Brain correlates of music-evoked emotions

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Abstract | Music is a universal feature of human societies, partly owing to its power to evoke strong emotions and influence moods. During the past decade, the investigation of the neural correlates of music-evoked emotions has been invaluable for the understanding of human emotion. Functional neuroimaging studies on music and emotion show that music can modulate activity in brain structures that are known to be crucially involved in emotion, such as the amygdala, nucleus accumbens, hypothalamus, hippocampus, insula, cingulate cortex and orbitofrontal cortex. The potential of music to modulate activity in these structures has important implications for the use of music in the treatment of psychiatric and neurological disorders.

Music
Structured sounds that are produced by humans as a means of social interaction, expression, diversion or evocation of emotion.

Functional neuroimaging
Functional neuroimaging methods, such as functional MRI (fMRI) or positron emission tomography (PET), use indirect measures (for example, changes in regional blood flow) to localize neural activity in the brain.

Otolith organs
The two otolith organs, the saccule and utricle, are vestibular organs that sense linear acceleration (and its gravitational equivalent).

Vestibular nuclei
Nuclei that are located in the brainstem and receive information from the vestibular nerve.

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Music is a universal feature of human societies: in all cultures that we know about, humans make (or made) music. Newborn infants show limbic responses to music[1], and 5-month-old infants enjoy moving in synchrony with music[2]. For adults, the prime motivations for engaging with music are experiencing, and regulating, emotions and moods[3] (a neurobiological definition of emotion is provided in BOX 1).

Although researchers still debate the degree of overlap between music-evoked emotions and emotions evoked in everyday life, there is now evidence that music can evoke changes in the major reaction components of emotion, including subjective feeling, physiological arousal (autonomic and endocrine changes), motoric expression of emotion (such as smiling) and action tendencies (for example, dancing, singing, playing an instrument, foot tapping and clapping, even if only covertly).

The potential of music to evoke emotions makes music a valuable tool for the investigation of emotions and their neural correlates. During recent years, neuroscientific research on music-evoked emotions has rapidly progressed and increased our knowledge about neural correlates of human emotion in general. Here, I review this research and summarize the findings by providing a meta-analysis of functional neuroimaging studies on music-evoked emotions. Findings to date indicate that the superficial amygdala has a central role in the processing of stimuli with universal socio-affective significance (such as music), that music-evoked pleasure is associated with activity of the dopaminergic mesolimbic reward pathway (including the nucleus accumbens) and that the hippocampal formation is involved in emotions related to social attachments. The power of music to change the neuronal activity within these brain structures has implications for the development of music-based therapies for the treatment of neurological and psychiatric disorders associated with dysfunction and morphological abnormalities in these structures.

Phylogenetic origins of sound-evoked emotions

The auditory system evolved phylogenetically from the vestibular system. Interestingly, the vestibular nerve contains a substantial number of acoustically responsive fibres. The otolith organs (the saccule and utricle) are sensitive to sounds and vibrations[4], and the vestibular nuclear complex exerts a major influence on spinal (and ocular) motor neurons in response to loud sounds with low frequencies or with sudden onsets[4,5] (FIG. 1). Moreover, both the vestibular nuclei and cochlear nuclei project to the reticular formation, and the vestibular nucleus also projects to the parabrachial nucleus, a convergence site for vestibular, visceral and autonomic processing[6,7]. Such projections initiate and support movements and contribute to the arousing effects of music. Thus, subcortical processing of sounds gives rise not only to auditory sensations but also to muscular and autonomic responses, and the stimulation of motor neurons and autonomic neurons by low-frequency beats might contribute to the human impetus to 'move to the beat' (REFS 5,8). Beyond these phylogenetically old brainstem systems, which are in part the basis for visceral reactions to music, several forebrain systems also contribute to music-evoked emotional experiences.

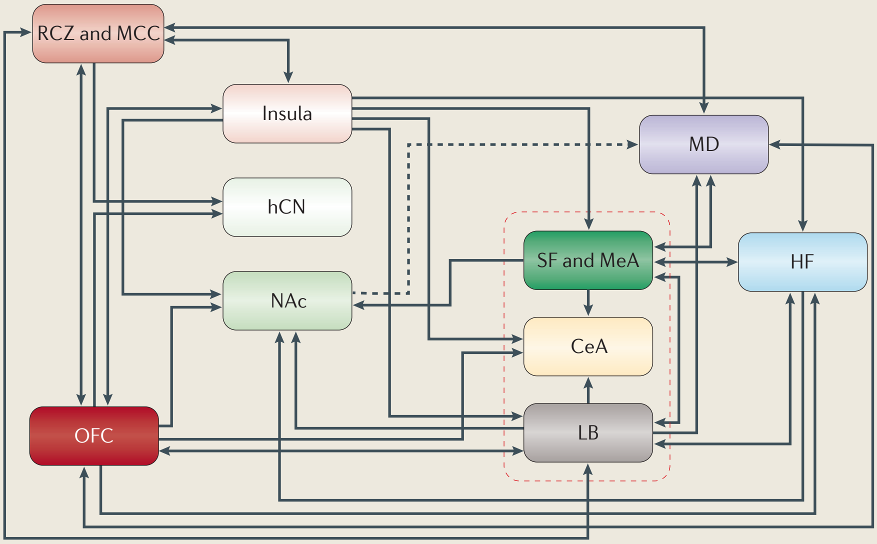
Box 1 | Brain structures involved in music-evoked emotions

Emotions are understood here to be the result of the integrated activity of affect systems (affect-generating brain systems such as the brainstem, diencephalon, hippocampus and orbitofrontal cortex (OFC)) and emotional effector systems (such as peripheral physiological arousal systems and motor systems producing actions, action tendencies and motoric expression of emotion). Information from the affect systems and sensory information resulting from activity of the effector systems (that is, interoceptive, proprioceptive and cutaneous exteroceptive information) is synthesized into an emotion percept (a pre-verbal subjective feeling), which is represented in areas such as the insular cortex, cingulate and secondary somatosensory cortex. An emotion percept can be reconfigured into a symbolic code such as language (analogous, for example, to the reconfiguration of an auditory percept into language). Conscious appraisal (possibly related to neural activity within Brodmann area 7) can regulate and modulate, and to a certain extent even initiate, activity of affect systems and effector systems (and perhaps even of neural activity associated with the representation of an emotion percept). The functional interconnections of the brain structures involved in the affect systems, effector systems, language or conscious appraisal are not yet well understood. As described in the main text, research on emotion with music has revealed some of these connections.

The figure illustrates the anatomical connections between the limbic and paralimbic brain structures highlighted by the meta-analysis in this article. Anatomical connections were drawn according to REFS 31,124,125. The projection from the nucleus accumbens (NAc) to the mediodorsal thalamus (MD) (dashed arrow) is relayed via the ventral pallidum (not shown), which is the main efferent target of the NAc. This striatal–pallidal–thalamic pathway forms part of the limbic loop, which also includes the OFC[31]. The red dashed rectangle denotes structures within the amygdala. MCC, middle cingulate cortex.

Below is a summary of the functional significance of brain structures highlighted in this article.

- Superficial amygdala (SF) and medial nucleus of the amygdala (MeA): sensitive to socio-affective information and modulate approach–-withdrawal behaviour in response to such information
- Laterobasal amygdala (LB): codes the positive or negative reward value of music and regulates neural input into the hippocampal formation (HF)
- Central nuclei of the amygdala (CeA): involved in autonomic, endocrine and behavioural responses, and expression of emotion
- HF: regulates hypothalamus–pituitary–adrenal axis activity, is vulnerable to emotional stressors and generates attachment-related emotions
- MD: modulates corticocortical communication, movement control and approach–withdrawal behaviour
- Auditory cortex: computational hub in an affective–attentional network with limbic, paralimbic and neocortical connections
- Brodmann area 7: involved in processing conscious appraisal, conscious subjective feeling and attentional functions
- Brodmann area 8: involved in response competition and has a putative role in musical tension owing to prediction difficulty and uncertainty
- Pre-supplementary motor area (SMA): involved in complex cognitive motor programming and preparation of voluntary action plans — for example, to dance
- Rostral cingulate zone (RCZ): convergence zone for interoceptive awareness, internal selection of movements and autonomic regulation
- Insula: involved in autonomic regulation and sensory interoceptive representation of bodily reactions accompanying emotions
- Head of the caudate nucleus (hCN): involved in the initiation and patterning of somatomotor behaviour, anticipation of frissons
- NAc: sensitive to rewards and motivates, initiates and invigorates behaviours to obtain and consume rewards
- OFC: involved in the control of emotional behaviour and automatic (non-conscious) appraisal and is activated by breaches of expectancy



Music changes activity in core emotion networks

FIGURE 2 shows the results of a meta-analysis of functional neuroimaging studies on music-evoked emotion[9–29] (for details, see Supplementary information S1 (box)). The studies included in this analysis used various experimental approaches, such as investigating music-evoked experiences of intense pleasure[10,22], emotional responses to consonant or dissonant music[9,14,19,23], happy or sad music[12,15,24,25], joy- or fear-evoking music[16,28], musical expectancy violations[18] and music-evoked tension[29]. Despite this methodological diversity, the meta-analysis shows clusters of changes in activity in various regions in response to music, including the superficial and laterobasal nuclei groups of the amygdala, the hippocampal formation, the right ventral striatum (including the nucleus accumbens) extending into the ventral pallidum, the head of the left caudate nucleus, the auditory cortex, the pre-supplementary motor area (SMA), the cingulate cortex and the orbitofrontal cortex. Thus, music can evoke activity changes in the core brain regions that underlie emotion. Below, the role of the amygdala, the nucleus accumbens and the hippocampus in music-evoked emotions is discussed in detail. Further information on the connections between, and functions of, the brain structures indicated in the meta-analysis can be found in BOX 1.

Cochlear nuclei
Nuclei that are located in the brainstem and receive information from the cochlear ('auditory') nerve.

Forebrain
The forebrain (also called the prosencephalon) comprises the diencephalon, the telencephalon impar and the telencephalon (cerebrum).

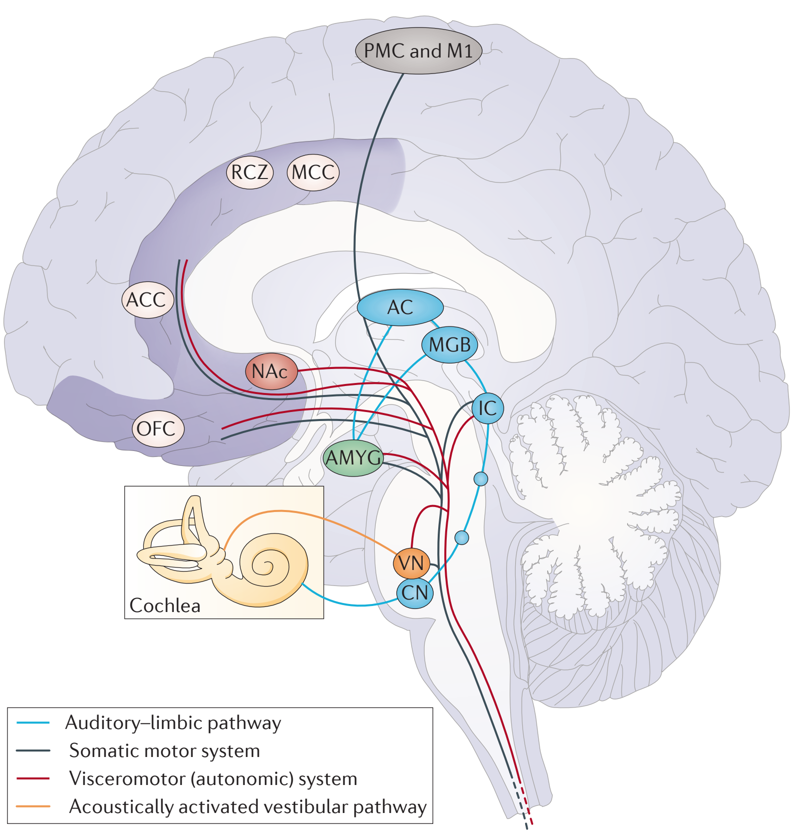


Figure 1 | **The main pathways underlying autonomic and muscular responses to music.** Note that the auditory cortex (AC) also projects to the orbitofrontal cortex (OFC) and the cingulate cortex (projections not shown). Moreover, the amygdala (AMYG), OFC and cingulate cortex send numerous projections to the hypothalamus (not shown) and thus also exert influence on the endocrine system, including the neuroendocrine motor system. ACC, anterior cingulate cortex; CN, cochlear nuclei; IC, inferior colliculus; M1, primary motor cortex; MCC, middle cingulate cortex; MGB, medial geniculate body; NAc, nucleus accumbens; PMC, premotor cortex; RCZ, rostral cingulate zone; VN, vestibular nuclei.

Affective prosody
The non-lexical expression of emotion in speech, as characterized, for example, by pitch height, pitch range, pitch variability, loudness, velocity, rapidity of voice onsets and voice quality.

Eigenvector centrality
A measure of centrality (often used as a measure of the relative importance, or influence, of a node within a network); it assigns a large value if a node is connected with many other nodes that are themselves central within the network.

Amygdala. FIGURE 2a shows clusters of bilateral activity changes in the amygdala in both superficial and laterobasal nuclei groups. The local maxima of these clusters were located in the left superficial amygdala and in the right laterobasal amygdala (see Supplementary information S1 (box) for coordinates). The superficial amygdala mainly comprises the cortical nuclei[30], and some authors also include the medial nuclei in the superficial group[31,32]. Anatomically, both cortical and medial nuclei have three layers of neurons and are thus reminiscent of the three-layered cortex of the hippocampus. The superficial amygdala receives projections from the olfactory bulb and has been implicated in intraspecies communication via olfactory stimuli[33]. Studies in humans have shown that the superficial amygdala is also sensitive to faces[34], sounds[35] and music (in particular to music that is perceived as pleasant or joyful)[10,23,28]. This could be because music is perceived as a stimulus with social significance owing to its communicative properties[36–38] and its acoustic similarity with affective prosody[39]. Basic emotions expressed by olfactory signals, faces, vocalizations and music are universally recognized[39,40], suggesting that the superficial amygdala is sensitive to signals that convey basic socio-affective information between conspecifics.

The superficial amygdala seems to be particularly sensitive to socio-affective signals that encourage approach: music-evoked joy (compared with music-evoked fear) elicits stronger blood-oxygen-level-dependent (BOLD) responses[28] and is associated with higher network centrality[41] in the superficial amygdala. Functional connections between the superficial amygdala and the nucleus accumbens, as well as between the superficial amygdala and mediodorsal thalamus, are stronger during joy-evoking music than during fear-evoking music[28]. This suggests that the superficial amygdala, nucleus accumbens and mediodorsal thalamus constitute a network that modulates approach–withdrawal behaviour in response to socio-affective cues such as music.

The laterobasal amygdala (which consists of lateral, basolateral, basomedial and paralaminar nuclei)[30] is the main amygdala input structure for auditory information as well as for sensory information from other modalities[42]. The laterobasal amygdala has been implicated in the evaluation and learning of both positive and negative stimuli[42–45] and is involved in the generation of expectancies of reinforcers that guide goal-directed behaviour in response to such stimuli[44]. Activity changes in the (right) laterobasal amygdala were observed in response to joyful music in some studies[23,28] and in response to unpleasant or sad music in other studies[14,15]. Thus, activation of the laterobasal amygdala in these studies was probably due to coding of the positive or negative reward value of music. Notably, the laterobasal amygdala receives direct projections from the auditory cortex (in addition to projections from the auditory thalamus)[42] (FIG. 1), and by virtue of such projections the auditory cortex modulates laterobasal amygdala activity in response to complex sounds with emotional valence[35].

The amygdala has high network centrality[46] within emotion networks: it has high structural centrality[47,48], and both the superficial and laterobasal nuclei groups have high functional eigenvector centrality during music-evoked emotion (that is, the amygdala is connected with several other computational hubs)[41]. Thus, the amygdala is in a key position to modulate and regulate emotion networks with regard to initiating, maintaining and terminating emotions, in addition to its function in integrating cognitive and emotional information[48,49].

Nucleus accumbens. Several studies have shown signal changes in the ventral striatum (including the nucleus accumbens) in response to pleasant music[10,11,14,22,26,50] (FIG. 2b). Two studies showed activity in the nucleus accumbens during intense feelings of music-evoked pleasure and reward — so-called 'chills' or 'musical frissons' (REFS 10,22), often involving experiences of shivers or goose-bumps. Importantly, the nucleus accumbens is not only active during frissons but is also activated as soon as music is experienced as pleasurable[11,14,26,50].

The nucleus accumbens is sensitive to primary rewards (such as food, drink or sex) and secondary rewards (for example, money or power)[51]. It is involved in representing

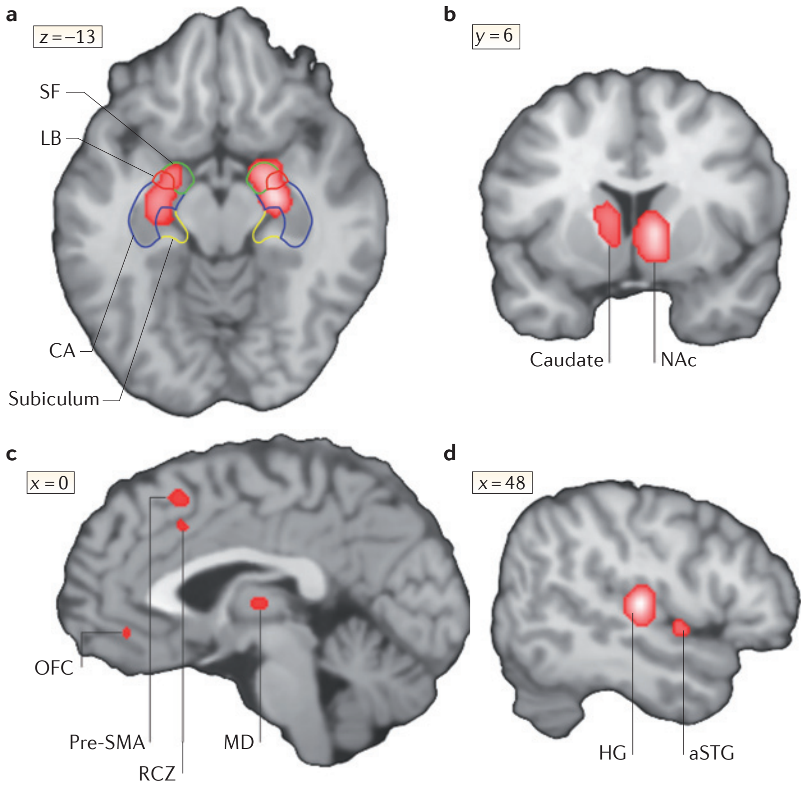


Figure 2 | **Neural correlates of music-evoked emotions.** A meta-analysis of functional neuroimaging studies that shows several neural correlates of music-evoked emotions[9–29]. The analysis indicates clusters of activity changes reported across studies in the amygdala (local maxima were located in the left superficial amygdala (SF), in the right laterobasal amygdala (LB)) and hippocampal formation (panel **a**), the left caudate nucleus and right ventral striatum (with a local maximum in the nucleus accumbens (NAc)) (panel **b**), pre-supplementary motor area (SMA), rostral cingulate zone (RCZ), orbitofrontal cortex (OFC) and mediodorsal thalamus (MD) (panel **c**), as well as in auditory regions (Heschl's gyrus (HG) and anterior superior temporal gyrus (aSTG)) (panel **d**). Note that, owing to the different experimental paradigms used in these studies, limbic and paralimbic brain areas that have not been indicated in this meta-analysis may nevertheless contribute to music-evoked emotions. Outlines of anatomical structures in panel **a** are adapted from probability maps according to REF. 143 (the SF is shown in green, the LB is shown in red, the CA is shown in blue and the subiculum is shown in yellow). Clusters were computed using activation likelihood estimation (ALE) as implemented in GingerALE[144,145] (false discovery rate-corrected $p < 0.01$, 339 foci of 44 contrasts obtained from 21 studies with 319 participants). None of the contrasts included music with lyrics, and none of the contrasts included a comparison of music against a non-stimulus rest condition (for details, see Supplementary information S1 (box)). Images are shown according to neurological convention, and coordinates refer to Talairach space. Coordinates of local maxima of clusters are provided in Supplementary information S1 (box).

hedonic value, and motivates, initiates and invigorates behaviours aimed at obtaining and consuming rewards (for example, by virtue of projections via the ventral pallidum to the tegmentum and to the mediodorsal thalamus; see BOX 1)[31]. In addition to the cluster in the right ventral striatum, FIG. 2b also shows a cluster in the left dorsal striatum (caudate nucleus). The pattern of co-activation in the right ventral and left dorsal striatum corresponds exactly to activations in response to food, money and erotic rewards reported in a recent meta-analysis on the processing of primary and secondary rewards[51]. In addition to these striatal activations, food, monetary and erotic rewards engage the ventromedial orbitofrontal cortex, pre-genual cingulate cortex, amygdala, anterior insula and mediodorsal thalamus[51]. Strikingly, all of these structures were also identified in the present meta-analysis of music-evoked emotions, showing that music-evoked pleasure is associated with the activation of a phylogenetically old reward network that functions to ensure the survival of the individual and the species[31,51]. During rewarding experiences of music, this network seems to be functionally connected with the auditory cortex: while listening to music, the functional connectivity between the nucleus accumbens and the auditory cortex (as well as between the nucleus accumbens and orbitofrontal cortex) predicts whether individuals will decide to buy a song[27].

A positron emission tomography investigation on musical frissons (using $[^{11}\text{C}]$raclopride to measure dopamine availability) indicated that neural activity in both the ventral and dorsal striatum involves increased dopamine availability (probably released by mesencephalic dopaminergic neurons mainly located in the ventral tegmental area (VTA)). Together with evidence showing activity changes in the VTA during musical frissons[10], this indicates that music-evoked pleasure is associated with activation of the mesolimbic dopaminergic reward pathway. Moreover, dopamine availability has been shown to increase in the dorsal striatum during the anticipation of a musical frisson and in the ventral striatum during the experience of the frisson[22]. Thus, different striatal regions are involved in anticipation and experience of reward.

Hippocampus. In striking contrast to monetary, food-related and erotic rewards, which do not activate the hippocampus (as evident from the meta-analysis on reward processing reported in REF. 51), an overwhelming number of studies on music-evoked emotions have reported activity changes within the hippocampal formation[10,13–16,23,26] (FIG. 2a). This indicates that music-evoked emotions are not related to reward alone. Most research on the hippocampal formation has been carried out with regard to learning, memory and spatial orientation. However, in some music studies, hippocampal activity was not simply due to processes related to memory or learning because, for example, only responses to highly familiar pieces were analysed[10].

Hippocampal activity was associated in some studies with music-evoked tenderness[26], peacefulness[26], joy[23], music-evoked frissons[10] or sadness[15]. In other studies[14,16], hippocampal activity changes were associated with both positive (joy) and negative (unpleasantness and fear) emotions. Emotion-related activity changes in the hippocampal formation are consistent with mounting evidence indicating that the hippocampal formation is substantially involved in emotion, owing to its role in the regulation of the hypothalamus–pituitary–adrenal (HPA) axis-mediated stress response[52,53]. Functional connectivity between the hypothalamus and the hippocampal formation has been shown in response to music-evoked joy[41], which supports the notion that the hippocampus is involved in music-evoked positive emotions that have endocrine effects associated with a reduction of emotional stress, such as lower cortisol levels[54,55]. Moreover, the hippocampus is vulnerable to severe,

$[^{11}\text{C}]$raclopride
$[^{11}\text{C}]$raclopride is a radiolabelled D2 dopamine receptor antagonist that is used in positron emission tomography studies.

chronic emotional stressors that lead to feelings of helplessness and despair[45,56]. In humans, structural damage of the hippocampus has been observed in patients with depression[57], individuals with post-traumatic stress disorder (such as war veterans who witnessed extreme violence or committed extremely violent acts)[58] and individuals who were sexually abused during childhood[59]. Such structural damage is due to stress-induced loss of hippocampal neurons and reduced neurogenesis in the dentate gyrus[56]. The involvement of the hippocampal formation in emotion has also been shown in studies investigating neural correlates of tender positive emotion (encompassing joy and attachment-related emotion, such as love, compassion and empathy)[60,61]. These studies show that individuals with a reduced tendency to experience tender positive emotions have a reduced hippocampal volume[60] and exhibit reduced neuronal activity in the hippocampal formation in response to musical stimuli[60,61]. Notably, chronic acoustic stressors can also lead to both structural and functional changes in the hippocampus (and the amygdala)[62].

Besides its vulnerability to stress and regulation of HPA axis stress responses, animal studies indicate that the hippocampus has a role in attachment-related behaviours, such as grooming and nursing of offspring[63–66]. The role of the hippocampus in these behaviours is consistent with the observation that the hippocampus hosts oxytocin receptors and that it is involved in the regulation of oxytocin release into the bloodstream by the pituitary gland[67]. These findings suggest that another emotional function of the hippocampus in humans, beyond stress regulation, is the formation and maintenance of social attachments. Attachment-related emotions (such as love) and emotions that can arise owing to the experience of social attachments (such as joy and happiness) have positive valence, and are hence probably associated with neural activity in the ventral striatum (which receives a large number of direct projections from the hippocampal formation; see also BOX 1)[31]. Conversely, loss of social attachments leads to sadness. This is consistent with music studies showing changes in hippocampal activity during music-evoked tenderness, peacefulness, joy and sadness[15,26,28]. Signal changes in the hippocampus in response to strongly unpleasant[14] or fear-evoking music[16] are perhaps due to automatic inhibitory processes, which might prevent hippocampal damage in response to acoustic stressors[14,62]. For example, the laterobasal amygdala is involved in the regulation of neural input into the hippocampal formation[31,45], in the inhibition of fear responses to faces[68] and in the downregulation of hippocampal neural activity in response to loud or unpleasant sounds[69].

The evocation of attachment-related emotions by music seems to be related to the social functions of music, which establish, maintain and strengthen social attachments (BOX 2). In numerous social contexts, and for most of human history, ‘music’ means actively participating in musical activity (for example, by singing, clapping, playing instruments and dancing). Such musical activity engages several social functions that support the survival of the individual and the species, such as communication, cooperation and social cohesion (BOX 2). Moreover, during engagement with music in a group (whether playing, dancing or simply listening), individuals have a shared goal, joint attention, shared intentionality, joint action and joint emotionality. Corroborating the link between hippocampal activity and engagement in social functions, hippocampal activity increases even when simply tapping in synchrony with a (virtual) partner[70].

Music can also simultaneously support a range of social functions, and owing to the engagement in these social functions, the sense of a communal ‘we’ emerges among the participants involved in a musical activity. Note that the social functions of music have a role even when merely listening to music: listeners automatically engage social cognition[37], interpret music as a communicative signal[36,38] and often feel impulses to move to the music[26,71,72] (also reflected in activity of the pre-SMA, as indicated in FIG. 2c), thus stimulating social interaction during music listening. Music triggers engagement in social functions and is thus directly related to the fulfilment of basic human needs, such as contact and communication with other humans, cooperation, social cohesion and social attachments[73,74]. Strengthening inter-individual attachments and increasing cooperation as well as social cohesion was probably an important adaptive function of music in the evolution of humans[36,75].

Neuropsychological findings. Evidence from patients with brain lesions or degenerative diseases shows that the changes in activity observed in functional neuroimaging studies are not merely correlational: recognition of music expressing joy, sadness, anger or fear is impaired in patients with frontotemporal lobar degeneration, and the degree of impairment is associated with grey matter volume loss (atrophy) in the amygdala, orbitofrontal cortex, cingulate cortex and retro-insular cortex[76]. FIGURE 3 illustrates that these areas show a remarkable overlap with the regions involved in music-evoked emotions, as indicated by the present meta-analysis of functional neuroimaging studies of healthy individuals. Similarly, in patients with semantic dementia, impairment in emotion recognition of music (happy, peaceful, sad or scary) is associated with temporal pole atrophy[77]. Impaired emotion recognition of music has also been shown in patients with unilateral damage of the amygdala and the adjacent hippocampal formation[78,79] and in a patient with a bilateral lesion in the amygdala[80].

Patients with lesions in the parahippocampal cortex and the subiculum of the hippocampal formation find dissonant music pleasant (in contrast to healthy controls, who find such music unpleasant)[81]. Moreover, blunted emotional reactions to music (loss of musical frissons) have been reported for a patient with lesions in the left insula (and the left amygdala)[82]. This is consistent with activation of the anterior insula in several functional neuroimaging studies on music-evoked emotions[10,13,14,26,50] and with the role of the insula in autonomic regulation as well as in the representation and integration of emotionally relevant interoceptive sensory information[83], including visceral reactions accompanying music-evoked emotions.

Frontotemporal lobar degeneration
A term used to describe a group of focal non-Alzheimer dementias that are characterized by selective atrophy of the frontal as well as temporal lobes of the brain. It includes syndromes led by behavioural and semantic disintegration, often accompanied by strikingly impaired understanding of emotional and social signals.

Box 2 | Social functions of music: the seven Cs

Music is an activity that involves several social functions. The ability, and the need, to engage in these social functions is part of what makes us human, and the emotional effects of engaging in these functions include experiences of reward, fun, joy and happiness. Exclusion from engaging in these functions has deleterious effects on health and life expectancy[74].

These functions can be categorized into seven areas. First, when individuals make music, they come into contact with each other. Social contact is a basic need of humans, and social isolation is a major risk factor for morbidity and mortality[74,126].

Second, music automatically engages social cognition. Social cognition involving the attempt to understand the composer's intentions is associated with activity in the anterior frontomedian cortex, temporal poles and the superior temporal sulcus[37]. Interestingly, individuals with autism spectrum disorder (ASD) seem to be surprisingly competent in social cognition in the musical domain[24,111]. This supports the notion that music therapy can aid the transfer of sociocognitive skills in the musical domain to non-musical social contexts in individuals with ASD[111].

Third, engaging with music can lead to co-pathy: individuals of a group can be empathically affected in such a way that inter-individual emotional states become more homogeneous. Co-pathy refers to the social function of empathy, including a decrease in conflicts and promotion of group cohesion[75]. Co-pathy can increase the well-being of individuals during music making or during listening to music[127] and is an important means of the emotional identification of individuals with particular lifestyles, subcultures, ethnic groups or social classes[128].

Fourth, music involves communication. Neuroscientific and behavioural studies have revealed considerable overlap between the neural substrates and cognitive mechanisms underlying the perception and production of music as well as of language[38,129]. For infants and young children, musical communication during parent–child singing seems to be important for social and emotional regulation, as well as for social, emotional and cognitive development[130,131]. Because music is a means of communication, active music therapy can be used to develop (non-verbal) communication skills.

Fifth, music making also involves coordination of actions. This requires individuals to synchronize to a beat and keep a beat. Children as young as 2.5 years of age synchronize more accurately to an external drum beat in a social situation (that is, when the drum beat is presented by a human play partner) than in non-social situations (when the drum beat is presented by a drumming machine or via a loudspeaker)[132]. This effect might originate from the pleasure that emerges when humans coordinate their movements with each other[75,133,134] or to a musical beat[2,72]. The capacity to synchronize movements to an external beat seems to be specific to humans among primates, although other mammals and some song birds might also possess this capacity[4]. Synchronization of movements while playing a beat increases trust and cooperative behaviour in both adults[135] and children[136]. Performing identical movements also gives rise to a sense of group identity.

Sixth, a convincing musical performance by multiple players is only possible if it also involves cooperation. Cooperation implies a shared goal as well as shared intention, and engaging in cooperative behaviour is a source of pleasure (and is associated with activation of the nucleus accumbens)[137]. Cooperation between individuals increases inter-individual trust and the likelihood of future cooperation between these individuals[138,139].

Seventh, music leads to increased social cohesion of a group[140]. A wealth of studies showed that humans have a 'need to belong' — that is, a need to feel attached to a group — and that they have a strong motivation to form and maintain enduring interpersonal attachments[73]. Meeting this need increases health and life expectancy[74,126,141]. Social cohesion also strengthens the confidence in reciprocal care[130,142] and the confidence that opportunities to engage with others in the mentioned social functions will also emerge in the future. Social cohesion has aesthetic quality because it can be experienced as beautiful, and the engagement in social functions can lead to 'aesthetic emotions' such as transcendence and spirituality.

Dominant
A functional denotation of a chord built on the fifth scale tone.

Principles underlying music-evoked emotions

In the previous sections, I described changes in neural activity in response to music and discussed the engagement of social functions as one principle underlying the evocation of emotion by music. Next, I describe two further principles — tension (including musical expectancy) and emotional contagion. A feature that these principles have in common is that emotional effects are due to the music itself (and not, for example, due to memories associated with music or appraisals that are not related to the music itself; these principles are discussed elsewhere[38,84]).

Musical expectancy and tension. Musical sounds are not random and chaotic but are structured in time, space and intensity. Such structuring applies to single tones, simultaneous tones (such as chords) and sequential sounds, from melodies to symphonies. Perceiving musical structures has emotional effects that only emerge from the music itself, without reference to the extra-musical world of concepts, memories or social relationships. The concept of musical tension relates to the different emotions that arise from processing intra-musical structure.

Several structural factors give rise to musical tension. On the perceptual level, acoustic factors, such as sensory consonance or dissonance, loudness and timbre can increase or decrease tension owing to an increase or decrease in (un)pleasantness. Sensory consonance or dissonance is already represented in the auditory brainstem[85] and modulates activity within the laterobasal amygdala[86]. In addition, the perception of acoustic information leads to low-level acoustic predictions[87] and is itself modulated by higher-level predictions and inferences[88]. The combination of acoustic elements leads to the build-up of musical structure, and the interest in this structure (for example, its continuation, its underlying regularities or its logic) is one aspect of musical tension.

The stability of a musical structure also contributes to tension, such as a stable beat or its perturbation (for example, by an accelerando or a ritardando, syncopations, off-beat phrasings, and so on)[89]. In tonal music, the stability of a tonal structure is related to the representation of a tonal centre[90]. Moving away from a tonal centre creates tension, and returning to it evokes relaxation[91–93]. FIGURE 4a illustrates how the entropy of the frequencies of occurrences of tones and chords determines the stability of a tonal structure and thus the ease, or difficulty, of establishing a representation of a tonal centre.

In addition to the stability of musical structure, the extent of a structural context contributes to tension[94]. FIGURE 4b shows the bigram (context-dependent) probabilities of certain chords following other chords in a corpus of Bach chorales. For example, the red bars indicate that, after a dominant, the next chord is most likely to be a tonic. The uncertainty of predictions for the next chord (and thus the entropy of the probability distribution for the next chord) is relatively low during the dominant, intermediate during the tonic and relatively high during the submediant. The entropy values of the probability distributions for chords following these three chord functions, as well as probability distributions for chords following other chord functions, are shown in FIG. 4c. Progressing tones and harmonies thus create an 'entropic flux' that gives rise to a constantly changing (un)certainty of predictions. The increasing complexity of regularities (and thus the increase of entropic flux) requires an increasing amount of (usually implicit) knowledge about musical regularities to

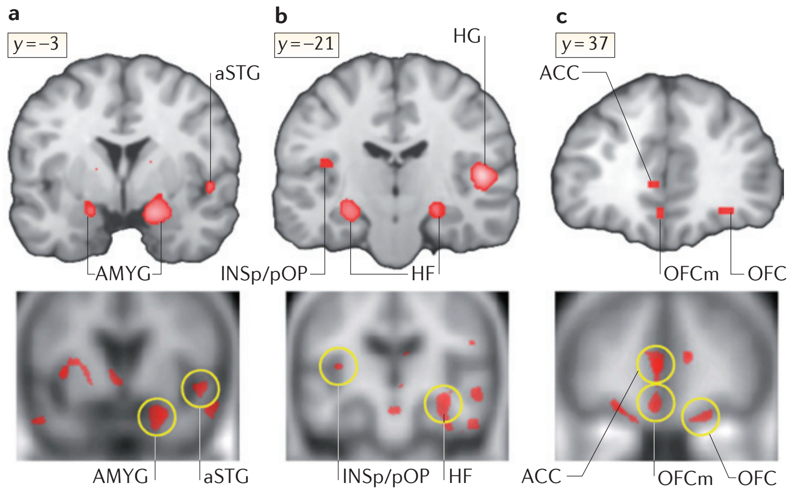


Figure 3 | **Comparison of neural correlates of music-evoked emotions revealed in functional imaging studies with neuropsychological data.** The upper row of images shows the results of the meta-analysis (see also FIG. 1 and Supplementary information S1 (box); *y* coordinates refer to Talairach space), the lower row of images shows grey matter loss associated with impaired recognition of emotions expressed by music in frontotemporal lobar degeneration. Note the overlap (indicated by the yellow circles) between the amygdala (AMYG) and temporal cortex (panel **a**), the posterior insula (INSp)/parietal operculum (pOP) and hippocampus (panel **b**) and the lateral and medial orbitofrontal cortex (OFCm) and pre-genual anterior cingulate cortex (ACC) (panel **c**). This overlap indicates that activations of these structures in functional neuroimaging studies have a causal role in music-evoked emotions. Images are shown according to neurological convention. aSTG, anterior superior temporal gyrus; HF, hippocampal formation; HG, Heschl's gyrus. The images in the lower row for panels **a**, **b** and **c** are modified, with permission, from REF. 76 © (2011) Elsevier.

make precise predictions about upcoming events[95]. Tension can emerge from the suspense about whether a prediction proves true (and correct predictions in more complex systems are probably perceived as more rewarding). Thus, different musical systems and styles can produce different degrees of tension, depending on the sociocultural purpose of music (for example, tension and release are important for a religious chorale as metaphors for sin and redemption, whereas musical tension is less important for a polka dance).

Tension can be further modulated by a structural breach: that is, an event that is unpredicted given the model of regularities mentioned above (such as a deceptive cadence in tonal music). The unpredicted event has high information content[96] (and might be perceived as rewarding because such events help to improve the model[97]). The emotional effects of the violation of predictions (related to free energy[88]) include surprise[98]. In contrast to everyday surprise, in tonal music, these surprising events also evoke tension that results from the delay of the resolution of the sequence. Interestingly, violations of predictions occur despite veridical knowledge of a piece, owing to the automatic (non-intentional) application of implicit knowledge (thus, despite repeated listening to a piece, irregular events still elicit emotional effects). Irregular (unexpected) chord functions evoke skin conductance responses, and the amplitude of such responses is related to the degree of unexpectedness[98,99]. Moreover, unexpected chord functions evoke activity changes in the superficial amygdala[18] and lateral orbitofrontal cortex[100,101], and activity in these two regions correlates with ratings of felt tension while listening to pieces of classical piano music[29]. Thus, music studies can inform us about emotional effects of predictions, predictive coding and prediction errors[102]. Note that not all kinds of unpredicted events evoke such emotional effects (for example, random chaotic stimuli usually do not evoke surprise).

A structural breach is usually followed by a transitory phase, which leads to the resolution of the breach. If a structural breach is not resolved, the musical information is perceived as unpleasant and arousing[98]. Breaches of expectancy give rise to the anticipation of an emotion (for example, anticipation of the relaxation related to the return to the tonic)[94]. Similar anticipatory processes can also be evoked by structural cues without a preceding structural breach — for example, by a dominant seventh chord (which has a markedly high probability for being followed by a tonic, thus evoking the anticipation of release). Such anticipation of relaxation might involve dopaminergic activity in the dorsal striatum[18,22].

The resolution of a sequence (for example, in tonal music, by returning to the tonic) is associated with relaxation[91,93] and thus presumably with feelings of reward[97]. The structural factors mentioned above build a tension arc (that is, build-up, breach, transitory phase and resolution). The overlap of several tension arcs leads to large-scale structures, and the maximum amount of relaxation due to the processing of intra-musical structural relations is reached when all tension arcs are closed at the end of a piece. The degree of tension evoked by intra-musical structure and the development of tension and release owing to the composition of interwoven tension arcs are important aspects of the aesthetic experience of music.

Emotional contagion. Another emotional effect arising from the music itself is emotional contagion: the expression of an emotion with music (such as joy or sadness) can trigger physiological processes that reflect the emotion. For example, 'happy' music triggers zygomatic muscle activity (and an increase in skin conductance and breathing rate), whereas 'sad' music leads to the activation of the corrugator muscle[103,104]. The physiological feedback of such muscular and autonomic activity is thought to evoke the corresponding subjective feeling (for example, joy or sadness)[103,105]. In previous neuroimaging studies using music expressing emotions such as joy, sadness or fear[12,15,16,24,25,28], brain activations were presumably at least partly due to emotional contagion in response to music.

Interestingly, there are acoustic similarities between the expression of emotions in Western music and affective prosody[39]. For example, the acoustic characteristics of speech when expressing joy (such as fast tempo, high sound level and high pitch variability) are similar to those found in music expressing joy[39]. Similarly to affective prosody, which is universally understood[39], even individuals who are naive to Western music can recognize the expression of basic emotions (joy, sadness and fear) in Western music[40]. Thus, music (not necessarily just Western music) and affective prosody feature universal acoustic signals for emotional expression and can therefore evoke processes of emotional contagion.

Tonic
A functional denotation of a chord that is built on the first scale tone.

Submediant
A functional denotation of a chord built on the sixth scale tone.

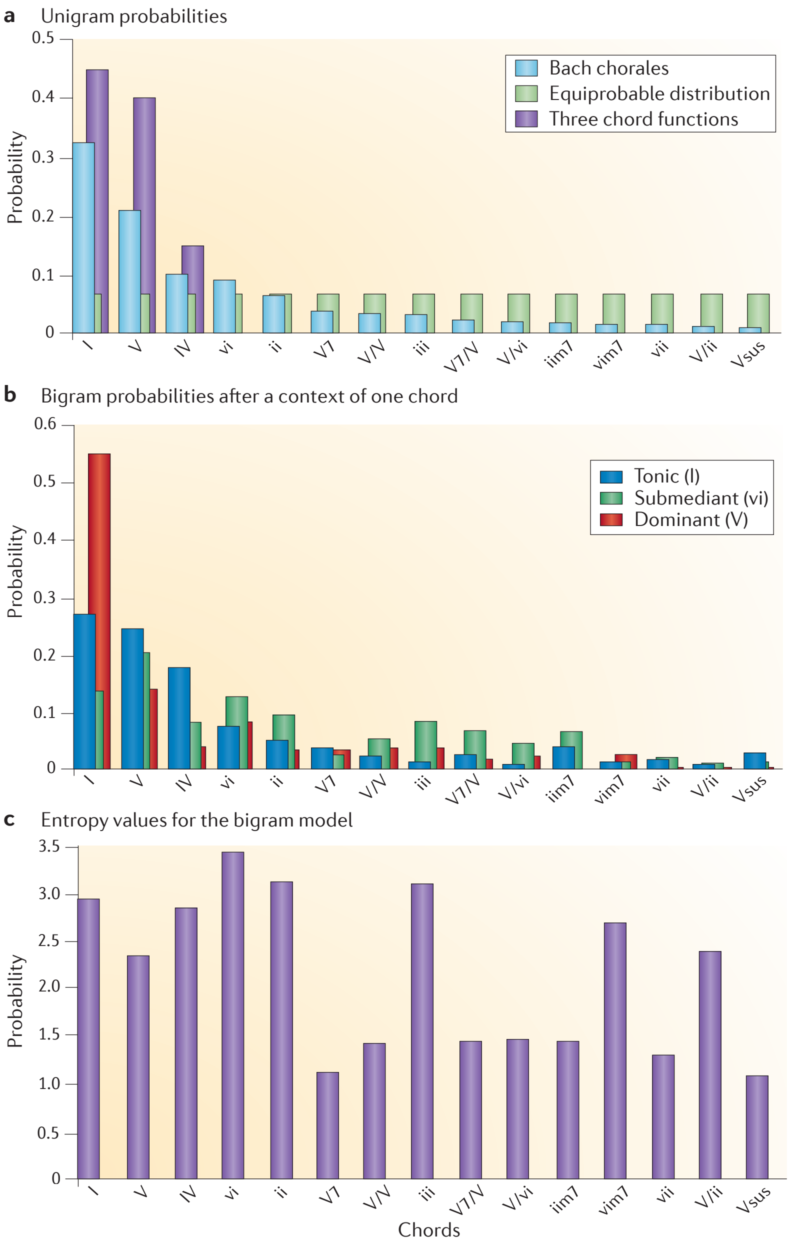


Figure 4 | **Probability distributions of chords and chord progressions.** **a** | The light blue bars show the frequencies of occurrence of chord functions in a corpus of Bach chorales (data from REF. 146). The entropy of the resulting probability distribution is 3.1 bits per chord. The purple bars show an imaginary probability distribution with only three chord functions (as would be typical, for example, for a piece of polka music); here, the tonal centre is easier to extract and the entropy is considerably lower (1.5). The green bars show an imaginary probability distribution in which all chord functions occur with the same probability. The tonal centre is difficult to extract, and the entropy of that distribution is high (3.9). **b** | This graph shows the context-dependent bigram probabilities for the corpus of Bach chorales (data from REF. 146). Blue bars show probabilities of chord functions following the tonic (I), green bars following the submediant (vi) and red bars following a dominant (V). The entropy values (and thus the uncertainty of predictions for the next chord) for these three probability distributions are 2.9 (during tonic), 3.4 (during submediant) and 2.3 (during dominant). **c** | These entropy values, as well as entropy values for the probability distributions for chords following other chord functions, are shown in the graph. IV, subdominant; ii, supertonic; V7, dominant seventh; V/V, secondary dominant; iii, mediant; V7/V, secondary dominant seventh; V/vi, secondary dominant of submediant; iim7, supertonic seventh; vim7, submediant seventh; vii, leading tone; V/ii, secondary dominant of supertonic; Vsus, suspended dominant.

Audio–visual interactions and visual imagery

Several functional neuroimaging studies have investigated how music influences, and interacts with, the processing of visual information[13,16,106–108]. These studies show that combinations of film clips[16,107] or images[13] with music expressing joy[16], fear[13,16] or surprise[107] increase BOLD responses in limbic and paralimbic brain structures, such as the amygdala, hippocampus or insula. Many individuals report that even mere visual imagery of objects, facial and gestural expressions, or of movements, such as dance movements, intensifies their emotional responses to music[84].

During music-evoked fear, the auditory cortex shows emotion-specific functional connectivity with the visual cortex (Brodmann areas 17 and 18), insula, the rostral cingulate zone and Brodmann area 7 of the superior parietal lobule[28]. Both the visual cortex and Brodmann area 7 are also functionally connected with the superficial amygdala during music-evoked fear[28]. Thus, both the auditory and visual cortices are part of an affective–attentional network that might have a role in visual alertness, visual imagery and an involuntary shift of attention during the perception of auditory signals of danger. The role of the auditory cortex in music-evoked emotions in limbic–attentional networks is highlighted in the meta-analysis, which indicated clusters of activity in the auditory cortex bilaterally (see Heschl's gyrus and the anterior superior temporal gyrus in FIG. 2d).

Potential use for therapy

Dysfunction and structural abnormalities in limbic and paralimbic structures (such as the amygdala, hippocampus, medial thalamus, accumbens area, caudate and cingulate cortex) are characteristic of a number of psychiatric and neurological disorders, including depression, pathological anxiety, post-traumatic stress disorder, Parkinson's disease, schizophrenia and neurodegenerative diseases[76,109]. The findings that music can change activity in these structures should encourage a more thorough investigation of the neural correlates of the therapeutic effects of music in the treatment of these disorders and diseases. High-quality studies are needed in this area to provide convincing evidence that music has such therapeutic effects[110].

Another condition in which music could have therapeutic effects is autism spectrum disorder (ASD). Despite their socio-emotional impairment in everyday life, individuals with ASD have a near to normal ability to recognize, experience and process emotional aspects of music[24,111,112]. While listening to happy or sad music, individuals with ASD show activations in cortical and subcortical brain regions that are known to be deficient in this patient group with regard to non-musical emotional stimuli[24]. In addition, children with ASD do not show activation of frontal language areas in response to speech but do show activation of these regions during the processing of music[113]. Music therapy could help patients with ASD to develop a vocabulary for their experiences of music-evoked emotions and to transfer this vocabulary, and related socio-emotional skills, from music to non-musical situations in everyday life[111].

With regard to neurodegenerative disease, some patients with Alzheimer's disease (AD) have almost-preserved memory of musical information (they remember familiar, popular tunes)[114–116]. Moreover, learning of sung lyrics (even on unfamiliar melodies) might lead to better retention of words in patients with AD[117], and anxiety levels of these patients can be reduced with the aid of music. Owing to the colocalization of memory functions and emotion in the hippocampal formation, future studies are needed to systematically investigate how music (and music making) is preserved in patients with AD and whether music can be used to ameliorate the neurological and psychological effects of AD or other neurodegenerative diseases[118]. In addition to therapeutic applications, music has also been suggested as a diagnostic device to differentiate frontotemporal dementia from AD in the early stages of dementia, because recognition of emotions expressed by music seems to be more strongly impaired in frontotemporal dementia than in AD[76,119].

Music has also been shown to be effective for the reduction of worries and anxiety[54], as well as for pain relief in clinical settings (although the effect sizes for pain relief are relatively small compared to analgesic drugs)[120]. Interestingly, stroke patients who regularly listened to music for a period of 2 months soon after stroke onset show a reduction in negative emotions as well as less impaired verbal memory and focused attention[121]; the latter effects might be, in part, due to neurochemical effects associated with positive emotion[54,55].

Conclusions

As has been shown consistently across studies, music can evoke changes in activity in the core structures underlying emotion. Lesioning of these structures leads to impairment of emotional responses to music, indicating causal involvement of these structures in music-evoked emotions. Moreover, music-evoked emotions can give rise to autonomic and endocrine responses as well as to motoric expression of emotion (for example, facial expression), action tendencies (in order to move to music) and subjective feelings. Thus, music can trigger changes in the major reaction components of emotion, indicating that music can evoke real emotions (not merely subjective feelings). This holds true even for emotions that are due to the music itself, such as surprise and tension arising from the breach of an intra-musical structural regularity, or emotions due to emotional contagion.

The degree of overlap between music-evoked emotions and so-called everyday emotions remains to be specified. Some music-evoked emotions may be identical to everyday life emotions (such as surprise or joy), some have different motivational components (for example, the motivation to experience sadness in music, owing to positive emotional effects such as consolation, but not in everyday life), some emotions are sought in music because they might occur only rarely in everyday life (such as transcendence or wonder) and some so-called 'moral emotions' occur in everyday life but usually not music (such as shame or guilt). Importantly, music-evoked emotions have goal-relevant consequences for everyday life, such as the regulation of emotions and moods, or engagement with social functions.

Regardless of the overlap between music-evoked and everyday emotions, and regardless of whether the music itself or associations trigger emotions, the fact that music elicits activity changes in limbic and paralimbic brain structures opens up the possibility of numerous applications for music-based therapy. In addition, the beneficial emotional effects of music also call for more systematic research for the use of music in both children and ageing populations. In children, neural correlates of beneficial effects of musical training on socio-emotional skills (such as emotion regulation or empathy) have remained unexplored. With regard to ageing populations, musical education can raise the quality of life, as indicated by musicians showing less age-related decline in auditory perceptual capabilities[122], including enhanced speech-in-noise perception[123] and greater auditory working memory capacity[123]. Given that musical memory is independent from semantic and episodic memory[118], and surprisingly well preserved in individuals with AD[115,116], experience of preserved mnemonic functions in the area of music can probably considerably enhance life quality in patients capable of actively engaging with music. Thus, policies that espouse music education will, in the long run, prove to be of considerable value for society.

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Competing interests statement

The author declares no competing interests.

SUPPLEMENTARY INFORMATION

See online article: S1 (box)

ALL LINKS ARE ACTIVE IN THE ONLINE PDF

Supplementary information S1 (box)

To visualize the main findings of previous functional neuroimaing studies on music-evoked emotions, and to provide coordinates for directed hypotheses of future studies, a meta-analysis was computed. The selection of studies was based on a search using *ISI Web of Knowledge* (Thomson Reuters, N.Y., USA) with keywords "music" AND "emotion" AND ["fMRI" OR "PET"] (May 2013), and two in-press studies from our group, which have since been published. Inclusion criteria were whole-brain analysis, provision of stereotaxic coordinates (MNI or Talairach space), use of a music stimulus, and at least one measure assessing the subjective feeling component evoked by that stimulus. None of the contrasts included music with lyrics, and none of the contrasts included a comparison of music against a non-stimulus rest condition. 21 studies [REFs. 1-21] with 319 participants, and 339 foci of 44 contrasts were included in the analysis. The analysis was computed using GingerALE.[22,23] Detailed results of the analysis are provided in Table S1. The list of studies and contrasts included in the analysis is provided in Table S2.

Structure	mm^3	Studies	Coord. (x y z)
Cluster 1	3328	2,5-8,13,15,18,20,21	
r hippocampal formation (90% CA)[1]			22 -14 -14
r amygdala (60% LB)[1]			20 -7 -16
Cluster 2	2648	2,5,6,13,15,18-20	
l hippocampal formation (70% CA)[2]			-24 -16 -14
l amygdala (70% SF)[2]			-18 -8 -12
l hippocampal formation (60% FD)[2]			-24 -26 -8
l hipp (70% SUB)[2]			-16 -26 -8
Cluster 3	2352	6,7,14,17-20	
r nucleus accumbens			10 6 2
Cluster 4	1528	5-7,19-21	
r auditory cortex (TE 1.0 80%)			48 -18 8
Cluster 5	1176	5,10,14,19,21	
l caudate nucleus			-8 8 8
Cluster 6	1072	6,13,16,20,21	
l auditory cortex (TE 1.1 60%)[4]			-38 -28 14
Cluster 7	464	2,9	
pre-SMA[3]			2 16 48
frontomedian cortex (area 8)[3]			8 20 46
rostral cingulate zone (area 32)[3]			2 16 36
Sub-threshold clusters			
pre-genual cingulate cortex		12,20	-5 38 6
middle cingulate cortex (area p24)		7,9,16,19	-4 -12 38
medial orbitofrontal cortex		2,5	-2 38 -7
lateral orbitofrontal cortex		8,19	28 36 -6
l anterior insula		2,20	28 8 10
mediodorsal thalamus		2,20	2 -16 5
SPL (area 7)		1,9,19	20 -52 61

[1] The cluster including right CA and LB had two local max.

[2] The cluster including left CA, SF, FD, and SUB had four local max.

[3] The cluster including pre-SMA, area 8 and area 32 had three local max.

[4] The cluster in the left auditory cortex extended into the retroinsular cortex

Table S1. Results of meta-analysis. Structures observed in the analysis are listed in the outermost left column (with anatomical probabilities according to REF. 24 in parentheses). The middle-left column indicates the volume of clusters, the middle-right column lists studies contributing to the clusters (note that more than one contrast of a study can contribute to a single cluster). The outermost right column indicates coordinates of local maxima within clusters in Talairach space. Statistical significance threshold for Clusters 1 to 7 was $p < .01$ (FDR-corrected with a minimum cluster size of 200 cubic mm). Clusters significant at $p < .01$ (FDR-corrected) without cluster size threshold are listed in the lower panel to generate directed anatomical hypotheses for future studies. Note that, due to the different experimental paradimgs used in the included studies (and the associated risk for false negatives), limbic/paralimbic brain areas not indicated in this meta-analysis may nevertheless contribute to music-evoked emotions. Abbreviations: l: left; r: right; CA: cornu ammonis; FD: dentage gyrus of hippocampal formation; LB: laterobasal group of amygdala; SF: superficial group of amygdala; SMA: supplementary motor area; SPL: superior parietal lobule; SUB: subiculum of hippocampal formation; TE 1: primary auditory cortex.

Table S2: List of studies and contrasts included in the meta-analysis.

Study	Modality	Number of subjects	Number of foci	Contrast
Blood & Zatorre (1999)[1]	PET	10	3	Positive Correlations with dissonance
			5	Negative Correlations with dissonance
Blood & Zatorre (2001)[2]	PET	10	9	Positive correlations with ratings of pleasantness
			6	Negative correlations with ratings of pleasantness
			8	Positive correlations with ratings of emotional intensity
			7	Negative correlations with ratings of emotional intensity
Menon & Levitin (2005)[3]	fMRI	13	3	Unpleasant > pleasant
Khalfa et al. (2005)[4]	fMRI	13	3	Minor vs. major
Baumgartner et al. (2006)[5]	fMRI	9	27	Pictures with music > pictures without music
Koelsch et al. (2006)[6]	fMRI	11	3	Pleasant > unpleasant
			3	Unpleasant > pleasant
Mitterschiffthaler et al. (2007)[7]	fMRI	16	11	Happy > neutral
			7	Sad > neutral
Eldar et al. (2007)[8]	fMRI	14	10	Negative combination effect
			11	Positive combination effect
Mizuno & Sugishita (2007)[9]		18	8	Major – neutral
			5	Minor – neutral
			6	Major – minor
			3	Minor-major
Koelsch et al. (2008)[10]	fMRI	11	4	Irregular > regular
Suzuki et al. (2008)[11]	PET	13	1	Consonance vs. dissonance
			3	Dissonance vs. consonance
			1	Minor vs. major
Green et al. (2008)[12]	fMRI	21	4	Minor vs. major
Chapin et al. (2010)[13]	fMRI	13	2	Emotional arousal
			9	Emotional arousal x experience
Salimpoor et al. (2011)[14]	PET	10	7	Pleasure – neutral
	fMRI	10	2	Pleasure > neutral
Mueller et al. (2011)[15]	fMRI	20	7	Pleasant > unpleasant
Caria et al. (2011)[16]		14	20	Happy favorite music > happy standard
Brattico et al. (2011)[17]	fMRI	15	6	Sad vs. happy
Trost et al. (2012)[18]	fMRI	16	13	Positive correlations with arousal ratings
			3	Negative correlations with arousal ratings
			11	Positive correlations with valence ratings
			3	Negative correlations with valence ratings
Salimpoor et al. (2013)[19]	fMRI	19	8	Music purchased vs. music not purchased
			39	Emotion-specific functional connectivity (increase in reward value)
Koelsch et al. (2013)[20]	fMRI	18	4	Joy > fear
			1	Fear > joy
			12	Interaction contrast of emotion (joy vs. fear) x time
			30	Emotion-specific functional connectivity (joy > fear)
Lehne et al. (in press)[21]	fMRI	25	1	Positive correlation with tension
			2	Tension (versions with dynamics) > tension (versions without dynamics)
			8	Tension increase > tension decrease

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