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Investigating the Neural Encoding of Emotion with Music

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Does our understanding of the human brain remain incomplete without a proper understanding of how the brain processes music? Here, the author makes a passionate plea for the use of music in the investigation of human emotion and its brain correlates, arguing that music can change activity in all brain structures associated with emotions, which has important implications on how we understand human emotions and their disorders and how we can make better use of beneficial effects of music in therapy.

Are Emotions Evoked by Music Real?

Curiously, I often have to justify that I use music to investigate the brain. It is not an uncommon notion, even among some scientists, that a psychological process evoked by music is merely an aesthetic phenomenon and thus not really suitable for the study of human behavior in the real world. This notion is so fallacious that it hurts. In most musical traditions, the two fundamental structural principles of music are "beat" (i.e., a tactus, the fundament of meter and rhythm) and scale (i.e., an organization of a few pitch classes in ascending or descending order). The ability to synchronize movements (including vocalizations) flexibly in a group to an external pulse (the tactus) is uniquely human, and I believe that this ability is the simplest cognitive function that just separates us from animals. This would make music the decisive evolutionary step of the *Homo sapiens*, maybe even of the genus homo. Music immediately affords, by virtue of its fundamental structural principles, that several individuals produce sounds together; this is in contrast to language, which also has many musical features (such as speech melody, timbre, rhythm, etc.) but is best understood when produced by one individual at a time. In this sense, language is the music of the individual, and music is the language of the group. Making music in a group is a potent elicitor of social bonding, associated with emotions that are often very intense, pleasurable, and moving, and the power of music to promote cooperation and social cohesion was (and still is) probably an important evolutionarily adaptive function of music. Thus, at its core, music is not a cultural epiphenomenon of modern human societies, but at the heart of what makes us human.

Music can evoke changes in all five organismic subsystems (or components) of emotion: (1) the evaluation, or appraisal, of music gives rise to emotions such as pleasure or displeasure (cognitive component); (2) music can induce strong action tendencies such as dancing or participating (motivational component); (3) music can change peripheral physiological activity associated with relaxation or arousal (physiological component); (4) music affects the expression of emotion, e.g., facial expression of emotion while music making or while listening to music (expression component); and (5) music evokes feelings such as joy, being moved, courage, nostalgia, peacefulness, sadness, surprise, tension, etc. (subjective feeling component). In addition, as will be described below, music can change activity in virtually all brain structures implicated in emotions. In some cultural practices, such as listening to classical music in a concert hall, the motivational and expression components are only minimally engaged. However, other cultural practices, such as dancing and grooving together to music in a dance club or at a rock concert, can powerfully fulfill the need to experience social connection and express social belonging, and it can give rise to clear expressions of emotions (other principles underlying the evocation of emotions with music are reviewed in Juslin et al., 2014). Thus, emotions evoked by, or with, music are "real" emotions, and these emotions can be exceptionally intense (as, e.g., when accompanied by goosebumps or tears). This makes music a highly valuable tool for the investigation of emotions. In fact, given the ubiquity of music across cultures, and most probably across human history, our understanding of emotions will remain incomplete without a proper understanding of music-evoked emotions.

Neural Correlates

A meta-analysis of functional neuroimaging studies on music and emotion published in 2014 (Koelsch, 2014) reported activity changes in numerous brain structures known to be crucially involved in emotion (Figures 1A–1C). The functional neuroimaging studies published since then are consistent with the findings of that meta-analysis, and they substantiate the findings that music-evoked emotions change activity in the (anterior) hippocampal formation, the amygdala, the auditory cortex, the nucleus accumbens/ventral striatum, the dorsal striatum, the medial and lateral orbitofrontal cortex, and the anterior cingulate cortex as well as in the anterior insula, pre-SMA, rostral cingulate zone, and mediodorsal thalamus. In addition, brainstem structures of the auditory pathway are involved in music-evoked emotions: for example, the very first auditory processing stages in the brainstem, the cochlear and vestibular nuclei, project into the reticular formation (contributing to the arousing or calming effects of music). Moreover, the inferior colliculus encodes consonance and dissonance (as well as auditory signals evoking fear or feelings of security), and this encoding is associated with preference for consonant over dissonant music. Notably, in addition to its projections to

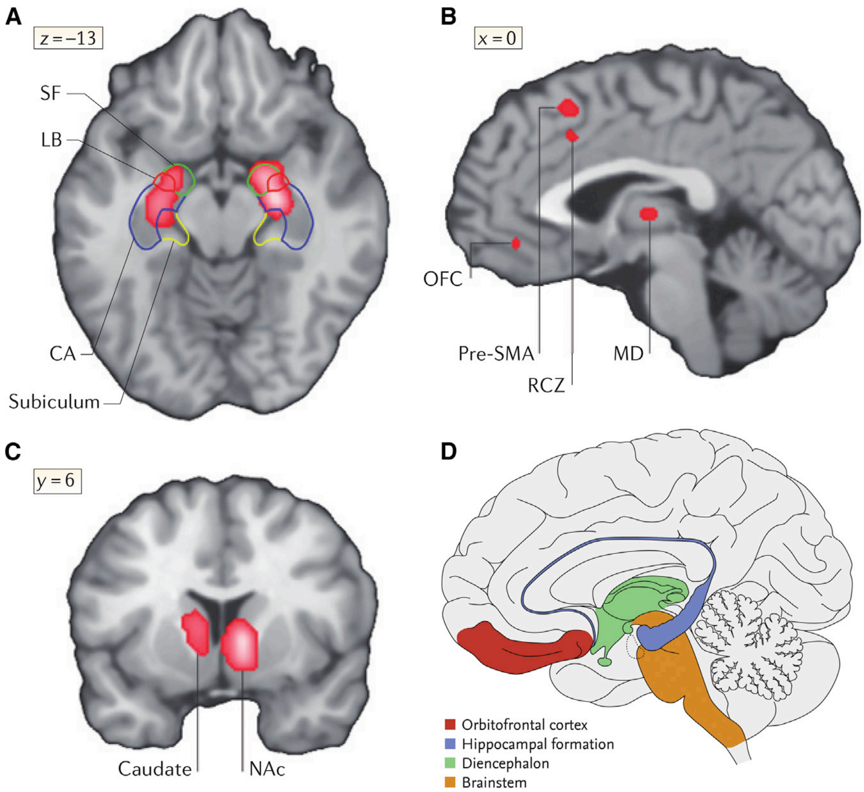

Figure 1. Brain Correlates of Emotions Evoked by Music

(A–C). Results of a meta-analysis of functional neuroimaging studies on music-evoked emotions (Koelsch, 2014). (A) indicates clusters of activity changes reported across studies in the anterior hippocampal formation (cornu ammonis, CA, and subiculum), the amygdala (with local maxima in the left superficial amygdala, SF, and the right laterobasal amygdala, LB). (B) shows clusters in the orbitofrontal cortex (OFC), mediodorsal thalamus (MD), pre-supplementary motor area (SMA), and rostral cingulate zone (RCZ). (C) shows clusters in the right ventral striatum (with a local maximum in the nucleus accumbens, NAc) and the left caudate nucleus. Additional clusters were observed in both left and right auditory cortex, anterior insula, anterior cingulate, and lateral orbitofrontal cortex (not shown). The results of this meta-analysis have been corroborated by studies published since then (see main text). Images are shown according to neurological convention, and coordinates refer to Talairach space.

(D) illustrates four affect systems according to the Quartet Theory (Koelsch et al., 2015): brainstem-centered (orange), diencephalon-centered (green), hippocampus-centered (blue), and orbitofrontal-centered (red) systems. Music can change activity in all these affect systems as well as in emotional coordination systems (including the amygdala, basal ganglia, insula, and cingulate cortex). This capacity of music needs to be investigated in the future with regard to its therapeutic effects in the treatment of psychiatric, neurological, and somatic disorders and diseases.

the auditory thalamus, the inferior colliculus hosts numerous other projections, e.g., into both the somatomotor and the visceromotor (autonomic) system, thus initiating and supporting activity of skeletal, smooth, and cardiac muscles. These brainstem connections are part of the basis of the visceral reactions to music.

The findings of neuroscience studies on music-evoked emotions thus show that music can change activity in the brain structures known to be crucially involved in emotion. Figure 1D illustrates the four affect centers as proposed recently in the “Quartet Theory of Human Emotions” (brainstem-, diencephalon-, hippocampus-, and orbitofrontal-centered affect systems) (Koelsch et al., 2015). The Quartet Theory proposes that these four affect centers generate different classes of emotions (such as activation and deactivation, pain and pleasure, attachment-related emotions, and moral emotions), and that their activity is coordinated by limbic/paralimbic coordination structures such as the amygdala, basal ganglia, striatum, insula, and cingulate cortex. It is important to note that, as reported above, music can change activity in all of these affect and coordination systems. This renders music, on the one hand, a valuable tool for the investigation of the neural correlates of emotions; on the other, it opens exciting new avenues for the use of music in the therapy of psychiatric and neurological disorders and diseases associated with dysfunction in these systems. For example, the finding that music can change activity in the anterior hippocampus gives rise to the investigation of the effects of music interventions on functional and plastic changes in this brain structure in patients with Alzheimer’s disease, depression, post-traumatic stress disorder, and chronic diseases of the immune system such as Crohn’s disease. Recent meta-analyses suggest positive effects of music therapy in patients with depression (Aalbers et al., 2017) and patients with dementia (Fusar-Poli et al., 2017), but there is dire need for randomized controlled trials substantiating these reports, and there is a shocking absence of high-quality neuroscience studies on these topics. Politicians and funding organizations need to be made aware of this nuisance and establish funding schemes for neuroscientific research on therapeutic effects of music.

The Role of the Auditory Cortex in Emotions

Importantly, activity differences in the auditory cortex associated with different emotions are not simply due to acoustical differences between, e.g., happy- and sad-sounding music: several recent music studies show that the auditory cortex plays a much more important role in emotions than previously believed, beyond the traditional view that sensory cortices have merely perceptual functions. For example, a recent study from my research group (Koelsch et al., 2018) suggests that the auditory cortex hosts regions that are influential within emotion networks associated with the processing of music evoking feelings of joy or fear. That study identified computational hubs with high eigenvector centrality in different regions of the auditory cortex and found that the functional connectivity between such processing hubs in the auditory association cortex and a number of limbic/paralimbic regions (ventral striatum as well as orbitofrontal, cingulate, parahippocampal, and insular cortex) interacted with the emotions elicited by the musical stimuli (joy or fear). Thus, it appears that neurons in the auditory cortex directly incite and modulate emotional processes, consistent, e.g., with work from LeDoux (2000) and colleagues showing that inputs from the auditory cortex to the (lateral) amygdala mediate fear conditioning. This sheds new light on the role of sensory cortices in emotion and suggests that the auditory association cortex not only processes perceptual information, but also influences emotional processes as a function of perceptual input (the neural origins of the appraisal processes that give rise to such influence remain to be specified—possible candidates are brainstem, thalamus, auditory cortex, and higher-order cortices). Consistent with these results, a study by Liu et al. (2017) reported auditory-limbic functional connectivity during listening to pop/rock songs, and a study by Salimpoor et al. (2013) reported increased functional connectivity between the (right) auditory cortex and the ventral striatum/nucleus accumbens with increasing reward value of music (as measured by the amount of money participants were willing to spend on the music they heard in the fMRI scanner), thus predicting reward value. Correspondingly, functional connectivity between the auditory cortex and the nucleus accumbens is reduced in individuals with "specific musical anhedonia," whereas individuals with average or greater-than-average reward sensitivity to music show enhanced connectivity between these structures.

The Role of the Hippocampus in Emotions

Most studies on the hippocampus have investigated its role in cognitive functions such as memory, navigation, and exploration (leading to a Nobel Prize in 2014, awarded to John O'Keefe, May-Britt Moser, and Edvard I. Moser). Notably, neuroscience studies on emotion with music reveal that the (anterior) hippocampus also plays a crucial role in human emotions. This became evident in the substantial proportion of music studies reporting activity changes in the anterior hippocampal formation: the largest clusters in the meta-analysis on music-evoked emotions (Koelsch, 2014) were located in the anterior hippocampal formation (see Figure 1A), a finding that is substantiated by the fact that a large number of studies on music-evoked emotions published since then have also reported activity changes in this structure.

Future research needs to specify the emotions associated with activity changes in the hippocampus (beyond negative emotions such as anxiety reported in animal studies). I have previously put forward the notion that the (anterior) hippocampus is the neural substrate of attachment-related emotions (Panksepp's CARE system), which give rise to subjective feelings such as joy, happiness, and being moved when social attachments are experienced, or to feelings such as sadness when social attachments are severed. The activation of hippocampal activity with music might be due to the extraordinary capacity of music to engage social functions associated with social attachment and social bonding.

Music and Social Bonding

Increasing evidence also shows us that music is a potent elicitor of social bonding. For example, synchronization of movements to a beat with other individuals has social effects such as increase in trust and cooperation (Tarr et al., 2014) and is associated with positive emotional effects (Trost et al., 2017) and possibly with activation of the endogenous opioid system (Tarr et al., 2014). Correspondingly, intranasal application of oxytocin can improve synchronized tapping. Thus, experiments on music and emotion are often social bonding experiments (even if not intentionally designed that way). This is relevant for the interpretation of functional neuroimaging results: for example, it is tempting to speculate that the activity changes in the anterior hippocampus (as reported above and shown in Figure 1A) are, at least in part, due to social bonding and social attachment associated with synchronization of sensorimotor processes to the beat of the music (including neurochemical processes such as enkephalinergic innervation of the hippocampus, hippocampal innervation of the paraventricular nucleus of the hypothalamus and associated oxytocin release, and changes in hypothalamo-pituitary-adrenal axis activity). Given the scarce knowledge on the neural correlates of social bonding in humans, music appears to be a highly useful tool for a more systematic investigation of this issue—for example, with regard to the capacity of music to facilitate the emergence of trust, cooperation, sympathy, and empathy.

The Influence of Music on Conscious Cognition and the Unaware Mind

It is well known that consciously controlled thought can modulate and regulate emotions (an important cornerstone of clinical psychology). How emotions influence thought, on the other hand, is not well studied. It is, therefore, an interesting development that several studies during the past years have begun to investigate effects of music-evoked emotions on cognition, e.g., on evaluative processes, risk taking, or "mind wandering." For example, a behavioral study by Schulreich et al. (2014) suggests that music-evoked emotions modulate probability weighting during risky choices. In that study, participants chose riskier lotteries significantly more often after listening to happy-sounding music compared with sad-sounding music or random tones (specifically, participants showed significantly higher decision weights associated with larger payoffs after listening to happy-sounding music). Consistent with this finding, a neuroimaging study by Halko et al. (2015) reported that the hedonic value of music modulates risky choices and associated reward responses in amygdala and dorsal striatum. Finally, a study from my research group (Taruffi et al., 2017) suggests that music-evoked emotions modulate mind wandering (i.e., spontaneous, non-intentional thought). In that study, happy-sounding music (compared with sad-sounding music) was associated with less mind wandering and lower centrality of "default mode" network hubs (e.g., medial orbitofrontal, anterior cingulate, and posterior cingulate cortex). These findings are consistent with findings by Wilkins et al. (2014), who reported that the default mode network is most strongly connected when listening to preferred music.

The latter findings have a particular clinical relevance, because recurring spontaneous thoughts with negative content are a crucial problem in individuals with psychological disorders such as depression. Even in healthy individuals, "mind-wandering" is often associated with negative thought content, therefore making individuals often unhappy. The use of music to evoke emotions and moods influencing thoughts thus has huge potential for health and well-being. On the other hand, research on this topic (such as work by Emily Carlson and Suvi Saarikallio) can also inform us about unhealthy ways of using music for mood regulation, e.g., when music elicits rumination.

Future studies on this topic should consider that it is important to differentiate between consciously controlled thought (i.e., deliberate thought, with awareness of the control over thoughts) and "sub-conscious" thought (without awareness of the control over thoughts). With regard to neural correlates, we have described in our Quartet Theory (Koelsch et al., 2015) that the orbitofrontal-centered affect system (see red color in Figure 1D) is a system characterized by fast, effortless, emotional thought and absence of logical thought (the orbitofrontal cortex is not neocortex, but mostly 5-layered palaeocortex). We have proposed (Koelsch et al., 2015) that many cognitive biases (as, e.g., described in the prospect theory) are due to sub-conscious thoughts performed by the orbitofrontal cortex and that one type of cognitive operation processed in this system is the fast and automatic evaluation of objects and circumstances with regard to internalized social norms, values, and self-concept. Such sub-conscious cognitions can lead to the generation of moral emotions such as guilt, blame, shame, embarrassment and disgrace. Others have used the term "the unconscious mind" for this system, or the "sub-consciousness," and we have suggested the term "the unaware mind." The observation that music can change activity in the orbitofrontal cortex (see Figure 1B) and the observation that music can influence mind wandering both suggest that music can change sub-conscious thought, i.e., the activity of "the unaware mind." Thus, music is a highly interesting and promising tool for the investigation of the effects of emotions and moods on both sub-conscious and conscious thought. In particular, it will be a major advance to elucidate neural networks of negative versus positive non-intentional, spontaneous (sub-conscious) thought, and how the activity of these networks can be modulated by music.

Musical Anhedonia

Another interesting development during the last years was the discovery of "specific musical anhedonia" in healthy individuals by Ernest Mas-Herrero, Robert Zatorre, and colleagues. Specific musical anhedonia refers to the absence of feelings of pleasure in response to music, while pleasure and reward experiences to other stimuli (e.g., food, sex, or exercise) are normal. This phenomenon is associated with reduced activity changes in the nucleus accumbens (NAc) in response to music (and auditory-NAc functional connectivity), highlighting the role of the mesolimbic dopaminergic system in musical reward. A study by Mallik et al. (2017) found that both positive and negative emotions to music were attenuated after administration of naltrexone (NTX), a μ-opioid antagonist, suggesting that "endogenous opioids are critical to experiencing both positive and negative emotions in music, and that music uses the same reward pathways as food, drugs and sexual pleasure" (Mallik et al., 2017). Moreover, a study by Keller et al. (2013) reported that trait anhedonia is associated with reduced reactivity and connectivity of mesolimbic and paralimbic reward pathways in response to music. These findings are consistent with the observation that transcranial magnetic stimulation (TMS) over the left dorsolateral prefrontal cortex modulated fronto-striatal function bidirectionally together with measures of pleasure and motivation during music listening (Mas-Herrero et al., 2018). In the latter study, perceived pleasure, psychophysiological measures of emotional arousal, and the monetary value assigned to music were all increased by exciting fronto-striatal pathways, whereas inhibition of that system led to decreases in these variables. However, lesion studies on musical anhedonia do not yet provide a coherent picture: Belfi et al. (2017) recently reported one anhedonic patient with focal damage to the right striatum who showed a marked musical anhedonia following brain injury, but other cases of striatal damage (both right and left) did not develop full-blown musical anhedonia, and a previous case study by Satoh et al. (2011) reported musical anhedonia after damage of the inferior parietal lobule.

Methodological Advances

The investigation of emotion with music has methodologically advanced considerably during the last years, using, e.g., measures of real-time emotion ratings during listening to entire pieces and using such measures as continuous regressors in the analysis of functional neuroimaging data. Results of such studies provide insight into neural correlates of inter-subject correlation of emotional processes during music listening; of musical tension, pleasure, and arousal; or of emotional processes that take a while to unfold (e.g., stress reduction and associated hypothalamic activity). In a study of my own research group (Koelsch and Skouras, 2014), we used one single stimulus block of 4 min duration for each experimental condition (e.g., music evoking joy or fear-evoking music) and then performed eigenvector centrality mapping on the fMRI data to identify computational hubs in the brain that are influential within the brain networks of interest. We found, e.g., high eigenvector centrality in different nuclei of the amygdala during joy (compared with fear), supporting the notion that the amygdala is an emotional coordination structure with an influential, or central, position within emotion networks.

Other Recent Developments and Future Challenges

Other recent developments and future challenges include, for example, the investigation of aesthetic emotions (such as feelings of beauty or the sublime, being moved, tension and suspense, amusement, fascination, awe, wonder, boredom, anger, interest, etc.). Recently, we proposed to define "aesthetic emotions" as emotions that are associated both with subjectively felt aesthetic pleasure or displeasure and with subjectively perceived and evaluated aesthetic appeal—and thus with subjectively perceived aesthetic liking or disliking. Surprisingly, only little research has investigated aesthetic emotions with regard to both aesthetic evaluation and subjective feeling, calling for more systematic research in this area. A thorough investigation of aesthetic emotions and their neural correlates is relevant for several reasons: aesthetic emotions are frequently elicited in our everyday lives, they are often exceptionally strong, they have a clear positive preponderance, and their potential for therapy is not well understood. Aesthetic emotions also provide a new means to investigate neural correlates of "mixed emotions." For example, an artwork such as music can be evaluated as positive, despite evoking negative emotions such as sadness, and different brain networks can be identified associated with the experience of sad and happy emotions on the one hand (including, e.g., the orbitofrontal cortex), and (dis)liking on the other (including, e.g., the amygdala) (Brattico et al., 2016).

Likewise, neural correlates of emotions associated with predictive processes have so far received only little attention. Investigations within the predictive coding framework have a certain cognitive bias, often neglecting affective processes such as surprise, anticipation, tension, and resolution. For example, it is not known whether the (un)expectedness of musical events is associated with feelings of pleasure and activity of the reward network (including, e.g., mesolimbic dopaminergic projections to the nucleus accumbens) or which brain structures are associated with the (un)certainty of musical predictions.

Finally, two recent fMRI studies by Pehrs and colleagues (Pehrs et al., 2014, 2017) have used music in combination with film clips. Music accompanying film clips of romantic kissing scenes was reported to lead to a suppressive gating effect of the (mid-)superior temporal gyrus on fusiform-amygdalar connectivity. This suggests that film music modulates emotion elicitation by differentially changing preprocessed visual information to the amygdala. In a study using empathic film clips paired with sad music, preceded by some text providing information about the character in the film clip, it was observed that fusiform-amygdalar connectivity is also modulated by the temporal pole. This suggests that the temporal pole integrates different sources of socially relevant information (text, film, music) and that it top-down modulates lower-level perceptual areas in the ventral visual stream during social cognition.

Conclusions and Perspectives

Music is a highly valuable, valid, and reliable stimulus for the investigation of both everyday emotions and aesthetic emotions in the laboratory. This does not mean that music is ideal to investigate each and every different type of emotion (neither is any other experimental stimulus). For example, disgust or jealousy are difficult to evoke with music. However, emotions evoked by music can be highly intense, and music-evoked emotions can change activity in virtually all emotion structures in the brain. This has important therapeutic implications, because it suggests that music can help in the therapy of disorders and diseases with emotional components, or with dysfunction in limbic/paralimbic brain structures. This calls for more evidence-based research investigating these issues and for new funding schemes that support high-quality research on the therapeutic effects of music in the brain.

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REFERENCES

Aalbers, S., Fusar-Poli, L., Freeman, R.E., Spreen, M., Ket, J.C., Vink, A.C., Maratos, A., Crawford, M., Chen, X.J., and Gold, C. (2017). Music therapy for depression. Cochrane Database Syst. Rev. *11*, CD004517.

Belfi, A.M., Evans, E., Heskje, J., Bruss, J., and Tranel, D. (2017). Musical anhedonia after focal brain damage. Neuropsychologia *97*, 29–37.

Brattico, E., Bogert, B., Alluri, V., Tervaniemi, M., Eerola, T., and Jacobsen, T. (2016). It's sad but I like it: the neural dissociation between musical emotions and liking in experts and laypersons. Front. Hum. Neurosci. *9*, 676.

Fusar-Poli, L., Bieleninik, Ł., Brondino, N., Chen, X.-J., and Gold, C. (2017). The effect of music therapy on cognitive functions in patients with dementia: a systematic review and meta-analysis. Aging Ment. Health. https://doi.org/10.1080/13607863.2017.1348474.

Halko, M.L., Mäkelä, T., Nummenmaa, L., Hlushchuk, Y., and Schürmann, M. (2015). Hedonic context modulates risky choices and reward responses in amygdala and dorsal striatum. J. Neurosci. Psychol. Econ. *8*, 100–115.

Juslin, P.N., Harmat, L., and Eerola, T. (2014). What makes music emotionally significant? Exploring the underlying mechanisms. Psychol. Music *42*, 599–623.

Keller, J., Young, C.B., Kelley, E., Prater, K., Levitin, D.J., and Menon, V. (2013). Trait anhedonia is associated with reduced reactivity and connectivity of mesolimbic and paralimbic reward pathways. J. Psychiatr. Res. *47*, 1319–1328.

Koelsch, S. (2014). Brain correlates of music-evoked emotions. Nat. Rev. Neurosci. *15*, 170–180.

Koelsch, S., and Skouras, S. (2014). Functional centrality of amygdala, striatum and hypothalamus in a "small-world" network underlying joy: an fMRI study with music. Hum. Brain Mapp. *35*, 3485–3498.

Koelsch, S., Jacobs, A.M., Menninghaus, W., Liebal, K., Klann-Delius, G., von Scheve, C., and Gebauer, G. (2015). The quartet theory of human emotions: an integrative and neurofunctional model. Phys. Life Rev. *13*, 1–27.

Koelsch, S., Skouras, S., and Lohmann, G. (2018). The auditory cortex hosts network nodes influential for emotion processing: An fMRI study on music-evoked fear and joy. PLoS ONE *13*, e0190057.

LeDoux, J.E. (2000). Emotion circuits in the brain. Annu. Rev. Neurosci. *23*, 155–184.

Liu, C., Brattico, E., Abu-Jamous, B., Pereira, C.S., Jacobsen, T., and Nandi, A.K. (2017). Effect of explicit evaluation on neural connectivity related to listening to unfamiliar music. Front. Hum. Neurosci. *11*, 611.

Mallik, A., Chanda, M.L., and Levitin, D.J. (2017). Anhedonia to music and mu-opioids: evidence from the administration of naltrexone. Sci. Rep. *7*, 41952.

Mas-Herrero, E., Dagher, A., and Zatorre, R.J. (2018). Modulating musical reward sensitivity up and down with transcranial magnetic stimulation. Nat. Hum. Behav. *2*, 27.

Pehrs, C., Deserno, L., Bakels, J.H., Schlochtermeier, L.H., Kappelhoff, H., Jacobs, A.M., Fritz, T.H., Koelsch, S., and Kuchinke, L. (2014). How music alters a kiss: superior temporal gyrus controls fusiform-amygdalar effective connectivity. Soc. Cogn. Affect. Neurosci. *9*, 1770–1778.

Pehrs, C., Zaki, J., Schlochtermeier, L.H., Jacobs, A.M., Kuchinke, L., and Koelsch, S. (2017). The temporal pole top-down modulates the ventral visual stream during social cognition. Cereb. Cortex *27*, 777–792.

Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A., and Zatorre, R.J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. Science *340*, 216–219.

Satoh, M., Nakase, T., Nagata, K., and Tomimoto, H. (2011). Musical anhedonia: selective loss of emotional experience in listening to music. Neurocase *17*, 410–417.

Schulreich, S., Heussen, Y.G., Gerhardt, H., Mohr, P.N., Binkofski, F.C., Koelsch, S., and Heekeren, H.R. (2014). Music-evoked incidental happiness modulates probability weighting during risky lottery choices. Front. Psychol. *4*, 981.

Tarr, B., Launay, J., and Dunbar, R.I. (2014). Music and social bonding: "self-other" merging and neurohormonal mechanisms. Front. Psychol. *5*, 1096.

Taruffi, L., Pehrs, C., Skouras, S., and Koelsch, S. (2017). Effects of sad and happy music on mind-wandering and the default mode network. Sci. Rep. *7*, 14396.

Trost, J.W., Labbé, C., and Grandjean, D. (2017). Rhythmic entrainment as a musical affect induction mechanism. Neuropsychologia *96*, 96–110.

Wilkins, R.W., Hodges, D.A., Laurienti, P.J., Steen, M., and Burdette, J.H. (2014). Network science and the effects of music preference on functional brain connectivity: from Beethoven to Eminem. Sci. Rep. *4*, 6130.