

Music, Feelings, and the Human Brain

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Music of varied kinds consistently triggers a large range of drives and emotions, which, in turn, induce a particular class of mental experiences known as feelings. The feelings are often pleasurable, though not necessarily. Neuroimaging and electrophysiological studies, in normal individuals as well as in patients with focal neurological lesions, reveal that music can change the state of large-scale neural systems of the human brain. The changes are not confined to brain sectors related to auditory and motor processing; they also occur in regions related to the regulation of life processes (homeostasis), including those related to emotions and feelings, most prominently in the insula and cingulate cortices, in the ventral striatum, in the amygdala, and in certain upper brainstem nuclei. The ease with which music leads to feelings, the predictability with which it does so, the fact that human beings of many cultures actively seek and consume music, and the evidence that early humans engaged in music practices lead us to hypothesize that music has long had a consistent relation to the neural devices of human life regulation. It is conceivable that, as a result, music-induced feelings can be informative and nourishing at the individual level and can also operate as significant promoters of sociocultural organization. We venture that the close relationship between music and feelings along with music's effectiveness in certain personal and social contexts, that is, its roles in homeostasis, explain, at least in part, the considerable degree of selection and replication of music-related phenomena, both biologically and culturally. As the invention of music forms continued and as intellectual analysis of compositions and reflection on music expanded, the practices and uses of music became less closely aligned with its affective and homeostatic aspects and, to a certain degree, gained autonomy relative to those aspects. This may account for the varied panorama of music invention, practice, and consumption that can be found today.

Keywords: music, emotions, feelings, brain, neuroimaging

Researchers interested in the brain's processing of music agree that music evokes a wide range of feelings (Sloboda, O'Neill, & Ivaldi, 2001) and have, understandably, devoted considerable effort to the investigation of music-related affect (for a comprehensive review see *Music and Emotion, Theory, Research, Applications* edited by Patrick Juslin & John Sloboda, 2010). In most treatments of music-related affect, however, feelings (along with emotions, the phenomena that are commonly and unfortunately taken as their equivalent) are only considered from psychological or sociocultural perspectives, without consideration of the fact that feelings are also neurobiological phenomena and play a central role in life regulation, that is, in homeostasis. There is no doubt that music needs to be investigated from psychological and sociocultural perspectives. Still to address the underpinnings of music experience comprehensively and because feelings are so central to that experience, we believe that the research effort also requires the inclusion of a neurobiological perspective. To that end, in the pages ahead, we introduce a general neurobiological framework; we explain why feelings and emotions should be regarded as distinct phenomena; we relate music to the neurobiological per-

spective; and we review relevant findings concerning the neural counterparts of music-evoked affects.

Neurobiological Framework

The mammalian central nervous system (CNS) continuously monitors the body's interior and exterior environments. Changes in the interior environment (such as the mechanical or chemical conditions that lead to pain or the chemical imbalances behind thirst and hunger) are sensed by the interoceptive system (Craig, 2002), and signaled to sensory regions of the CNS dedicated to the governance of body functions. The signals are then displayed as neural maps of the body, within specific sensory regions whose integrity is required for the mental experience of feelings of the body state to occur (Damasio, 2001). Changes in the external environment are sensed by the exteroceptive systems (hearing, taste, smell, touch, and sight) and are displayed in separate sensory regions as neural maps of the external world. Their integrity is also required for the mental experience of signals from the external world (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2012; Kobatake & Tanaka, 1994; Udin & Fawcett, 1988). These two distinct systems, inwardly and outwardly oriented, operate interactively. Certain perceptual configurations, as displayed in neural maps of either the interior or the exterior, can trigger innate physiological action programs, which include *drives* and *emotions* (see Glossary). The trigger points are in a variety of regions largely located below the cerebral cortex. Drives are aimed at satisfying basic instinctual physiological needs and correcting the detected imbalances relative to basic body states. They include hunger,

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thirst, libido, the avoidance of pain, exploration and play, care of offspring, and attachment to mates (Berridge, 2004; Panksepp, 1998). Emotions, on the other hand, are largely triggered by the perception or recall of exteroceptive stimuli and include not only basic responses such as disgust, fear, anger, sadness, joy, but also socially complex responses such as shame, jealousy, compassion, admiration, and awe. The engagement of the latter emotions has a major effect on social regulation (Ekman & Friesen, 1971; Immordino-Yang, McColl, Damasio, & Damasio, 2009; LeDoux, 1996). Clearly all these action programs are ultimately aimed at maintaining or restoring homeostatic balance, not only at individual level—the principal task of drives and basic emotions—but, importantly, also at social levels, where social emotions play a major role by reducing the impact of negative conditions (e.g., compassion) or enhancing positive effects (e.g., admiration) (Damasio, 2001, 2011; Sanabria, 2006; Wright, 2010).

The range of actions in these programs is wide. An incomplete list includes visceral responses (e.g., changes in cardiac rhythm, respiration, blood pressure, rearrangement of blood distribution relative to the skin, and striated muscles), endocrine responses, and complex behaviors ranging from basic fight and flight routines to complex, socially oriented responses that involve specific facial expressions, as well as, for example, avoidance or nurturing behaviors (Damasio, 1999). Of note, each particular action program, that is, action programs for fear, joy, anger, or compassion is distinctive in terms of the profile of responses it includes as well as in the degree of engagement of each component response. Signals from the entire collection of body states—both the body states that prompted a homeostatic action program response, in the first place, as well as the body states which result from the executed programs themselves—are conveyed and mapped in neural structures of the brainstem and of the cerebral cortex, which are distinct from those where the triggering of drives and emotions occurs. These maps are believed to be a major component of the neural substrate for the mental experiences known as feelings (Craig, 2002; Damasio, 1999; Damasio & Carvalho, 2013).

It is apparent from the above account that feelings are functionally distinct from drives and emotions and from the simpler body states that result, for example, from a wound or a lack of nutrients. Feelings are *mental experiences*, closely connected to activity in certain brain regions capable of mapping body states; by contrast, drives and emotions are integrated *action sequences*, triggered from regions of the brain distinct from those that map body states. The two sets of phenomena are, of course, closely related, given that the mental experience follows the deployment of the actions.

The fact that both feelings of “body states” (the feelings that arise from basic regulation of body states such as hunger, thirst, pain) as well as “emotional feelings” (the more complex variety that arises from emotions changing the configuration of the body states) play a role in life regulation is inescapable and is a well-known part of human experience. For example, we depend on feeling pain to respond to it adequately and it is well known that pathological disruption of pain sensitivity poses major risks (Thrush, 1973). Obviously, to survive and flourish, we depend on feeling hunger and thirst, and on feeling a wide range of emotions that varied individual or social situations can trigger. Feelings, that is, mental experiences grounded on neural maps of body states, are thus indispensable sentinels in the comprehensive processes of life regulation.

Musical Experience in the Perspective of the Neurobiological Framework

At first glance, music may have no obvious relevance to the survival of individual humans or the species. Music does not feed us, save us from harm, or fight one's arguments. Nevertheless, the following facts are well established: (1) music evokes a broad range of emotions and feelings from joy and peacefulness to sadness and fear (Sloboda, O'Neill, & Ivaldi, 2001); and (2) music-related affects are accompanied by physiological and behavioral changes (Bartlett, 1996; Scherer & Zentner, 2001). Music listening changes the state of the autonomic nervous system indexed by, among others, heart and respiration rates, galvanic skin responses, and temperature (Blood & Zatorre, 2001; Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011; Trost, Ethofer, Zentner, & Vuilleumier, 2012), it can clearly modify the state of the body and subsequently modify body maps in the areas of the CNS related to homeostatic regulation, for example, in the brain stem nuclei, the insular cortices (Brown, Martinez, & Parsons, 2004; Koelsch, Fritz, Cramon, Müller, & Friederici, 2006; Menon & Levitin, 2005; Trost et al., 2012), and the cingulate cortices (Blood & Zatorre, 2001; Menon & Levitin, 2005). A significant part of the feelings related to music listening emerge from this functional chain, and such music-induced feelings can contribute to individual well-being (Cepeda, Carr, Lau, & Alvarez, 2006; MacDonald, 2013; Nilsson, 2008) and, not uncommonly, to a wide range of beneficial social experiences (Chanda & Levitin, 2013; DeNora, 2000; Koelsch, 2010; Sloboda, O'Neill, & Ivaldi, 2001).

For many music pieces and for many listeners, music-induced feelings derive from the direct emotive competence of musical sounds and compositional structure, while for other music pieces and listeners, feelings derive from layers of interposed cognitive steps, such as memory, evocations, processing of recalled contents (Scherer, 2004), and analysis of musical structure (scheme). We note, however, that these interposed cognitive steps have, in of themselves, the power to induce emotions. The term, “esthetic emotions” would apply to this more complex evocation process although we expect the core physiology of such emotions and subsequent feelings to conform to the general scheme of emotional evocation and subsequent emergence of feelings as discussed earlier.

It has been argued that music cannot induce basic “everyday” emotions related to survival, and that music-evoked emotions should be categorized separately, as “aesthetic,” and contrasted to “utilitarian” emotions (Scherer, 2004; Zentner, Grandjean, & Scherer, 2008). Moreover, the related notion that listeners might be able to perceive the emotional expression of music without necessarily feeling that emotional experience has been under debate (Juslin & Sloboda, 2010). For example, it has been suggested that because listeners are usually safely removed from threats, dangers, and the possibility of losses, negative emotions, including fear, sadness, or anger would be perceived as expressive properties of music instead of actually becoming felt responses to music (Zentner et al., 2008). However, even, “aesthetic” emotions cannot be regarded as entirely disembodied (Scherer, 2004). Music demonstrably produces physiological changes (Scherer & Zentner, 2001). We hypothesize that music can engage innate physiological action programs and, by doing so help restore the physiological state to a range of relative homeostatic balance. The change in body states

that result from these action programs are displayed in both the upper brainstem and cerebral cortex (i.e., insular and cingulate cortices) and are experienced as a whole range of feelings including of sadness, joy, and fear (Brattico et al., 2011; Koelsch et al., 2013; Sloboda, O'Neill, & Ivaldi, 2001). This is an important issue that deserves further experimental probing to be conclusively resolved.

The average individual elects to spend a considerable amount of time listening to music (DeNora, 2000; Skånland, 2013). Reports from cross-cultural studies have also shown that listeners from different parts of the world can relate emotionally to unfamiliar music from varied cultures (Balkwill & Thompson, 1999; Balkwill, Thompson, & Matsunaga, 2004; Fritz et al., 2009) raising the possibility of a considerable universality of musical emotions. They certainly indicate that music of varied kinds can prompt "emotive" reactions and ensuing feelings that may become individually and socially significant suggesting that a homeostatic influence is likely. Such an influence is not confined to adults as there is evidence of affective reactions to music by infants as young as two months (Trainor, Tsang, & Cheung, 2002). Perhaps not surprisingly, music plays a virtually obligate and significant part in a number of signal social events, for example, religious ceremonies, weddings, and a variety of other celebrations.

Of relevance to the argument that music could play a role in life regulation is the fact, known from studies of animal vocalizations, that a variety of mammals and birds signal their weakness and defeat by producing high or rising pitch vocalizations, whereas strength, aggression, and territorial dominance are communicated using vocalizations with low or falling pitches (Morton, 1977; see also Hinton, Nichols & Ohala, 1994). The close connection between emotive and social-related behaviors and manipulations of acoustic frequency, a central element of music-making, is inescapable. Also, the direction of tonal movement in music implies an "affective code" in relation to frequency. From a historical standpoint, it is conceivable that the usage of pitch rises and falls in music may have begun as a biological device for conveying a particular emotive state but, as multiple musical dimensions including melody, harmony, rhythm, and timbre evolved and became more complex, the "meanings" of sounds became less closely related to homeostatic value. Still, the autonomic nervous system activation that we feel when we hear well-crafted music may be related in part to the variation of acoustic frequency present in the music (see Cook, 2011). Taken together, the above facts suggest, that a major reason for music's universal appeal may arise from the emotional/feeling effects that music produces in composers, players, and listeners, along with the social consequences of these effects.

We believe the facts discussed above are compatible with the hypothesis that the emotions and feelings evoked by music can be connected to the fundamental process of life regulation or homeostasis. We have ventured that early humans discovered that certain frequencies of sound and certain combinations of sound elicited predictable emotions and feelings. Accordingly, for example, the singing human voice, drumming, and the playing of a simple flute could have been used for seduction and for compensatory consolation following loss and disease (Damasio, 2010, Ch.11; pp: 290–297). Music may have facilitated social functions such as group organization and general communication (Koelsch, 2010) and fostered engagement in anticipatory interplay of expectancy

and reward (Gebauer, Kringelbach, & Vuust, 2012). In brief, music may have prevailed in human history largely because of its contribution to well-being and relatedly to survival. This possibility is entirely compatible with the intellectually and culturally autonomous status of elaborate varieties of music creation and listening.

A Selective Review of Literature on the Neural Basis of Music-Evoked Feelings

It is reasonable to expect from the forgoing that there are anatomically and functionally separate systems involved in music perception, in the motivational and emotive states that music provokes, and in the ensuing feelings. The traditional view of the perception of music has focused on regions of the primary and secondary auditory cortices (Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Peretz & Zatorre, 2005; Tramo, Shah, & Braid, 2002) and of the inferior frontal regions (Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Koelsch, 2009; Tillmann, Janata, & Bharucha, 2003), but it has been shown that additional areas including nuclei in the brain stem (Bidelman, Krishnan, & Gandour, 2011; Griffiths, Uppenkamp, Johnsrude, Josephs, & Patterson, 2001), and along the multistep auditory pathways (Koelsch, 2011), are involved as well. The study of affect-related consequences of music perception, on the other hand, has pointed to a large number of cortical and subcortical regions usually known by the traditional designation of "limbic and paralimbic" (Brattico, Bogert, & Jacobsen, 2013; Koelsch, 2010; Zatorre & Salimpoor, 2013). Surveying the large number of excellent studies published on this topic during the past two decades, it appears that some fundamental facts have been established firmly, while, not surprisingly, a number of important questions await investigation. For example, to date, the investigations have concentrated on cerebral cortical sites and on subcortical but telencephalic sites, such as the dorsal and ventral striatum and the amygdala, while leaving out brain stem structures, which house several auditory processors in addition to the core mechanism of homeostatic regulation. This is understandable given the technical difficulties involved in brain stem imaging, on the one hand, and the chronic lack of theoretical treatments of the role of brain stem structures in both hearing and homeostasis.

In this section, we review functional neuroimaging and lesion studies of music and emotion in the perspective of the neurobiological framework outlined above. We describe these studies first from the point of view of the emotion/feeling that the musical stimulus used in each study was meant to induce in the listener. We then report on the brain regions and systems correlated with the processing of these stimuli (see Table 1). Importantly, the brain regions reviewed below are not only related to auditory and motor processing but they are engaged in regulating homeostasis. The data address our hypothesis that music, via its close relationship to feelings, is able to influence the neural devices of life regulation. We begin the section by reviewing studies that have investigated the pleasurable aspects of music listening, followed by studies focusing on the negative aspects of music listening such as the sensation of dissonance. Finally, we discuss two studies that have explored how combining music with visual stimuli, such as static images or video clips, can enhance the emotional experience of those stimuli.

Table 1

List of Brain Structures Correlated With Music Induced Emotions and Feelings as Identified by Functional Neuroimaging and Lesion Studies

Structure	Study
Insular Cortex	Baumgartner et al. (2006); Blood and Zatorre, (2001); Brown et al. (2004); Koelsch et al. (2006); Mitterschiffthaler et al. (2007); Trost et al. (2012)
Anterior Cingulate Cortex	Blood and Zatorre (2001); Caria et al. (2011); Green et al. (2008); Menon and Levitin (2005); Mitterschiffthaler et al. (2007); Trost et al. (2012)
Ventromedial Prefrontal Cortex	Blood and Zatorre (2001); Green et al. (2008); Khalfa et al. (2005)
Parahippocampal Cortex	Baumgartner et al. (2006); Blood and Zatorre (1999); Gosselin et al. (2006); Green et al. (2008); Koelsch et al. (2006); Mitterschiffthaler et al. (2007); Trost et al. (2012)
Striatum	Blood and Zatorre (2001); Brattico et al. (2011); Brown et al. (2004); Koelsch et al. (2006); Menon and Levitin (2005); Mitterschiffthaler et al. (2007); Salimpoor and Zatorre (2011, 2013); Suzuki et al. (2008); Trost et al. (2012)
Amygdala	Baumgartner et al. (2006); Blood and Zatorre (2001); Eldar et al. (2007); Gosselin et al. (2005, 2007); Koelsch et al. (2006, 2008, 2013); Lehne et al. (2013); Mitterschiffthaler et al. (2007)
Hippocampus	Baumgartner et al. (2006); Blood and Zatorre (2001); Brown et al. (2004); Eldar et al. (2007); Koelsch et al. (2006); Mitterschiffthaler et al. (2007); Trost et al. (2012)

Pleasurable Feelings Evoked by Music

Musical pleasure, chills, and the striatum. Music listening can be highly pleasurable. The hedonic aspects of music listening, which include the experience of “chills,” have been shown in a number of neuroimaging studies to activate limbic and paralimbic structures including the ventromedial orbitofrontal cortex (Blood & Zatorre, 2001), the ventral striatum, and its nucleus accumbens (Blood & Zatorre, 2001; Brown et al., 2004; Menon & Levitin, 2005; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007; Salimpoor et al., 2013, 2011; Trost et al., 2012), the anterior cingulate cortex (Baumgartner, Lutz, Schmidt, & Jäncke, 2006; Blood & Zatorre, 2001; Brown et al., 2004; Menon & Levitin, 2005; Salimpoor et al., 2013; Trost et al., 2012), the insular cortex (Baumgartner et al., 2006; Blood & Zatorre, 2001; Brown et al., 2004; Mitterschiffthaler et al., 2007; Salimpoor et al., 2013; Steinbeis, Koelsch, & Sloboda, 2006; Trost et al., 2012), and the hypothalamus (Menon & Levitin, 2005).

The activation of the limbic system during pleasurable music listening was first reported in a study by Blood and Zatorre (2001). Using positron emission tomography (PET), they measured the regional cerebral blood flow (rCBF) during the experience of “chills” when participants were presented with their own personally selected musical passages chosen because of their known pleasurable effects. Each participant’s favorite music was used as one of the control conditions for all the other participants in the study. Compared with the control condition, the experience of “chills” was associated with an increase in heart and respiration rates. Moreover, an increase in the intensity of chills correlated with increases in rCBF in ventral striatum, orbitofrontal cortex, insular and anterior cingulate cortices, and with decreases in rCBF in the amygdala, hippocampus, and ventral medial prefrontal cortex (VMPFC). The authors proposed that, as in the case of other responses to rewarding stimuli such as drugs of abuse, pleasurable music activated the dopaminergic reward system. This was a reasonable interpretation even though their study only measured changes in rCBF and not dopamine release directly. In a recent and remarkable study, however, using a combination of functional MRI (fMRI) and PET techniques, Salimpoor and Zatorre (2011) investigated the time course of brain activity during “chills” and

did target dopamine directly by taking advantage of the dopamine-specific binding potential of [^{11}C] raclopride. As in their previous work, for the PET study, participants made their own selection of highly pleasurable music passages and each participant’s favorite music was used as a neutral condition for others. During the PET scanning, levels of arousal were assessed by measuring changes in heart and respiration rate, skin conductance, and temperature. To examine the time course of dopamine release, the authors complemented the PET study with fMRI using the same stimuli and participants. They measured changes in the blood oxygenation level dependent (BOLD) response in the regions that had been identified with dopamine release via PET [^{11}C] raclopride imaging during epochs that were indicated by participants as anticipation and peak pleasure experience periods and compared it with periods in which participants reported feeling neutral during the same musical excerpt. The results of the physiological measures, collected during the PET scanning and consistent with their previous findings (Salimpoor, Benovoy, Longo, Cooperstock, & Zatorre, 2009), showed that during the pleasurable condition the participant’s self-reported intensity of experienced chills correlated positively with the degree of autonomic nervous system changes. This included increases in heart rate, respiration, and skin conductance and decreases in temperature. Comparing peak pleasurable music to neutral music, the PET study revealed an increase in endogenous dopamine release (measured by inverse [^{11}C] raclopride binding), bilaterally, in both the dorsal and ventral striatum with the highest percentage increase in the right caudate nucleus and the right nucleus accumbens. Using fMRI the authors also investigated the time course of activation within the dopamine releasing regions (as identified by PET) and showed an intriguing functional dissociation between the anticipation phase and the actual pleasure phase of the chill experience. During the experience of peak pleasure, neural activity measured by the BOLD response increased in the nucleus accumbens. By contrast, during the anticipation of chills, within the time window immediately preceding the report of pleasure, an increase BOLD response was observed in the right caudate (Salimpoor et al., 2011). Finally, the subjects’ self-report of the intensity of chills was shown to correlate with the amount of dopamine release in the nucleus accumbens. This is

consistent with the fMRI findings and the view that this region is involved in the process of experiencing highly pleasurable music. The self-reported number of chills was shown to also correlate with the amount of dopamine released in the caudate nucleus. These results are particularly interesting given the comparable findings of anatomically and temporally distinct dopaminergic activity in response to drugs of abuse in animal models (Volkow et al., 2006) and suggest that the anticipation of musical reward, similar to other rewarding stimuli, may be related to dopamine release in an anatomical region different from the one eventually associated with musical pleasure itself.

The fascinating findings of the Zatorre group need to be considered in the context of a recent and robust line of investigation primarily unrelated to the studying music that has revealed dopamine as related most directly to desire (the pleasure of anticipating) rather than the ultimate hedonic experience. Growing evidence suggests that dopamine is a key player in relation to reinforcement learning and reward-seeking behavior but not pleasure in of itself. Instead, the hedonic experience is best associated with endogenous opioid release in hedonic “hot spots” that have been identified in the core and medial shell of the nucleus accumbens (Berridge & Kringelbach, 2008). Consistent with this interpretation, it has been shown that the experience of chills caused by music can be blocked by naloxone, a well-known opioid antagonist (Goldstein, 1980). It should then be noted that owing to the limited temporal resolution of PET, the functional distinction of anticipation versus peak pleasure reported by Salimpoor and Zatorre (2011) using fMRI may not match the spatially and temporally distributed dopamine release measured by PET (Gebauer et al., 2012). While dopamine release may be related to the anticipation of pleasure, the peak of the pleasure experience may depend on the release of other neurotransmitters such as opioids in the nucleus accumbens (Berridge & Kringelbach, 2010).

The increase of activity in the limbic and paralimbic systems is not confined to the experience of music-induced chills. Salimpoor et al. (2011) showed that even in the absence of chills, there is a direct relationship between increases in pleasure during music listening and hemodynamic activity in the right nucleus accumbens. In a recent fMRI study, Trost and colleagues (2012) showed that music deemed to have positive emotional valence engages the ventral striatum selectively but in a lateralized fashion. Musical stimuli with positive valence and low arousal, for example, those leading to tenderness, increases activity in the right ventral striatum, whereas musical stimuli with high valence and arousal, such as those leading to joy, are correlated with increased activity in the left ventral striatum. Activation of the ventral striatum in relation to pleasant music listening was also observed in fMRI studies by (Menon & Levitin, 2005) and (Koelsch et al., 2006), and in PET studies (Brown et al., 2004 and Suzuki et al., 2008).

In the Menon and Levitin study, the authors compared listeners' responses to classical musical excerpts with responses to scrambled pieces that were created by randomly cutting and concatenating excerpts from the same musical pieces. Relative to the scrambled pieces, the musical stimuli elicited activation in ventral striatum, the hypothalamus, and the ventral tegmental area. In addition, using connectivity analysis, the authors showed significant interactions between the three structures, suggesting that activation of the ventral striatum in response to pleasurable music

is modulated by the activity in the ventral tegmental area of the brainstem and the hypothalamus (Menon & Levitin, 2005).

In the Koelsch study, pleasant music, in comparison with unpleasant dissonant counterparts, elicited activity in the ventral striatum. The activity increased during the presentation of music, indicating that the pleasure responses to music can build up gradually and follow an extended time course (Koelsch et al., 2006). In studies using PET, Brown and colleagues (2004) observed activation of the ventral striatum, albeit not reaching significant level, associated with listening to unfamiliar pleasant pieces contrasted with a resting condition, whereas Suzuki et al. (2008) found that comparing sequences of consonant chords rated as beautiful with ugly dissonant ones, elicited activity in the ventral striatum and substantia nigra. In a new fMRI study, Salimpoor and Zatorre (2013) reported significant functional connectivity of the ventral striatum with auditory sensory cortices in a music auction paradigm in which participants were asked to evaluate previously unheard music. Interestingly, the amount that listeners were willing to spend on new music directly correlated with the degree of activity in the ventral striatum (Salimpoor & Zatorre, 2013).

Pleasant music and the role of anterior cingulate and insular cortices. The pleasant quality of music can be related to its ability to alter the degree of arousal and change state of the autonomic nervous system, and these physiological changes have been shown to be associated with activity in the anterior cingulate cortex and the insular cortex (Damasio, 2001). Several studies using PET or fMRI have reported activity changes in both structures during the experience of pleasurable music listening. In their 2001 study, Blood and Zatorre had shown that the intensity of physiological responses (including heart rate, muscular activity, and respiration rate) increased along with the experience of increased chill intensity, and occurred concurrently with a rise in cerebral blood flow within the insular and anterior cingulate cortices bilaterally. In a recent study, using fMRI, Trost and colleagues (2012) showed that listening to classical instrumental music identified as high in arousal level and positive in valence (such as joy), led to increased respiration rate together with increased activity in the insular cortex. By contrast, listening to musical excerpts that were rated low in level of arousal, regardless of valence, correlated with increased activity in the anterior cingulate cortex. Increased activation of the insula was also observed when pleasant versus unpleasant musical excerpts were contrasted (Koelsch et al., 2006), and when joyful music was contrasted with a rest condition (Brown et al., 2004). Finally, Menon and Levitin (2005) observed greater activity in the anterior cingulate cortex when responses to standard musical pieces from the classical repertoire were contrasted with scrambled unmusical excerpts.

The insular and the anterior cingulate cortices, which are joined by mutual connections (Mesulam & Mufson, 1982), are the main regions of the cerebral cortex involved in the processing of feelings (Damasio, 1999). Given their significant roles in relation to visceral function and production of body maps, it is not surprising that listening to pleasurable music is associated with activity in these regions. Of course, several subcortical regions are also engaged in the system whose activation correlates with musically induced feelings. This is also not surprising given that, the state of body maps in the insular cortex during the experience of music-induced pleasure is likely to be modified by the release of a variety

of molecules in the striatum as a consequence of activity in the ventral tegmental area of the brainstem.

Unpleasant Music: Dissonance, Fear, and Sadness

The studies reviewed thus far have revealed much about the brain systems involved in musical pleasure, but the feelings induced by music are not always pleasurable. Music can evoke unpleasant feelings such as anxiety, frustration, fear, and sadness. Composers have successfully manipulated musical components such as melodic intervals, harmonic progressions, modes, timbre, texture, rhythm, and tempo to evoke such feelings. In general, musical pieces that listeners rate as sad are often in minor mode and are typically expressed by soft dynamics, legato articulation, and slow tempos, whereas fear-causing music has relatively faster tempi and irregular rhythm (Juslin, 2000). In addition, one way to induce unpleasantness with music is using dissonant stimuli. Perception of sensory dissonance, an irritating sensation, occurs early within the peripheral sensory system. The human sensory system, at the level of the cochlea's basilar membrane of the inner ear does not have sufficient spatial resolution. Therefore, tones that are too close in pitch (such as one semi tone difference in a minor second) create an irritating sensation when they are heard at the same time (Juslin, Liljeström, Västfjäll, & Lundqvist, 2010; Helmholtz, 1877). In addition, Tramo, Cariani, Delgutte, & Braid, (2001) have shown that the experience of dissonance is also related to the fine temporal structure of firing pattern of auditory nerve neurons (Tramo, et al. 2001). However, these facts alone do not satisfactorily explain how or why the poor acoustic resolution of the basilar membrane prompts negative emotions and feelings in listeners, and it raises the possibility that subsequent brain regions are involved in the processing of dissonant stimuli. As shown by a number of neuroimaging and lesion studies, regions involved in perceptual analysis of dissonant stimuli include the cortices in the superior temporal gyri bilaterally (Fishman et al., 2001; Peretz, 2001). The processing of the affective aspect of sensory dissonance, on the other hand, as shown in the studies reviewed in the next section, primarily engages the parahippocampal gyrus.

The role of the parahippocampal cortex in the processing of dissonance. The parahippocampal gyrus seems to have a role to play in the processing of dissonance in musical stimuli as shown both by functional neuroimaging (Blood, Zatorre, Bermudez, & Evans, 1999; Koelsch et al., 2006) and lesion studies (Gosselin et al., 2006). Using PET, Blood, Zatorre and colleagues (Blood et al., 1999) investigated the dimension of unpleasantness versus pleasantness in nonmusicians. They used unfamiliar melodies that varied in the degree of dissonance by manipulating the harmonic structures of the chords to create six versions of (otherwise) the same musical passage. Musical passages with the highest degree of dissonance were perceived as the most unpleasant and increasing unpleasantness correlated with activity in the right parahippocampal gyrus and precuneus while decreasing unpleasantness correlated with activation of orbitofrontal cortex, frontal pole, and subcallosal cingulate cortex. Similarly, Koelsch et al. (2006) reported activity changes in the parahippocampal cortex related to the unpleasant dissonant music (although in their study the changes were marked on the left side). In a lesion study involving patients with surgical resections of the anteromedial section of the temporal lobe, which result in removal of the cortex in the para-

hippocampal gyrus, Gosselin and colleagues showed that the absence of parahippocampal cortex resulted in diminished sensitivity to unpleasant dissonant music. Of interest, the size of the removal of the parahippocampal cortex correlated positively with the diminished response to unpleasant dissonance but did not affect emotional judgments of music more generally. In contrast, patients' evaluation of happy and sad music, provided it was consonant, did not differ from control participants, suggesting that the parahippocampal cortex is specifically involved in processing dissonance (Gosselin et al., 2006). Of related interest, a recent fMRI study Trost and colleagues (2012) also observed increased activity in the right parahippocampal cortex in response to musical stimuli with negative valence regardless of arousal level, whereas perception of both tension and sadness while listening to music activated the right parahippocampal gyrus.

A role for the amygdala in musical processing. Several functional imaging and lesion studies have implicated the amygdala in responses to unpleasant music. Using fMRI, Koelsch and colleagues (Koelsch et al., 2006) investigated the neural correlates of responses to unpleasant music compared with consonant pleasant music. The unpleasant stimuli in their study were dissonant versions of joyful excerpts of instrumental dance tunes, while the pleasant stimuli were the nonmanipulated tunes. By using identical and equally novel stimuli for all nonmusician participants, the authors circumvented two important factors of variance in comparable studies, namely, the participants' degree of familiarity with a piece and their preference for a certain kind music. Compared with the pleasant excerpts, unpleasant excerpts elicited increased activation in the left amygdala, hippocampus, parahippocampal cortex, and the right temporal pole cortex as measured by the BOLD response. Koelsch and colleagues (Koelsch, Fritz, & Schlaug, 2008) also observed increased activity in the amygdala in response to unexpected irregular chord sequences ending in the Neapolitan 6th chord. From the standpoint of musical syntax, a sequence of chords ending in the Neapolitan sounds irregular although the Neapolitan chord is not dissonant in of itself. The Koelsch et al. results therefore showed that a simple irregularity of music syntax can lead to unpleasant feelings and activation of the amygdala.

Involvement of the amygdala in the processing of musically induced emotion has been inferred from lesion studies as well. A patient with damage to the left amygdala showed a selective loss of pleasurable experiences for music although the emotional responses to unpleasant music were not assessed. The lesion, however, also included the left insular cortex and extended to the frontal lobe, making it unclear whether the lesion to the left amygdala was truly necessary or sufficient in contributing to the loss of pleasurable experience from music (Griffiths, Warren, Dean, & Howard, 2004). Along the same line, it has been reported that patients with unilateral (Gosselin et al., 2005) or bilateral (Gosselin, Peretz, Johnsen, & Adolphs, 2007) medial temporal lobe resections that included the amygdala and varied amount of hippocampus and temporal pole, have impairment in identifying fear in music, while their recognition of happiness in music was normal. Of note, patients' impaired judgment of fearful music was not a consequence of impaired perceptual abilities because all patients performed highly in an error detection task that used the same stimuli as the emotional task (Gosselin et al., 2005). Still, even though the impairment was attributed to amygdala damage,

the lesion encompassed temporal and paralimbic regions including the parahippocampal gyrus, where cortex is clearly implicated in the processing of dissonant music (Blood et al., 1999; Koelsch et al., 2006). Moreover, compared with control participants, patients with such lesions rated fearful music as being less arousing, and yet their judgment of valence was not affected by the deficit—they still recognized the negative valence, just found it to be less arousing. In particular, all participants, including the patients, rated scary music as unpleasant relative to other categories, and rated happy and peaceful music to be more pleasant than sad music (Gosselin et al., 2005).

Ventromedial prefrontal cortex. Neuroimaging studies have also investigated the role of VMPFC in processing musical stimuli with negative valence. Blood and Zatorre (2001) reported a negative correlation with the activation of VMPFC and intensity of chill experience. Comparing feelings of sadness with happiness using minor and major modes, respectively, Green et al., (2008) and Khalfa, Schon, Anton, & Liégeois-Chauvel (2005) showed increased activation of the left medial frontal cortex (centered on Brodmann area 10) when minor modes were contrasted to major. The VMPFC is typically recruited in relation to the processing of self-referential information including the integration of sensory information with self-knowledge and the retrieval of autobiographical memories (Araujo, Kaplan, & Damasio, 2013). Popular music associated with autobiographical memories has been reported to engage the medial prefrontal cortex (especially in its dorsal sector), and the response to music is shown to correlate with the salience of personal autobiographical memories (Janata, 2009). Given the use of familiar music from the classical repertoire in some of the studies that have reported involvement of the VMPFC, the observed activity may be related to the overall familiarity and to a sense of nostalgia, rather than to unpleasantness per se. In fact, emotional responses to perceived pleasantness of a short consonant passage have been also shown to modulate activity in the same area (Blood et al., 1999).

The hippocampus. The hippocampus is known to play a significant role in learning and memory. Accordingly, remembering situations in which certain kinds of music or specific music passages were associated with certain emotions and feelings is likely to be one of the mechanisms through which music produces its affective responses (Juslin et al., 2010). In addition, the hippocampus is densely connected to structures involved in homeostatic regulation. A network comprising hippocampus, parahippocampal gyrus, amygdala, and the cortices in the temporal poles has been proposed by Koelsch (2010) for the processing of music-evoked emotions. But even after placing the relationship between hippocampus and music-evoked emotions in the context of memory processing, the correlations remain equivocal.

Increased activity in the left hippocampus was correlated with decreased chill intensity (Blood & Zatorre, 2001) and with responses to unpleasant versus pleasant melodies (Koelsch et al., 2006). By contrast, a right hippocampus activation was reported for sad as contrasted to happy music (Mitterschiffthaler et al., 2007), and for musical stimuli with positive valence but with low arousal levels leading to feelings of nostalgia, tenderness, and peacefulness (Trost et al., 2012). Some studies have also found increased activation in the hippocampus during listening to music with a positive valence (Brown et al., 2004; Koelsch et al., 2007).

Music and Visual Stimuli

Music is widely used in conjunction with visual stimuli to enhance the negative or positive emotional experience of movies. Examples of fear-evoking film music include Bernard Herrmann's score for several movies of Alfred Hitchcock, most notably for *Psycho* (1960) and John Williams' music for *Jaws* (1975). Examples of positive emotional enhancement abound in movie comedies and in advertisement. However, to the best of our knowledge, only two functional neuroimaging studies to date have investigated brain areas involved in the combined processing of music and visual stimuli. Baumgartner and colleagues (2006) explored how fearful or sad music can enhance the feelings of fear or sadness evoked by congruent images. They showed that when sad or fearful images were presented together with congruent musical stimuli, as compared with pictures presented alone, emotional responses and the corresponding brain activations were stronger in the amygdala, parahippocampal cortex, and the hippocampus (Baumgartner et al., 2006). However, they did not present fearful or sad music alone, leaving open the possibility that the activation they observed might also be elicited by the music alone without the visual stimuli. Nevertheless, the findings of Baumgartner and colleagues were further supported by an fMRI study (Eldar, Ganor, Admon, Bleich, & Hendler, 2007) in which the authors investigated how combining fearful or joyful music with neutral film clips can change the perception of the neutral film clips. They showed that the increased activity in response to music in both the amygdala and anterior hippocampus was greater when negative music was presented in combination with neutral film clips compared with when the same clips were presented alone. The combination of positive music with neutral clips, compared with neutral clips alone, enhanced activity in the amygdala only. The authors also investigated the activation of the same regions of interest (amygdala and anterior hippocampus) in response to the fearful music alone (without the film clips) compared with a baseline condition. Although the participants rated the music condition alone as equally negative as the combined condition of negative music with neutral film clips, neither hippocampus nor amygdala was activated in response to music, compared with baseline, when it was presented without the film clips (Eldar et al., 2007).

Discussion

The studies reviewed above were informed by different theoretical approaches and made use of different designs and techniques. The technical diversity and the different theoretical approaches make it challenging to compare findings from different studies. In this section, we point out some of the differences between designs and frameworks across the reviewed studies and suggest ways to avoid inconsistencies.

One issue raised by some designs concerns the selection of participants with diverse levels of training in Western classical music. In their first study of the experience of chills, Blood and Zatorre (2001) only assessed musicians, whereas a combination of musicians and nonmusicians participated in the studies by Koelsch et al., 2008 and Salimpoor et al., 2011. By contrast, participants in the studies by Blood et al., 1999; Brown et al., 2004; Koelsch et al., 2006; Menon & Levitin, 2005; and Trost et al., 2012 did not have music training, and no information is

provided as to the participants' musical background in the studies by Baumgartner et al., 2006; Eldar et al., 2007; Green et al., 2008; and Khalfa et al., 2005. And yet training does play a significant role in how listeners perceive music. Musicians often listen to music more analytically (Habibi, Wirantana, & Starr, 2013; Johnson, 1977) and are also familiar with aspects of the structure of Western classical music such as the occurrence of increased tension and subsequent resolution of the expectation. Given that musical expectations are central to musical pleasure and that music can be experienced as pleasurable both when the expectations are fulfilled and violated (Gebauer et al., 2012; Meyer, 1956; Zatorre & Salimpoor, 2013), it is reasonable to assume that listeners with different levels of training and knowledge of the structure of music would at least experience music-derived pleasant emotions differently. Future studies would benefit from taking the musical training and background of the participants into consideration and investigate whether and how trained individuals experience music-related emotions compared with untrained participants and whether there are any differences in the neural correlates of the processing of affective response to music between the two groups.

Another issue concerns the choice of musical stimuli, and the participants' level of familiarity with those stimuli and their musical preferences. In a few studies, participants were allowed to select musical passages of varied genres (Blood & Zatorre, 2001; Salimpoor et al., 2011), but most studies have used commercially available instrumental excerpts, often from the classical repertoire (Khalfa et al., 2005; Menon & Levitin, 2005; Mitterschiffthaler et al., 2007; Trost et al., 2012), while Koelsch and colleagues (2008) and Suzuki and colleagues (2008) used unfamiliar chord progressions and Blood et al., 1999; Brown et al., 2004; and Green et al., 2008 used unknown single voice melodies. Finally, whereas some studies aimed at comparing musical stimuli related to different affective states (sad, happy, and fearful), others compared musical stimuli with a rest condition (Brown et al., 2004), or with scrambled nonmusical stimuli (Menon & Levitin, 2005), or with dissonant versions of the same stimuli (Blood et al., 1999; Koelsch et al., 2006). The lack of standardized means of selecting musical stimuli is a significant limitation of the studies we reviewed on music and emotion and we suggest that future work could benefit from controlling for the level of familiarity of the musical stimuli and selecting a compatible control condition such as emotionally neutral music.

Yet another significant difference across the studies concerned what was measured psychometrically and how. Participants were asked "how well they liked each melody" (Green et al., 2008), to rate "pleasantness versus unpleasantness of each melody" (Blood et al., 1999; Koelsch et al., 2006), to assess their feeling state from happy to sad (Khalfa et al., 2005; Mitterschiffthaler et al., 2007), or to judge the emotion represented in music according to a predefined scale in the Geneva Emotional Music Scale (Trost et al., 2012; Zentner et al., 2008). In addition to rating the arousal and pleasantness properties of music, further studies would benefit from including measurements of physiological response including heart rate, respiration rate, body temperature, and galvanic skin response, to better identify physiological and bodily changes to music-related emotions and feelings.

Closing Remarks

Given the methodological heterogeneity, it is noteworthy that the informative studies reviewed here revealed several consistent results and support some general conclusions. First, there is unequivocal evidence that the emotive states induced by music and the feelings states that follow them, engage homeostasis-related neural systems of the human brain and prompt physiological changes in several sectors of the body. The evidence is compatible with the hypothesis that music may have begun its long historical evolution because, by its effects in physiological states, it played a role in homeostasis, positive as well as negative, in both personal and social areas. As noted in the framework section of this review, such an origin would have allowed for a varied cultural evolution with several branches. Some music forms would have maintained stronger ties to homeostatic effects, while others would have been dominated by intellectual developments. Neither the homeostatic ties nor the intellectual bent would need to be exclusive.

Second, the studies reveal unequivocally that the activation of the ventral striatum and its nucleus accumbens, the anterior cingulate, and the insular cortices are consistently correlated with the pleasurable aspects of musical listening, while the activation of amygdala nuclei, hippocampal formation, and parahippocampal cortex are often correlated with listening to music deemed unpleasant (see Koelsch et al., 2013). Future studies, are likely to yield additional insights into how music can induce affective states and into the neural basis, at cortical, subcortical, and brain stem levels, of the complex relation of music and feelings. The progress achieved over the past two decades is most encouraging.

Glossary

Action Programs

A set of innate collection of physiological responses triggered by critical deviations in the internal or external environments that can produce the quality of biological function and survival. Action programs are aimed at maintaining or restoring homeostatic balance. The programs produce changes in viscera and internal milieu (e.g., alterations in heart rate, breathing, and temperature), striated muscle (e.g., facial expressions and running), and cognition (e.g., focusing attention on a particular target and favoring certain ideas and modes of thinking). The prime examples of action programs are drives and emotions.

Drives

Action programs that are aimed at satisfying basic instinctual physiological needs. Examples include hunger, thirst, libido, exploration and play, care of progeny, and attachment to mates.

Emotions

Action programs largely triggered by external stimuli, either perceived or recalled. Examples include disgust, fear, anger, sadness, joy, shame, contempt, pride, compassion, and admiration.

Feelings

The mental experiences that accompany the mapping of visceral and internal milieu states, as they naturally occur (body state feelings) or as they are produced by action programs (drives and emotions).

Homeostasis

A general term for the process of maintaining the body's physiological parameters (such as temperature, pH, hydration, and nutrient levels) within the range that facilitates optimal function and survival.

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