and paralimbic structures, and thus our understanding of emotion in general. This overview will mainly deal with functional neuroimaging and lesion studies (for EEG studies see Refs. [4–7]).

Limbic and paralimbic correlates of music-evoked emotions

Although not well defined, "limbic" and "paralimbic" structures are considered as core structures of emotional processing, because their lesion or dysfunction is associated with emotional impairment [8]. How limbic (e.g. amygdala and hippocampus) and paralimbic structures (e.g. orbitofrontal cortex, parahippocampal gyrus and temporal poles) interact, and which functional networks they form is still not well understood.

A central structure within the limbic/paralimbic neural circuitry is the amygdala, which has been implicated in the initiation, generation, detection, maintenance and termination of emotions that are assumed to be important for the survival of the individual [9]. Several functional neuroimaging [10–16] and lesion studies [17–19] have shown involvement of the amygdala in emotional responses to music (Figure 1). The first neuroimaging study showing activity changes in the amygdala was a positron emission tomography (PET) experiment by Blood and Zatorre [10], in which changes in regional cerebral blood flow (rCBF) were measured during "chills" (i.e. intense emotional experiences involving sensations such as goose bumps or shivers down the spine). Each participant listened to a piece of their own favorite music to which they usually had a chill experience. Increasing chill intensity correlated with rCBF decrease in the amygdala as well as the anterior hippocampal formation. An increase in rCBF correlating with increasing chill intensity was observed in the ventral striatum, the midbrain, the anterior insula, the anterior cingulate cortex and the orbitofrontal cortex (the functional significance of these structures is discussed in the following sections; see Refs. [20–22] for patient studies on music-evoked pleasure).

Even if individuals do not have intense "chill" experiences, music can evoke activity changes in the amygdala, the ventral striatum and the hippocampus. Investigating the emotional valence dimension with music, Koelsch *et al.* [11] compared brain responses to joyful instrumental tunes (played by professional musicians) to those evoked by electronically manipulated, permanently dissonant counterparts of these tunes (for other studies using consonant and dissonant music see Refs. [7,12,23–25]). During the presentation of pleasant music, increases in blood–oxygen level dependent (BOLD) signals were observed in the ventral striatum (presumably the nucleus accumbens, NAc) and the anterior insula (among other structures). Dissonant music, by contrast, elicited increases in BOLD signals in the amygdala, the hippocampus, the parahippocampal

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Box 1. Social functions of music: The seven Cs

Humans have a need to engage in social activities; emotional effects of such engagement include fun, joy and happiness, whereas exclusion from this engagement represents an emotional stressor and has deleterious effects on health [59,60]. Making music is an activity that involves several social functions: (1) when we make music, we make *contact* with other individuals (preventing social isolation); (2) music automatically engages *social cognition* [61]; (3) it engages *co-pathy* in the sense that interindividual emotional states become more homogeneous (e.g. reducing anger in one individual and depression or anxiety in another), thus promoting interindividual understanding and decreasing conflicts [62]; (4) music involves *communication* (notably, for infants and young children, musical communication during parent–child singing of lullabies and play songs is important for social and emotional regulation, as well as for social, emotional and cognitive development [63,64]); (5) music making also involves *coordination* of movements (requiring the capability to synchronize movements to an external beat) [65–67]. The coordination of movements in a group of individuals appears to be associated with pleasure (e.g. when dancing together), even in the absence of an explicit shared goal; (6) performing music also requires *cooperation* (involving a shared goal and increasing interindividual trust); notably, engaging in cooperative behavior is an important potential source of pleasure [68,69] and; (7) as an effect, music leads to increased *social cohesion* of a group [70], fulfilling the ''need to belong'' [71], and the motivation to form and maintain interpersonal attachments [60,72]. Social cohesion also strengthens the confidence in reciprocal care (see Ref. [64] for the caregiver hypothesis) and the confidence that opportunities to engage with others in the cited social functions will also emerge in the future. Music seems to be capable of engaging all of the ''Seven Cs'' at the same time, which is presumably part of the emotional power of music. In this regard, music does serve a goal, namely the goal to fulfill social needs that are of vital importance for the individual. Therefore, the notion that music evokes only aesthetic experiences without goal relevance is doubtful.

gyrus and the temporal poles (and decreases of BOLD signals were observed in these structures in response to the pleasant music). Notably, patients with unilateral resection of the medial temporal lobe including the parahippocampal cortex show diminished emotional sensitivity to dissonant music [24,25], consistent with activity changes within the parahippocampal gyrus observed in functional neuroimaging studies using stimuli with varying degrees of dissonance [11,23]. The results of these studies [11,23–25] suggest a specific role of the mid-portion of the parahippocampal gyrus for the processing of acoustic roughness, which is perhaps also relevant for the decoding of the affective content of vocal signals.

In an attempt to investigate the neural correlates of sadness, fear and joy, Baumgartner *et al.* [14] observed that auditory information interacts with visual information in several limbic and paralimbic structures, including the amygdala and the hippocampus (for other studies using joyful and sad music see Refs. [24–26]): activity changes in these structures were stronger during the combined presentation of fearful or sad photographs with fearful or sad music, compared to when only visual information was presented. The combined presentation of music and photographs also elicited stronger activation in the parahippocampal gyrus, and the temporal poles. Activity changes in the amygdala, hippocampal formation, parahippocampal gyrus and temporal poles were also found in two other functional magnetic resonance imaging (fMRI) studies [11,27], suggesting that these structures form a network which plays a prominent role in emotional processing (blue-colored structures in Figure 2).

Box 2. Relevance for therapy

Music therapy (MT) can have effects that improve the psychological and physiological health of individuals. A heuristic working factor model for music therapy [72] assumes five factors which contribute to the effects of MT. These factors refer to the modulation of emotion, attention, cognition, behavior and communication.

Given that music can change activity in brain structures that function abnormally in patients with depression (such as amygdala, hippocampus and nucleus accumbens; see main text), it seems plausible that music can be used to stimulate and regulate activity in these structures (either by listening to or by making music), and thus ameliorate symptoms of depression. However, so far the scientific evidence for effectiveness of MT on depression is surprisingly weak, because of the lack of high-quality studies, and the small number of studies with randomized, controlled trials [73].

Studies on neurological applications of MT have so far mainly dealt with the therapy of stroke patients. Recent evidence suggests that playing melodies either with the hand on a piano, or with the arm on electronic drum pads that emit piano tones, helps stroke patients to train fine as well as gross motor skills with regard to speed, precision and smoothness of movements [74]; it seems likely that an emotional component contributes at least partly to these effects, because this treatment was more effective than a standard rehabilitation. Electrophysiological data suggest that these effects are due to enhanced cortical connectivity and stronger activation of the motor cortex as a result of music-supported movement training [75].

Other studies showed that isometric musical stimuli have the capability of regulating gait and arm control in patients with stroke and Parkinson's disease, presumably as a result of music-evoked arousal and priming of the motor system via auditory stimulation, as well as a result of entrainment of the motor system to the beat of the music [75,76]. Moreover, positive emotions elicited by preferred music can decrease visual neglect (possibly by increasing attentional resources) [77], and listening to self-selected music after stroke appears to improve recovery in the domains of verbal memory and focused attention (along with less depressed and confused mood) [78]. The neural mechanisms for such effects, however, remain to be specified.

The findings of Baumgartner *et al.* [14] received support from a study by Eldar *et al.* [13], who showed that when either positive (joyful) or negative (fearful) music was played simultaneously with an emotionally neutral film clip, it evoked stronger signal changes in the amygdala, and in areas of the ventrolateral frontal cortex, compared to when only music or only film clips were presented. Moreover, the combination of negative (but not positive) music and neutral film clips evoked stronger signal changes in the anterior hippocampal formation compared to when only music or only film clips were presented. Subjective ratings showed that the music plus film conditions were not perceived as significantly more positive or negative than when music was presented alone. Therefore, the functional significance of the increase in signal change (in the amygdala and hippocampal formation) remains unclear. However, the findings that the visual system modulates signal changes in the amygdala are corroborated by data showing that simply closing the eyes during listening to fearful music also leads to increased amygdalar activity [16].

Another important finding by Eldar *et al.* [13] was that activity changes in the amygdala were observed in response to both positive and negative stimulus combinations. This supports the view that the amygdala is not

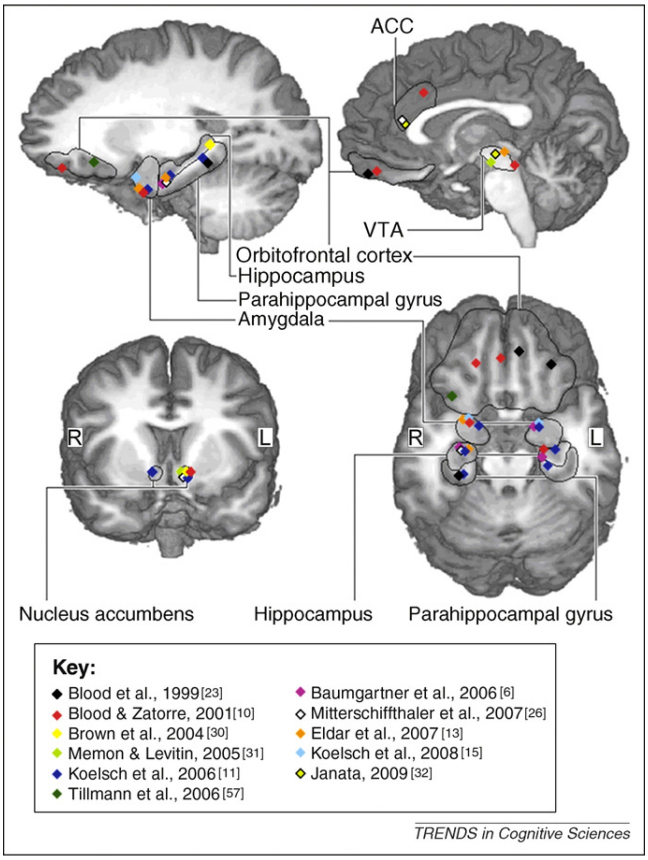

Figure 1. Illustration of some structures belonging to the limbic/paralimbic system. The diamonds represent music-evoked activity changes in these structures (see figure legend for references). Note the repeatedly reported activations of amygdala, nucleus accumbens and hippocampus, reflecting that music is capable of modulating activity in core structures of emotion. Top left: view of the right hemisphere; top right: medial view; bottom left: anterior view; bottom right: bottom view.

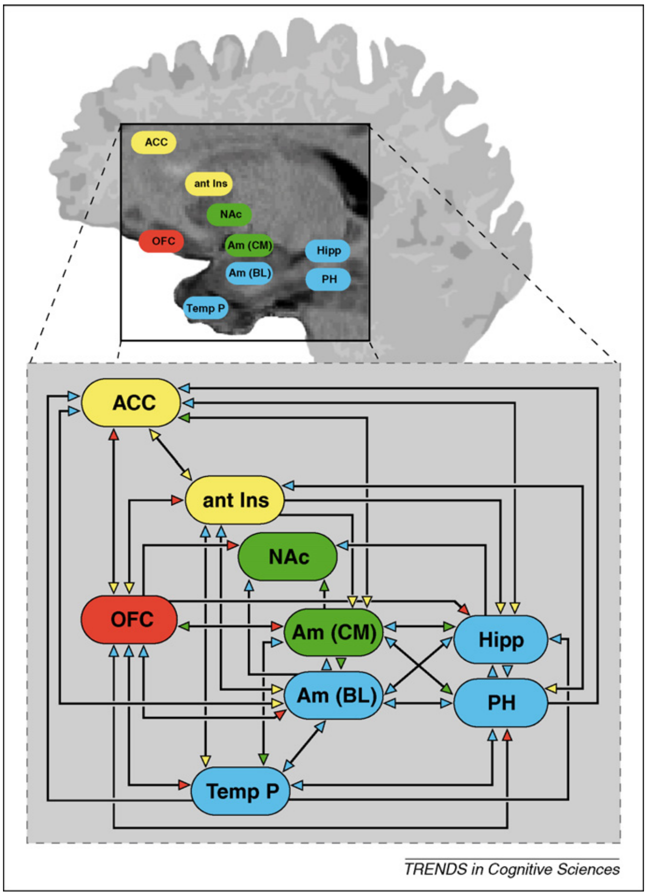

Figure 2. Schematic representation of anatomical connections of some limbic and paralimbic structures involved in the emotional processing of music (Figure 1 and main text). ACC: anterior cingulate cortex; ant Ins: anterior insula; Am (BL): basolateral amygdala; Am (CM) corticomedial amygdala (including the central nucleus), Hipp: hippocampal formation; NAc: nucleus accumbens; OFC: orbitofrontal cortex; PH: parahippocampal gyrus; Temp P: temporal pole. Connectivity is depicted based on Refs. [37,79–81].

only involved in negative but also in positive emotions [28], clearly challenging the rather simplistic view that the amygdala is primarily a "fear center" in the human brain. Notably, the amygdala is not an anatomical unity: it is composed of several distinct nuclei (the lateral, basal, accessory basal, central, medial and cortical nuclei), and although the amygdala has become one of the most intensely studied brain structures, the functional significance of these nuclei, as well as their interaction with other structures, is not well understood [29]. A music study by Ball *et al.* [12] was the first to provide insight into different functional properties of different subregions of the human amygdala in response to auditory stimulation. This study used original (mainly consonant) piano pieces as pleasant stimuli, and permanently dissonant versions of these stimuli as unpleasant stimuli (similar to other studies investigating the valence dimension with music [7,11,23]). The authors investigated signal changes in the amygdala in response to both consonant and dissonant music. A BOLD signal increase was observed in the basolateral amygdala (to both types of music), and signal decrease in a superior region of the amygdala. Also using consonant and dissonant music, Fritz and Koelsch [27] reported BOLD signal decreases with increasing emotional valence in a central aspect of the amygdala (presumably lateral and/or basal nuclei), whereas BOLD signals increased with increasing valence in a superior aspect of the amygdala (including the substantia innominata). Importantly, the central aspect of the amygdala was found to be functionally connected to the temporal pole, the hippocampus and the parahippocampal gyrus, whereas the superior aspect of the amygdala (presumably the corticomedial amygdala) was functionally connected with the ventral striatum and the orbitofrontal cortex. This suggests that different nuclei of the amygdala are involved in modulating activity of different emotion networks.

As mentioned above, the amygdala and related limbic structures play a critical role for emotions that are assumed by some to have survival value for the individual and the species [9]. The studies cited in this section provide compelling evidence that music can evoke activity changes in these brain structures, suggesting that at least some music-evoked emotions involve the very core of evolutionarily adaptive neuroaffective mechanisms. This challenges the notion that music-evoked emotions are merely illusions, rather than real emotions (reviewed in Refs. [2,3]; Box 1). The next section provides further support for the view that music is capable of evoking real emotions by illustrating neural correlates of music-evoked pleasure.

Music affects dopaminergic neural activity

Several studies have shown that listening to pleasant music activates brain structures implicated in reward and experiences of pleasure (perceived pleasantness evoked by the engagement in social functions during making, and listening to, music is addressed in Box 1). Blood and Zatorre [10] reported that the ventral striatum (presumably the NAc; Figure 1) is involved in intensely pleasurable "chill" responses to music. Similarly, another PET study by Brown *et al.* [30] reported activation of the ventral striatum (in addition to the subcallosal cingulate cortex, the anterior insula and the posterior part of the hippocampus) during listening to two unfamiliar, pleasant pieces contrasted with a resting condition. Activation of the ventral striatum in response to pleasant music was also observed in three studies using fMRI (one investigated the valence dimension [11], another examined differences in pleasantness as a result of the predictability of music [31], and the third investigated music-evoked memories [32]). One of these studies [31] reported that activation of the ventral striatum was connected to activity in the ventral tegmental area (VTA) and the hypothalamus. This suggests that the hemodynamic changes observed in the ventral striatum reflected dopaminergic activity: the NAc is innervated in part by dopaminergic brainstem neurons (located mainly in the VTA as well as in the substantia nigra) and is part of the so-called 'reward circuit' [33]. This circuit includes projections from the lateral hypothalamus via the medial forebrain bundle to the mesolimbic dopamine pathway involving the VTA with projections to the NAc [34]. Further support for the assumption that the hemodynamic changes in the ventral striatum reported in Refs. [10,11,30–32] involved dopaminergic neural activity stems from a recent PET study [35] showing that strong music-evoked pleasure (including "chill" experiences) lead to increased dopamine binding in the NAc.

Importantly, activity in the NAc (as well as activity in the ventral pallidum [33]) correlates with motivation- and reward-related experiences of pleasure, for instance during the process of obtaining a goal, when an unexpected reachable incentive is encountered, or when individuals are presented with a reward cue (reviewed in Refs. [33,36]). In humans, NAc activity has been reported for sexual activity, intake of drugs, eating of chocolate and drinking water when dehydrated [33,36]. It has, therefore, previously been suggested that NAc activity correlates with the subjective experience of fun [3], but more detailed information about the functional significance of the NAc is needed to determine the role that the NAc possibly plays for other emotions as well.

The NAc also appears to play a role in invigorating, and perhaps even selecting and directing, behavior in response to stimuli with incentive value, as well as in motivating and rewarding such behavior [36]. The NAc is considered as a 'limbic motor interface' [37], because (i) the NAc receives input from limbic structures such as amygdala and hippocampus; (ii) injecting dopamine in the NAc causes an increase in locomotion; and (iii) the NAc projects to other compartments of the basal ganglia, which play an important role for the learning, selection and execution of actions. This motor-related function of the NAc puts it in a key position for the generation of a drive to move to, join in and dance to pleasant music, although the neural basis for this drive needs to be specified.

It is important to note that in three of the cited studies [11,30,31] participants did not report chill responses during music listening, suggesting that dopaminergic pathways including the NAc can be activated by music as soon as it is perceived as pleasant (i.e. even in the absence of extreme emotional experiences involving chills). Results from the reviewed studies indicate that music can easily evoke experiences of pleasure, or fun, associated with the activity of a reward pathway involving the hypothalamus, the VTA and the NAc. This emotional power of music needs to be explored to provide more systematic knowledge that could be used in support of the therapy of affective disorders related to anhedonia (such as depressive disorders or Parkinson's disease; Box 2). It has previously been argued that music cannot only evoke subjective experiences of fun (involving the NAc) but also experiences of joy and happiness [3]. The next section puts forward the hypothesis that the latter experiences involve different neural systems than those involved in experiences of fun.

Music and the hippocampus

Compared to studies investigating emotion with stimuli such as emotional faces, affective pictures, pain stimuli or reward stimuli, the number of studies reporting activity changes within the (anterior) hippocampal formation in response to music [10,11,13,14,26,27,30] is remarkably high (Figure 1). It is well established that the hippocampus plays an important role for learning and memory [38], as well as for novelty and expectedness [39] (for relations between music-evoked emotions and memory processes see Refs. [32,40,41]). However, at least in some of the functional neuroimaging studies that used music to investigate emotion, it is unlikely that the hippocampal activations were simply a result of memory processes. For example, in the fMRI study by Mitterschiffthaler *et al.* [26], in which sad (as compared to neutral) music elicited changes in the anterior hippocampal formation, participants were probably comparably familiar with neutral and sad pieces. Similarly, participants were presumably equally unfamiliar with the happy and fearful musical pieces used in the study by Eldar *et al.* [13].

Therefore, studies on music and emotion remind us of James W. Papez's view that the hippocampus also plays an important role for emotional processes [42], a notion which is at least around 70 years old, but has unfortunately fallen into abeyance. The hippocampus has dense reciprocal connections with structures involved in the regulation of behaviors essential for survival (such as ingestive, reproductive and defensive behaviors), and with structures involved in the regulation of autonomic, hormonal and immune system activity [37]. Such structures include the amygdala, hypothalamus, thalamic nuclei, the septal-diagonal band complex, the cingulate gyrus, the insula and autonomic brain stem nuclei (Figure 2). Efferent connections project to the NAc, other parts of the striatum, as well as to numerous other limbic, paralimbic and non-limbic structures [37]. The functional significance of these connections places the hippocampus (along with the amygdala and the orbitofrontal cortex) in a pivotal position for emotional processing, and it has previously been noted that the key to understanding the function of the hippocampus lies in the fact that it has major projections not only to cortical association areas but also to subcortical limbic structures [37].

The notion that the hippocampus is involved in emotional processes (in addition to its more cognitive functions such as memory and spatial representation) is supported by significant empirical evidence. First, individuals with depression show structural as well as functional abnormality of the hippocampus (reviewed in Refs. [43,44]). Second, the hippocampus is unique in its vulnerability to emotional stressors. In animals, chronic stress related to helplessness and despair leads to death of hippocampal neurons and related hippocampal atrophy [44], consistent with studies on humans that show reduced hippocampal volume in individuals suffering from childhood sexual abuse [45] and post-traumatic stress disorder (PTSD) [46]. The loss of hippocampal volume during and after emotional traumatization, or during depression, is assumed to be partly due to both a downregulation of neurogenesis in the hippocampus and death of hippocampal neurons [44]. Third, activity changes in the anterior hippocampal formation (as well as in the amygdala) in response to pleasant and unpleasant music are reduced in individuals with reduced "tender positive emotionality" (i.e. with reduced capability of producing tender positive feelings that can be described as soft, loving, warm and happy) compared to individuals of a normal control group [47].

Although only little specific information about the involvement of the hippocampus in the processing of emotions is yet available, the results of the study by Koelsch *et al.* [47] (as well as of studies showing hippocampal dysfunction and structural damage in depressive individuals) encourage the hypothesis that the hippocampus is a critical structure for the generation of tender, positive emotions, such as joy and happiness. This hypothesis relates feelings of happiness (supposedly involving the hippocampus, presumably in connection with the amygdala, parahippocampal gyrus and temporal poles) to a different neural network than the experiences of fun (involving the NAc, the VTA, and the hypothalamus; see previous section). Future neuroimaging studies of emotion should carefully control for familiarity, novelty and memory processes elicited by different stimulus categories to rule out the possibility that hippocampal activations are due to such factors.

Notably, owing to the capability of music to evoke activity changes in the hippocampus, it is conceivable that music therapy with depressed patients and with PTSD patients has positive effects on the upregulation of neurogenesis in the hippocampus, but this is still an open question (Box 3).

It is also worth noting that because of its particular sensitivity to emotional stressors, inhibition of neural pathways projecting to the hippocampus during the perception of unpleasant stimuli could represent a sensitive neural mechanism that serves the prevention of potential damage of hippocampal neurons [3,11]. Thus, it is possible that activity changes observed in the amygdala and the hippocampus during the presentation of unpleasant (or threatening) stimuli is not necessarily a result of the generation of fear (or other unpleasant emotions) but could well reflect inhibitory processes activated to prevent the hippocampus from traumatization during exposure to potentially harmful stimuli.

Box 3. Outstanding questions

- How can the emotion-evoking power of music be used in the therapy of affective disorders related to anhedonia, such as depressive disorders, or of Parkinson's disease?
- What are the neural correlates of the mechanisms underlying the evocation of emotions by music?
- How (and why) does the interaction of music and visual information impact on activity of the amygdala and the hippocampus?
- What is the neural basis of the drive to move and dance to (pleasant) music?
- Can modulation of hippocampal activity (and possible upregulation of neurogenesis in the hippocampus) with music be used for the therapy of depressed patients and patients with PTSD?
- What role does the ACC play for the synchronization of biological subsystems?
- What is the neural basis of beneficial effects of music listening in stroke patients?

Effects of music on insular and anterior cingulate cortex activity

Current theories of emotion emphasize the association between emotion and changes in physiological arousal (mainly involving changes in autonomic and hormonal activity). Changes in autonomic activity have been reported to be associated with activity changes in the anterior cingulate cortex (ACC) and the insular cortex [48–50], and music studies using PET or fMRI have observed activity changes in both of these structures (during music-evoked chills [10], as well as during experiences of fear and sadness [14]). Note, however, that activity changes in the ACC or insular cortex are not necessarily related to emotional processing (for the role of the ACC in performance monitoring and motor activity see Ref. [51]; for movement-related functions of the insula and the involvement of the insula in the perception of speech and music see Ref. [3,52]).

It has recently been proposed [3] that the ACC is involved in the *synchronization of biological subsystems* (such as physiological arousal, motor expression, motivational processes, monitoring processes and cognitive appraisal; [53]). The synchronization of these subsystems is likely to occur as an effect of every emotional instance and could even be indispensable for subjective emotional experiences (usually referred to as *feelings*). The ACC is in a unique position to accomplish such synchronization, owing to its involvement in cognition, autonomic nervous system activity, motor activity, motivation and monitoring.

Emotions are usually not only accompanied by autonomic but also by endocrine (i.e. hormonal) effects, which, in turn, have effects on immune system function [54,55]. With regard to music, such effects are particularly relevant when they are related to a reduction of stress or amelioration of depression and anxiety [56] (Box 2). However, more evidence of the emotional effects of music on autonomic, hormonal and immune system activity is needed for music therapy to be systematically employed in the treatment of diseases related to endocrine, autonomic or immune system dysfunction.

Concluding remarks

Despite active research in the area of affective neuroscience, the different roles of various brain regions involved in emotion are still not well understood. This review illustrates that music is an important, perhaps even indispensable, tool to gain such knowledge. Future work with music can contribute to the investigation of the neural networks underlying different emotions, with the particular advantage that music can be used to study a range of positive as well as negative emotions.

As yet only little is known about the neural correlates of different psychological processes underlying the evocation of emotion with music (such as emotional contagion [11], musical expectancy [15,57,58] or musical memories [2]). Specific knowledge can be gained by systematically manipulating different such processes to identify their neural correlates.

Finally, with regard to music therapy, future work needs to determine which types of music (taking into account individual experiences and preferences) are best suited to stimulate specific limbic and paralimbic brain structures (e.g. the hippocampus in depressive patients or dopaminergic system activity in patients with Parkinson's disease). Therefore, although several outstanding questions remain, better insight into the neural basis of emotions evoked by music will lead to a better understanding of how to employ music in the therapy of affective disorders.

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