Music and emotions: from enchantment to entrainment

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Producing and perceiving music engage a wide range of sensorimotor, cognitive, and emotional processes. Emotions are a central feature of the enjoyment of music, with a large variety of affective states consistently reported by people while listening to music. However, besides joy or sadness, music often elicits feelings of wonder, nostalgia, or tenderness, which do not correspond to emotion categories typically studied in neuroscience and whose neural substrates remain largely unknown. Here we review the similarities and differences in the neural substrates underlying these “complex” music-evoked emotions relative to other more “basic” emotional experiences. We suggest that these emotions emerge through a combination of activation in emotional and motivational brain systems (e.g., including reward pathways) that confer its valence to music, with activation in several other areas outside emotional systems, including motor, attention, or memory-related regions. We then discuss the neural substrates underlying the entrainment of cognitive and motor processes by music and their relation to affective experience. These effects have important implications for the potential therapeutic use of music in neurological or psychiatric diseases, particularly those associated with motor, attention, or affective disturbances.

Keywords: music; brain; emotions; entrainment; movement; rehabilitation

Introduction

Music is a remarkable human activity in many ways. Not only does it require sophisticated perceptual and motor skills, imbue many aspects of our lives and societies, and exhibit an amazing richness across cultures and times in history, but it also has a unique power to elicit strong and diverse emotions and, more generally, appears capable of engaging multiple cognitive functions and neural circuits in the brain. Understanding the neural mechanisms underlying such power of music is important for several reasons. In particular, this may allow harnessing these effects for the purpose of cognitive training and rehabilitation. There is indeed growing evidence that music can bring significant benefits in a variety of therapies or training protocols targeting both sensorimotor and higher level cognitive domains. In addition, unveiling the psychological and cerebral underpinnings of music processing and music-induced emotions may yield precious insights into the human mind and brain. This review illustrates some recent approaches and advances in this field and then presents some outlooks on potential implications for the therapeutic use of music in neurological diseases and aging.

Music-induced emotions

Recent neuroimaging research has illuminated several aspects of music-induced emotions (for a review see Refs. 1 and 2). Pioneer studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have consistently shown that pleasurable music activates brain regions usually responding to other pleasures and rewards such as the ventral striatum but also the orbitofrontal cortex (OFC) and anterior insula, together with frequent effects in parietal and somatosensory areas.³⁻⁵ The ventral striatum also activates in response to music evoking joy and happiness.⁶ Conversely, sad music has been reported to activate the hippocampus, amygdala, and neighboring medial temporal lobe areas.
that are implicated in negative affective states and anxiety. Comparing unpleasant dissonant to pleasant consonant music produces similar effects.\textsuperscript{7,8} Furthermore, elegant work combining pharmacological PET with fMRI showed that moments of higher pleasure during music correlate with dopamine release in ventral regions of the striatum (nucleus accumbens), distinct from more dorsal dopamine sites associated with anticipation of the corresponding musical moments.\textsuperscript{9} Feelings of “chills” triggered by pleasant music also correlate with increased activity in the striatum and insula, accompanied by transient reductions in activity in the amygdala, anterior hippocampus, and ventromedial prefrontal cortex.\textsuperscript{3} On the other hand, fear and tension evoked by music (as in horror movies) may increase activity in the amygdala.\textsuperscript{8,10–14} Interestingly, these responses overlap with those of other stimuli evoking similar emotions,\textsuperscript{10} and damage to the amygdala may impair recognition of fear as expressed in both music and faces.\textsuperscript{15} Altogether, these findings have been taken as evidence that music evokes “true” emotions rather than more abstract or intellectual states of mind due to cognitive connotations or memory associations as argued by some authors (e.g., see Ref. 16).

Yet, neuroimaging studies have often focused on dichotomous categories of musical emotions, such as pleasant/positive emotions in opposition to unpleasant/negative emotions, without fully exploiting the richness and originality offered by the music domain. Although music does produce pleasure\textsuperscript{3} and may convey feelings of sadness or even fear in a universal manner across different peoples,\textsuperscript{17} its effects appear broader and more diverse than the emotion categories classically highlighted by neuroscience and human neuroimaging work. Moreover, psychological models and philosophers have suggested that music may evoke specific kinds of “aesthetic” emotions distinct from basic “utilitarian” categories with adaptive functions such as pleasure or fear.\textsuperscript{18} The nature of these emotions remains unresolved, and their neural substrates underexplored.

**Music-specific emotions**

On the basis of comprehensive questionnaires given in both real-life and laboratory conditions, requiring listeners to describe their emotions while listening to music with a large variety of words and adjectives, researchers have proposed that nine main affective states are commonly elicited by music across different music genres and different Western populations.\textsuperscript{19} These emotion categories include emotions investigated in other domains, such as joy and sadness, but also other categories that might be more specific to music such as wonder, tenderness, nostalgia, tension, power, peacefulness, or transcendance (i.e., feelings related to sacred or divine domains). Further, it has been suggested that these emotions can be regrouped under higher order factors such as vitality, sublimity, and unease.\textsuperscript{19} Whereas vitality and unease are reminiscent of arousal and valence dimensions associated with emotions in many domains,\textsuperscript{20,21} the existence of a higher order factor such as sublimity (defined as a sense of beauty and perfection) suggests that the spectrum of emotional experiences evoked by music might require additional categories beyond the range of basic emotions. Moreover, this factor might not only concern the music domain but also characterize aesthetic feelings associated with the arts in general. However, even though such aesthetic experiences may be at the very heart of art and music, their neural substrates have not been studied in detail. How are these “complex” emotional experiences evoking “sublimity” instantiated at the brain level, and what components do they share with more “basic” emotions?

To address these questions we examined brain activity patterns with fMRI as well as subjective emotion ratings while music amateurs listened to a variety of classic music pieces that were carefully chosen to elicit specific kinds of aesthetic emotions.\textsuperscript{22} After each music piece, participants rated whether they felt any of the nine emotion categories described by Zentner and colleagues,\textsuperscript{19} as well as other affective dimensions such as valence, arousal, or familiarity. A factorial analysis of these ratings across pieces revealed an organization of these emotions in four main families that could be characterized in terms of their level of valence and arousal (Fig. 1A). Thus, joy, wonder, and power were all defined by positive valence and high arousal, whereas nostalgia, tenderness, or transcendance were also positively valenced but with low arousal. Such distribution accords with the bidimensional space of core affect observed for many other emotional domains, including face expression recognition or subjective response to emotional
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Figure 1. Valence and arousal dimensions of musical emotions. (A) Factorial analysis of subjective ratings along nine different categories showing a distribution along two main dimensions of arousal (increasing along horizontal axis, red) and valence (increasing along vertical axis, green). (B) Activations proportional to the valence dimension intensity. (C) Activations proportional to the arousal dimension intensity. Adapted from Trost et al.22

Nevertheless, the nine emotion ratings could reliably be discriminated from each other, confirming their subjective distinctiveness.19

Brain activation patterns revealed a similar segregation into distinct networks that responded to basic dimensions of valence and arousal—but with a differential recruitment of several areas according to the specific emotion category within each of the four main families. Parametric analyses were performed to identify activations that increased in direct proportion to the subjective ratings along each emotion dimension. Positive valence correlated with increases in activity in the ventral striatum and ventral tegmental area (VTA), corresponding to the well-known dopaminergic reward pathway,23 as well as the right insula (Fig. 1B), whereas negative valence correlated with increased activity in the lateral OFC, converging with other work on emotion processing in humans.24 Parametric effects of increasing arousal (Fig. 1C) were observed in several motor areas including motor and premotor cortex, cerebellum, and dorsal basal ganglia (caudate), but also in visual and auditory areas as well as anterior (ACC) and posterior (PCC) cingulate cortex involved in attention and alertness.25

In addition, systematic variations in the degree of these activations and specific combinations thereof were associated with specific emotion categories within a given family of similar valence and arousal. For instance, feelings of power (i.e., being heroic and triumphant) correlated with ventral striatum activation similar to joy, but with distinctive increases in the motor cortex and dorsal basal ganglia (Figs. 2 and 3A and B), possibly corresponding to a covert engagement of movement representations that may characterize the “march” style and the clear metrical structure of music eliciting this emotion. Cortical and subcortical motor structures are known to be highly sensitive to rhythmic structure.26–28 On the other hand, wonder (i.e., feeling allured and amazed) also activated the ventral striatum, but unlike joy and power, it activated the motor areas less and the right hippocampus more (Figs. 2 and 3B and C). This activation in the hippocampus was shared with positive emotions of lower arousal such as nostalgia or tenderness, which produced lower activation in the ventral striatum and instead recruited other memory-related areas including the ventromedial cortex (VMPFC) and parahippocampal cortex (PHG). Nostalgia
produced unique increases in extrastriate visual areas and right precuneus, previously implicated in visual imagery, whereas transcendence (i.e., impression of spirituality and divine) differentially activated the right medial temporal lobe and posterior parietal areas. These distinctive activation profiles nicely dovetail with characteristic psychological features of these emotions, including a mixture of self-centered introspection, autobiographical memory retrieval, and imagination, commonly associated with feelings of nostalgia. Individual proneness to tenderness has also been reported to correlate with greater modulation of the hippocampus and amygdala in response to music, attributed to better emotion regulation abilities. In addition, in our study, the hippocampus was differentially recruited by the more complex emotion categories associated with the higher order dimension of sublimity, such as wonder, tenderness, and transcendence. This suggests that music inducing these categories of emotion might solicit more complex associations partly based on personal memories that are thought to rely on hippocampal function. Finally, negative emotions of sadness and tension (i.e., uneasiness and nervousness) were associated with greater activation in the subgenual ACC for the former (Fig. 3D) and in corticosubcortical motor pathways and precuneus for the latter. The sgACC was previously found to respond to sad music and to be consistently linked to depressive mood and ruminations, possibly reflecting a general role in monitoring and regulating negative affective states. Activation in the precuneus during tension might reflect a modulation of attentional focus with greater absorption as observed in certain meditative or hypnotic states, whereas motor activation might reflect covert action preparedness associated with an anticipatory affective state. Note that we did not find reliable activation in the amygdala in this study, unlike previous findings of relative increases to music evoking fear and tension and/or decreases to happiness and chills. This might be because the amygdala is more sensitive to transient events corresponding to deviations or uncertainty in music structure or harmony. Moreover, because the amygdala plays a major role in detecting the...
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Figure 3. Distribution of activation across nine different emotion categories for different brain regions. Adapted from Trost et al.22

behavioral relevance or biological salience of sensory stimuli, it might be more strongly engaged when participants explicitly attend to specific music events but less modulated in a naturalistic listening condition as in our study.

Taken together, these data add support to the notion that aesthetic emotions elicited by music share core features with basic emotions that can be mapped onto independent dimensions of valence and arousal as observed in other affective domains, with distinct neural substrates in reward, attention, and sensorimotor networks. Despite a lack of clear amygdala activation in our study (but see Refs. 8, 10, 13, and 39), these complex music-specific emotions thus appear to emerge from the same brain architecture as more basic affective states with obvious adaptive and utilitarian aspects.18 However, a bidimensional space is not sufficient to account for finer differentiation into more specific emotion categories, particularly those evoking sublimity or other aesthetic experiences.19 These findings underscore the multidimensional nature of emotional reactions involving complex and dynamic configurations of activation across many distributed brain regions.42 Also noteworthy, these data reveal that specific emotion categories sharing similar valence and arousal may be distinguished by their profile of activation in brain regions outside those typically associated with emotion processing but usually associated instead with other cognitive, motor, or even sensory functions.

Entrainment of brain activity by music

A remarkable example of the powerful impact of music on the brain is the activation frequently observed in several relays of the motor system, which occurs without overt movement. However, it is a common experience that hearing music may often involuntarily induce movements in the listener, such as tapping the foot or swinging the head along to the beat. Further, motor activity during passive listening of music overlaps with active mental imagery of movement.43 These motor effects are not only dependent on rhythmic patterns in the music but also on the evoked emotional experience. In particular, joy is associated with a spontaneous urge for dancing19,44 and correlates with higher activity in the motor cortex and basal ganglia (caudate) relative to other pleasant emotions.22 Moreover, in our study of musical emotions,22 motor areas exhibited their strongest activation when music evoked feelings of power and triumph, which characteristically incite one to move and walk in synchrony with the rhythm.

In keeping with this, besides driving motor pathways and stimulating movement, music and music-induced emotions have been reported to produce powerful entrainment effects on several bodily and...
cognitive processes (for review see Ref. 45). Rhythmic entrainment refers to synchronization phenomena whereby neural activity in the brain and/or heart rate are modified by the rhythmic structure and tempo of auditory inputs such that they may eventually lock onto a common periodicity.46 It has been hypothesized that beat and meter perception itself may result from an entrainment of neuronal populations that resonate at the frequency of the rhythmic inputs from music.47,48 Moreover, entrainment might also constitute a potent emotion induction mechanism.46 At the motor level, entrainment can facilitate movements made on rhythms with a regular metrical rather than nonmetrical structure.48,49 Entrainment of brain activity by music may even extend to purely cognitive processes,45,50 particularly attention.51 According to the theory of dynamic attending (DAT), neural synchronization phenomena elicited by musical meter might entrain attention processes and lead to rhythmic oscillations in attentional levels following the music beats.51 This notion is supported by behavioral studies showing a facilitation in the detection of visual targets52 and enhancement of early visual evoked potentials (such as P1) when visual stimuli are presented in synchrony with auditory rhythms.49

We recently investigated the neural mechanisms of these entrainment effects by designing a visual detection task performed in different music contexts.53 We also asked whether these mechanisms would at least partly depend on the emotional state evoked by the music, as one might expect that more pleasant music should induce a greater attentional absorption of the listener in music and thus stronger entrainment. To these aims, we adapted a visuomotor paradigm previously shown to evoke reliable entrainment of attention performance.52 Participants had to detect occasional targets (such as a circle) appearing for 100 ms (~1 per 5–6 s) in the center of the screen and then press on a response key as quickly as possible on target detection. Classical piano music pieces were simultaneously played in the background but were task irrelevant. Critically, half of the targets appeared synchronously with a strong beat of the music meter, whereas the other half appeared on a weak beat (Fig. 4). None of the participants noticed any systematic association between the visual stimuli and music rhythm. In addition, orthogonally to this rhythmic manipulation, music was presented either in a normal/consonant harmony (emotionally pleasant conditions) or with an altered/dissonant harmony (emotionally unpleasant conditions). The latter procedure has previously been shown to reliably affect subjective pleasantness of music and modulate brain areas associated with emotion processing.8

Behaviorally, we found that visuomotor performance was facilitated by both the synchronization with meter (faster responses to targets appearing on strong than weak beats) and the pleasantness of music (faster responses to targets on strong or weak beats during consonant than dissonant music). However, at the brain level, our fMRI results indicated that these two effects were mediated by distinct neural mechanisms. Most remarkably, event-related activation to visual targets were selectively increased on strong compared to weak beats in the bilateral caudate nuclei (Fig. 5A), key components of the basal ganglia that play a major role in motor control and executive functions. Both the caudate and putamen have previously been shown to be activated by auditory rhythmic patterns and music.28,54 These structures are also recruited during working memory for musical tones55 and modulated by the emotional content of music and voices.22,56,57 Furthermore, the basal ganglia constitute a crucial relay within the cortico-subcortical motor loops that are deficient in patients with Parkinson disease and account for their motor impairment. The strong recruitment of the caudate by musical meter, as observed in this study, might provide a direct neural substrate for the well-known improvement in motor akinesia seen in Parkinsonian patients who often use rhythmic music to “unblock” their motor freezing.38–60 However, our results showed that this caudate activation to musical meter was not enhanced by music pleasantness. Instead, meter effects on caudate activity were stronger during dissonant than consonant music, presumably because only meter was capable of entraining brain activity in this condition, whereas pleasantness of consonant music could produce additional effects through distinct pathways.22,53

Indeed, besides meter effects, our fMRI analysis showed that visual targets evoked greater activation in parietal and frontal cortical areas during pleasant/consonant music relative to unpleasant/dissonant music (Fig. 5B). These areas overlap with those typically associated with top-down attention control61,62 and thus likely account for
the global visuomotor facilitation observed during pleasant music. These findings may thus also provide a substrate for previous reports that attention performance can be boosted by pleasant music in healthy people\(^63\)–\(^65\) as well as in patients with neurological deficits.\(^66\)–\(^68\) In particular, it has been reported that happy music can boost performance in speeded attentional tasks and reduce attentional blink.\(^65\) Neuropsychological results also indicate that left spatial neglect symptoms, characterized by deficits in orienting attention to the left side after right parietal damage, are partly alleviated when patients perform visual–spatial tasks during pleasant music.\(^67\)

Figure 4. Illustration of our visuomotor entrainment paradigm. Participants had to detect occasional visual targets (circles) on a screen while task-irrelevant music was played in the background. Targets could appear on either a strong or a weak beat of the music. Music could be either pleasant (consonant) or unpleasant (dissonant). Adapted from Trost et al.\(^53\)

Taken together, both behavioral and neuroimaging results converge to demonstrate that brain activation in motor areas and other brain circuits induced by music can in turn have a significant impact on motor or cognitive performance. Music thus appears endowed with the remarkable power to entrain neural activity in several brain circuits—but to different degrees depending on its rhythmic structure as well as its emotional content. Such entrainment may explain why music exposure or music training can influence various tasks, even when these are unrelated to music and when music is not directly relevant to the task.

Figure 5. Effect of background music on brain activity during our visuomotor task. (A) Event-related increase of BOLD signal evoked by visual targets appearing on a strong relative to weak beat, regardless of music type. (B) Event-related increase of BOLD signal evoked by visual targets appearing during pleasant relative to unpleasant music, regardless of synchronization with rhythm. Adapted from Trost et al.\(^53\)
Therapeutic potential of the effects of music on sensorimotor and cognitive processing

The capacity of music to engage various circuits in the brain makes it a powerful training tool to modulate behavior and cognition. In particular, the activation of motor pathways or attention control areas, as described, opens new avenues for useful applications in clinical conditions. Several studies reported that music-based therapies can be beneficial for patients with Parkinson disease by improving gait and movement difficulties. Musical activities in nonclinical elderly populations can also improve balance and reduce the risk of falling, which represents a major risk in this population.

In patients who suffer from motor impairment after a stroke, it has been shown that musical interventions can be valuably used as an adjunctive method for rehabilitation. In particular, the method of rhythmic auditory stimulation (RAS) may lead to significant benefits and help restore the capacity to perform movements and gait. In aphasia, using music in the form of melodic intonation therapy (MIT) has long been known to yield good success in brain-damaged patients.

Similarly, cognitive functions may also benefit from music exposure, including selective attention and executive function (for review see Ref. 77). Several studies found that music interventions can improve executive and emotion control in brain-injured patients. As noted earlier, in patients with left neglect after right hemisphere damage, listening to pleasant and arousing music can reduce attentional difficulties and diminish neglect symptoms.

In patients with dementia, music-based interventions may reduce general behavior disturbances and depressive symptoms and also increase well-being. In addition to the enhancement of attention networks by music, the activation of memory-related circuits and brain systems mediating the retrieval of self-related information, as observed in our fMRI study, might contribute to these effects and partly account for a reduction of confusion in these patients.

Music also has a positive impact on mood and depression, in keeping with its strong modulation of emotion systems. Furthermore, it can influence pain thresholds by lowering stress and anxiety levels, allowing reduction of sedative and analgesic drugs. Finally, it has also been suggested that music can be beneficial for the rehabilitation of persons in coma and with other disorders of consciousness by providing a stimulating environment with positive effects on arousal, memory, and attention and by engaging the patient into more pleasant emotional contexts.

Conclusions

Music provides a rich cognitive, sensory, and motor experience, with strong affective and motivational components. Beyond feelings of joy or sadness, which are also commonly studied in other domains of psychology and neuroscience, music tends to evoke a wide range of complex emotions that are more rarely considered from a neurobiological point of view, such as wonder, transcendence, or nostalgia (among others). These emotions may constitute a particular kind of aesthetic experience that appears partly shared with other forms of arts, associated with feelings of sublimity and engagement of more cognitive components, unlike more basic emotions. The neural substrates of these affective categories remain to be fully elucidated, but our neuroimaging results indicate that music-induced emotions are actually organized along the same two basic dimensions of valence and arousal as the other more basic emotions.

The combination of widespread activation in motor and cognitive systems, including memory, together with the concomitant recruitment of limbic circuits associated with basic dimensions of emotions and reward, might constitute the distinctive nature of music-induced responses and contribute to their unique subjective richness. Furthermore, by entraining neural activity in particular brain systems according to its rhythmic structure, music may have a direct influence on behavioral and cognitive processes mediated by these brain systems, which can in turn be harnessed for therapeutic purposes. Our work suggests that such entrainment may act on motor performance through activation of the basal ganglia or attention performance through activation of frontoparietal areas.

More research is needed to better identify the exact features in music that produce distinct emotions and more efficient cognitive–motor entrainment, not only to better understand the underlying mechanisms but also to optimize therapeutic applications. Beyond its position in culture and history,
reflecting the distinctive development of human skills and mind, music can thus certainly offer highly effective and pleasurable tools to further promote well-being and health.

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Conflicts of interest

The authors declare no conflicts of interest.

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