Pleasant and unpleasant emotions induced by music: A meta-analysis of functional neuroimaging studies

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February 15, 2023

Abstract

Prior neuroimaging studies of music-evoked emotions have shown that music listening involves the activation of cortical and subcortical regions. However, these regions could be differentially activated by music stimuli with different affective valence. To better understand the neural correlates involved in the processing of pleasant and unpleasant emotions induced by music, we conducted a quantitative activation likelihood estimate (ALE) meta-analysis. We performed separate ALE analyses for the overall brain activation during music listening (63 studies), for the brain activation during listening to unpleasant music (23 studies) and for the brain activation while listening to pleasant music (21 studies). Our results showed an activation of a range of cortical and subcortical regions, including the amygdala, insula, striatum, thalamus, parahippocampal gyrus, anterior cingulate gyrus and superior temporal gyrus. Moreover, our findings showed that pleasant and unpleasant music specifically activated different brain regions. Particularly, unpleasant music activated the amygdala, hippocampus and the anterior cingulate cortex, whereas pleasant music activated the striatum, thalamus and the hippocampus. The identification of brain networks preferentially activated during listening to pleasant and unpleasant music provide useful clinical information for the development of therapies in psychological disorders with emotion reactivity problems.

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# equal contribution

Running Head: A meta-analysis of the emotions induced by music

Abstract

Prior neuroimaging studies of music-evoked emotions have shown that music listening involves the activation of cortical and subcortical regions. However, these regions could be differentially activated by music stimuli with different affective valence. To better understand the neural correlates involved in the processing of pleasant and unpleasant emotions induced by music, we conducted a quantitative activation likelihood estimate (ALE) meta-analysis. We performed separate ALE analyses for the overall brain activation during music listening (63 studies), for the brain activation during listening to unpleasant music (23 studies) and for the brain activation while listening to pleasant music (21 studies). Our results showed an activation of a range of cortical and subcortical regions, including the amygdala, insula, striatum, thalamus, parahippocampal gyrus, anterior cingulate gyrus and superior temporal gyrus. Moreover, our findings showed that pleasant and unpleasant music specifically activated different brain regions. Particularly, unpleasant music activated the amygdala, hippocampus and the anterior cingulate cortex, whereas pleasant music activated the striatum, thalamus and the hippocampus. The identification of brain networks preferentially activated during listening to pleasant and unpleasant music provide useful clinical information for the development of therapies in psychological disorders with emotion reactivity problems.

Keywords: Emotion, Music, Brain activity, fMRI, ALE meta-analysis

Introduction

Music has been present in different cultures since ancient times. Listening to music, however, does not seem to be a survival-relevant activity, which implies the existence of other factors explaining the origin or evolution of music (Zatorre & Salimpoor, 2013). One of these possible factors is the capacity of music to convey, induce and regulate emotions (Hauser & McDermott, 2003). To this respect, prior research has demonstrated that music is capable of inducing powerful emotions, measurable at experiential, peripheral-physiological and brain levels (Blood & Zatorre, 2001; Fuentes-Sánchez et al., 2021a), which makes music a valid stimulus for investigating emotional processing (Koelsch, 2014), also offering some advantages over other emotional stimuli such as emotional scenes or faces (Baumgartner et al., 2006). Therefore, the powerful effect of music accounts for the large number of scientific studies that use this type of stimulation (Koelsch, 2020).

Previous meta-analyses in the field, such as those by Koelsch (2014, 2020), have been able to demonstrate the existence of a large body of work outlining the neural correlates of emotions evoked by music. In such works, it has been shown that music-evoked emotions not only activate emotion-related areas such as the amygdala, insula or striatum, but that they also activate the auditory cortex, the hippocampus and the secondary somatosensory cortex. This suggests that the latter areas, typically associated with more cognitive or perceptual processes, also have an important role in music-evoked emotions (Koelsch, 2020). However, in the aforementioned meta-analyses, the included studies were considered irrespective of the specific emotion induced and irrespective of the emotion model (discrete emotions vs. affective dimensions) employed, which does not allow for investigating whether these areas are activated independently of the specific discrete emotions or affective dimensions (e.g., pleasant/unpleasant emotions).

During the last decades, discrete and dimensional models have increasingly been used in the field of music and emotions (Eerola & Vuoskoski, 2011; Fuentes-Sánchez et al., 2021b; Song et al., 2016). The discrete emotion model argues for the existence of a limited number of basic emotions, which have specific and distinguishing neurophysiological and behavioral patterns from each other (Ekman, 1992). Findings obtained from this approach have shown that, generally speaking, each discrete emotion is associated with the activation of specific areas in the brain. For example, disgust typically evokes insula activation while fear predominantly activates the amygdala (Murphy et al., 2003; Vytal & Hamann, 2010). By contrast, the dimensional approach considers that all emotions underlie more general dimensions such as valence/arousal, positive/negative activation or approach/withdrawal (Bradley, 2000; Bradley et al., 2001; Barrett & Wager, 2006; Lang et al., 1997). From this approach, findings have revealed that some areas are activated by several emotions (e.g. Lindquist et al., 2012). For instance, the amygdala is activated not only by fear-inducing stimuli but also by more generally emotionally meaningful stimuli, even those with positive hedonic valence (Barrett & Wager, 2006).

In the existing literature, most studies do not tend to assess different discrete emotions/dimensions at the same time, making it difficult to extract specific brain areas related to these emotions (Hamann, 2012). For example, within the discrete approach model, studies have mainly focused on the contrast between happiness vs. fear (Koelsch & Skouras, 2014; Koelsch, 2021) or happiness vs. sadness (Brattico et al., 2011). Likewise, within the dimensional model, studies exist, for example, that have focused only on pleasant vs. unpleasant emotions (Koelsch, 2006), while others have focused on the relationship between pleasantness/unpleasantness and consonance/dissonance (Blood et al., 1999) or examined the relationship between some areas and the intensity of chills evoked by different pieces of music (Blood & Zatorre, 2001).

To our knowledge, no meta-analysis has been conducted so far that investigates the neural correlates of music-induced emotions considering the affective valence of music. Given that the neuroanatomy of emotions has been of great interest within the field of emotions and, considering the existence of other frequently cited meta-analyses in this line of research that have focused on other emotional stimuli (Barrett et al., 2006; Murphy et al., 2003; Wager et al., 2003), the motivation to carry out a valence-focused meta-analysis becomes apparent. To address the unresolved questions, the current meta-analysis had the aim to investigate the brain structures involved in pleasant and unpleasant emotions evoked by music. We refer to *pleasant* and*unpleasant emotions* as general labels that include both discrete and dimensional emotions. For example, within the label of pleasant emotions, we included studies that induced joy, happiness, pleasantness, liking, consonance, etc., whereas within the label of unpleasant emotions, we included studies inducing fear, sadness, unpleasantness, dislike, dissonance, etc. Likewise, this meta-analysis aims to replicate and supplement prior meta-analyses existing in the field of music and emotions (Koelsch, 2014, 2020).

2. Methods

2.1. Search method and study selection

The literature search was conducted through the following databases: PubMed (www.ncbi.nlm.nih.gov/pubmed), Scopus (Elsevier, Amsterdam, Netherlands) and Web of Science (https://www.webofscience.com). Additionally, citations and reference lists from relevant articles were reviewed. Eligible studies were experimental studies that investigated brain responses during the listening of music using fMRI (functional magnetic resonance imaging) or PET (positron emission tomography). The terms used to conduct the search were: [("Emotion" OR "Affect" OR "Mood") AND ("Music" OR "Excerpts" OR "Song") AND ("fMRI" OR "Functional Magnetic Resonance Imaging" OR "PET" OR "Positron Emission Tomography")].

Studies that investigated other psychological processes associated with explicit tasks during music listening (e.g., emotion regulation, memory, etc.) were not included. To circumvent complex interactions of language- and music-induced emotions, studies that used music with lyrics were also excluded. Additionally, to be included in the meta-analysis, studies had to target adult participants (>=18 years) and non-clinical samples[1]. Also, reviews, meta-analyses, dissertations, and conference abstracts were excluded. Lastly, taking into account the linguistic capacities of the authors, only studies published in English, Spanish or German languages were included, with no restrictions based on the year of publication (cutoff date: 23.08.2022).

For the ALE meta-analysis, the final inclusion criteria were that eligible studies should include whole brain analyses and not just specific regions of interest and should contain a complete list of stereotaxic coordinates (i.e., Montreal Neurological Institute [MNI] or Talairach space) (Talairach & Tournoux, 1988). In eligible studies where this information was missing, the authors were contacted.

The search generated a total of 1093 potential studies. Five additional studies were obtained from other relevant articles. Therefore, 1098 studies were identified. After retrieving duplicates (n = 428), a total of 670 studies were screened by two independent researchers (NF-S, SP), based on titles and abstracts. Of them, 129 studies were assessed for eligibility. After full article inspection, 63 studies were used for the final ALE meta-analysis (see Figure 1).

[FIGURE 1 ABOUT HERE]

The meta-analysis was performed following the methodological guidelines by Mueller et al. (2018) (see Figure 2).

[FIGURE 2 ABOUT HERE]

2.2. Data analysis

Relevant information (reference space, sample size, coordinates of activation, type of music, duration of music, etc.) was obtained by three researchers (NF-S, SP & AE-P) from the selected articles (N = 63) for the posterior analysis. All information was double-checked by a different researcher.

To identify consistent brain activation across studies, the activation likelihood estimation (ALE) approach (Eickhoff et al., 2009, 2012, 2017; Laird et al., 2005; Turkeltaub et al., 2012) was carried out. Talairach coordinates (Talairach and Tournoux, 1988) were converted to MNI using GingerALE, and all results were presented in MNI space. After preparing the selected contrasts, the ALE analysis was performed using GingerALE 3.0.2 software (http://brainmap.org/ale) (Lancaster et al., 2007). For the general analysis and sub-analyses, the family-wise error (FWE) method was used to correct for multiple comparisons using a significant cluster level threshold of $p < 0.05$ and a voxel-level cluster forming threshold of $p < 0.001$ (i.e., 1000 permutations).

The resulting peak coordinates are reported in MNI. To visualize the meta-analysis results, the resulting output were overlaid onto anatomical axial, coronal, and sagittal slice images in MNI space.

3. Results

3.1. Included articles

The final meta-analysis included 63 studies, with overall 3392 subjects and 1184 foci from 157 different contrasts (see Table 1). A complete list of studies and their characteristics can be seen in Supplementary Table 1. After the general analysis, two separate sub-analyses were conducted to investigate specific brain activations evoked by listening to unpleasant (in contrast to pleasant) and to pleasant (in contrast to unpleasant) music excerpts. In the former, 23 studies were included in an ALE analysis to investigate brain activity during listening to unpleasant (minus pleasant) music (with 628 subjects and 187 foci from 34 different contrasts). In the latter, 21 studies were included in an ALE analysis (with 632 subjects and 311 foci from 34 different contrasts) to investigate brain activity evoked by pleasant (minus unpleasant) music. The list of studies included in the sub-analyses is given in Supplementary Table 4.

[TABLE 1 ABOUT HERE]

3.2. Brain activity evoked during music listening (63 studies)

The ALE analysis identified 9 clusters for the general effect of music-evoked emotions. The list of peak coordinates and MNI coordinates can be found in Table 2 (see also the peaks of activations of the clusters in Supplementary Table 2 and the contrasts contributing to the clusters in Supplementary Table 3).

The first and the second clusters (Clusters #1 and #2) included peaks in the left and right superior temporal gyrus, the left transverse temporal gyrus and the supramarginal gyrus. Cluster #3 encompassed the right hemispheric amygdala, caudate, putamen, parahippocampal gyrus and substantia nigra, as well as the left thalamus. Clusters #4 and #5 revealed peaks in the left hemispheric amygdala, parahippocampal gyrus, lentiform nucleus (putamen and globus pallidus) and caudate nucleus. Clusters #6 and #7 encompassed peaks in the left hemispheric insula, claustrum and cingulate gyrus. Finally, Clusters #8 and #9 revealed peaks bilaterally in the anterior cingulate cortex (see Figure 3 and Table 2).

[TABLE 2 ABOUT HERE]

[FIGURE 3 ABOUT HERE]

3.3. Brain activity evoked by unpleasant contrasted to pleasant music (23 studies)

For specific brain activations during unpleasant > pleasant music listening, our analysis found 5 clusters (see Table 3; see also the contrasts contributing to these clusters in Supplementary Table 5). Particularly, activations were found in the right amygdala, in the left and right parahippocampal gyrus, in the bilateral anterior cingulate and the right hippocampus (see Figure 4).

[TABLE 3 ABOUT HERE]

[FIGURE 4 ABOUT HERE]

3.4. Brain activity evoked by pleasant contrasted to unpleasant music (21 studies)

The ALE analysis for brain activations during the listening of pleasant > unpleasant music identified 6 clusters (see Table 4; see also the contrasts contributing to these clusters in Supplementary Table 5). For these studies, clusters were found bilaterally in the superior temporal gyrus, in the right hemispheric parahippocampal gyrus, hippocampus, caudate and lentiform nucleus, as well as in the left thalamus (see Figure 4).

[TABLE 4 ABOUT HERE]

4. Discussion

The present ALE meta-analysis investigated brain activations evoked by listening to music fragments as well as the specific activations as a function of pleasant and unpleasant music-evoked emotions. Overall, this meta-analysis revealed peaks of activation and clusters across numerous cortical and subcortical regions related to emotional processing. Additionally, findings revealed that some areas are specifically activated depending on the type of emotion induced.

4.1. Overall music-evoked emotions effect

For the overall effect of music-induced emotion (general analysis without considering the hedonic valence of emotion), findings revealed clusters of activation in cortical and subcortical regions such as the auditory cortex, amygdala, striatum, insula, thalamus, parahippocampal gyrus and anterior cingulate cortex. This finding replicates results obtained in prior meta-analyses (Koelsch, 2014, 2020) and indicates that these brain areas are involved during the emotional processing induced by music.

In contrast to Koelsch's most recent meta-analysis (Koelsch, 2020), our general results did not reveal activations in the hippocampus and secondary somatosensory cortex regions, although we found hippocampus activations as specifically evoked by unpleasant and pleasant music, which will be discussed later. This finding suggests the importance of considering the affective valence of the stimuli as claimed by prior research (Fuentes-Sánchez et al., 2021c).

On the other hand, now extending the findings by Koelsch (2020), our results showed that listening to emotional music also activates the insula, an area related to the regulation and integration of autonomic reactivity (skin conductance, heart rate, pupil response, etc.) (Koelsch et al., 2010). This insula activation does in fact dovetail with well-established findings within other fields of emotion research (Barrett & Wager, 2006; Murphy et al., 2003; Phan et al., 2002) and also within the field of music research (Blood & Zatorre, 2001; Trost et al., 2012).

4.2. Brain activations as a function of unpleasant and pleasant emotions

The current sub-analyses also revealed some different activations as a function of the affective valence of music stimuli. Firstly, we observed that the amygdala was specifically activated during the listening of unpleasant music, but not during the listening of pleasant music. To this respect, prior research following the discrete emotion model has claimed that bilateral amygdala activation occurs preferentially with stimuli depicting fear (LeDoux, 2000; Murphy et al., 2003; Phan et al., 2002). In contrast, some studies from the dimensional approach have shown that the amygdala is similarly activated during the processing of positive emotions, such as reward (Barrett, 2006; Janak & Tye, 2015), indicating that this structure is associated with the processing of motivationally salient stimuli, irrespective of their specific valence. Our findings would, at least partially, support the former approach. However, in the present meta-analysis, we included direct contrasts not only between fear and other specific emotions (e.g., fear vs. joy) but also including other negative dimensions such as unpleasantness, dissonance or dislike. Therefore, the significant activation of the amygdala might not specifically be associated with fear, but is probably associated with negative mood in general. Interestingly, a recent meta-analysis that sought to investigate brain activations during food-induced pleasure and music reward showed that the amygdala was specifically activated during the food-induced pleasure but not during the music-induced pleasure (Mas-Herrero et al., 2021), also in accordance with our results. Following the hypothesis of the dimensional model of emotions, if amygdala activation is associated with the degree of emotional intensity of the stimulus (Lang & Bradley, 2013), another possible explanation of these findings could be that unpleasant music might be more emotionally intense in comparison to pleasant music. Notwithstanding, the fact that music is capable of inducing activation in the amygdala, a core structure of emotional processing, strengthens the basis for music-based clinical interventions, especially for the treatment of affective disorders, which are related to amygdala dysfunctions in music perception (Koelsch et al., 2010).

As mentioned before, an activation of the bilateral anterior cingulate cortex was found during music listening, independently of affective valence. The activation of this region has been shown as related to the regulation of emotional responses, including autonomic reactivity (Blood & Zatorre, 2001). Subsequently, when considering the type of induced emotions, our sub-analysis showed that the activation of that region appeared to be specifically evoked by unpleasant music. This finding aligns with prior work that suggests the implication of this region during the processing of negative emotions (Etkin et al., 2011; Shackman et al., 2011; Tikàsz et al., 2016). Moreover, a recent meta-analysis on neural correlates of music familiarity (Freitas et al., 2018) found activation of the right anterior cingulate cortex during listening to unfamiliar music compared to familiar music. Since unfamiliar music is usually rated as less preferent, and less preferent stimuli are typically rated as less pleasant (Fuentes-Sánchez et al., 2022), this finding of stronger cingulate cortex activation for unfamiliar music concords with preferential processing of negative/unpleasant emotions in this region as found here.

Our analysis further revealed clusters of activations in the dorsal striatum (i.e., caudate, putamen, lentiform nucleus) during the music-evoked emotions, independent of their valence, but also specifically during the processing of pleasant emotions (i.e., caudate, lentiform nucleus). These results replicate prior findings (Salimpoor et al., 2011, 2013; Trost et al., 2012) in that experiencing pleasure during music listening activates the reward network. In fact, prior work showed that the activation of the dorsal and ventral striatum was proportional to the reward value of the stimuli (Salimpoor et al., 2013). In this line, a more recent study showed that the dopaminergic system was involved during music reward (Ferreri et al., 2019).

However, despite mounting evidence for an involvement of the ventral striatum –particularly the nucleus accumbens– for music-induced emotions (Koelsch, 2014; Mantione et al., 2014; Salimpoor et al., 2013; Zatorre & Salimpoor, 2013), we did not find clusters of activation in that brain region. The non-activation of the ventral striatum and particularly the nucleus accumbens in the present meta-analyses does not, of course, mean that this structure is not activated during music listening per se. Overall, the activation of the dorsal striatum during music-evoked emotions suggests that musical stimuli might have similar properties to other rewarding experiences, such as food, sex or winning money (Belfi & Loui, 2019). These findings appear fascinating, as they open the door to the use of music for psychological treatment in pathologies showing an underactivation of the striatum, such as in anhedonia (e.g., Borsini et al., 2020) or major depressive disorder (e.g., Forbes et al., 2009).

In the same way, the present results showed activation of the left thalamus while listening to pleasant music, as well as while listening to music in general (without considering the hedonic valence). The activation of the thalamus is related to the modulation of emotional arousal (Anders et al., 2004). To this respect, a number of previous studies (Blood & Zatorre, 2001; Klepzig et al., 2020; Salimpoor et al., 2011) showed that this region was involved during chill response processing (response associated with a positive emotional response). These findings also align with those obtained using peripheral physiological measures (Fuentes-Sánchez et al., 2021a), as an enhanced reactivity of the sympathetic nervous system, a system related to emotional arousal, was found during listening to pleasant but also unpleasant music. Interestingly, in such work it was found that the sympathetic response was enhanced during the listening of pleasant music, which, in turn, was rated as more arousing, in comparison to the processing of unpleasant music (Fuentes-Sánchez et al., 2021a).

Additionally, our analysis showed an activation of the right hippocampus, both while listening to pleasant and unpleasant music. The role of the hippocampus on emotional processing has been met with mixed findings in the literature, with studies showing activations in that region while listening to unpleasant music (Koelsch et al., 2006; Mitterschiffthaler et al., 2007) but also to pleasant music (Koelsch et al., 2007, 2010; Trost et al., 2011). Despite these divergences, the hippocampus does seem to play some role in the processing of emotions (Koelsch, 2014, 2020), which is in line with our findings from this study. In fact, our results support the hypotheses proposed by Koelsch (2014, 2020), highlighting that the hippocampus as an important region for the generation of pleasant emotions (Koelsch et al., 2010; Koelsch, 2020). More specifically, in his last meta-analysis, Koelsch (2020) claimed that hippocampus activation is strongly associated with attachment-related emotions and social bonding elicited by music. In our analysis, pleasant music encompasses different emotions such as joy, pleasantness, wonder, tenderness or liking, emotions that have been demonstrated to activate regions such as the prefrontal cortex or the insula, which are brain areas related with social bonding (Greenberg et al., 2021). Therefore, these results suggest that music listening and, particularly listening to pleasant music, could provide an effective tool to facilitate social connection; as such, it could represent an effective intervention to social isolation, which affects a large and rapidly increasing percentage of the population, especially in the elderly (Fakoya et al., 2020).

Finally, our findings showed that the parahippocampal gyrus revealed activation during both pleasant and unpleasant emotions but with diverging laterality: While processing of pleasant emotions predominantly activated the right-sided parahippocampal gyrus, the processing of unpleasant emotions evoked this region bilaterally. The activation of the parahippocampal gyrus has been typically associated with the recognition of emotions and retrieval of strong emotional memory contents (Blood et al., 1999; Koelsch et al., 2006). Therefore, findings obtained in this work may demonstrate that the parahippocampal gyrus is involved in the recognition of music emotions, independent of their affective valence, in contrast to previous neuroimaging studies that associated the involvement of this regions in networks responsive to specifically unpleasant emotions (Blood et al., 1999; Koelsch et al., 2006). It should be mentioned that the valence lateralization obtained here in the parahippocampal gyrus is incongruent with the valence lateralization hypothesis, which assumes an asymmetric preferential involvement of the left anterior cerebrum in positive or approach-related affect, and the right anterior cerebrum in negative or avoidance-related affect (e.g., Davidson, 1992). However, meta-analyses of neuroimaging studies on emotion processing in general (Wager et al., 2003), and emotional face processing (Fusar-Poli et al., 2009) in healthy subjects, revealed bilateral activations of the parahippocampal gyri across valence conditions.

4.3. Limitations and future directions

Some limitations of the current study should be considered. First, regarding the studies included in the meta-analysis, it is important to highlight the great variability between studies at both conceptual and methodological levels. At the conceptual level, some studies focused on the discrete approach of emotions, focusing on specific emotions such as happiness, fear or sadness (e.g., Aubé et al., 2015; Bogert et al., 2016; Brattico et al., 2011), whereas others studies focused on the dimensional theoretical approach, considering broader dimensions such as pleasantness/unpleasantness or arousal (e.g., Bravo et al., 2020; Chapin et al., 2010; Flores-Gutiérrez et al., 2007). At the methodological level, studies selected for this meta-analysis presented different types of stimuli (e.g., instrumental music, film music, popular music, dissonant/consonant music), as well as different durations of music excerpts, ranging between 2 seconds and more than 1 minute. These methodological divergences could make the replicability and the interpretation of the data more difficult. Related to this issue, the analyzed studies in this meta-analysis included healthy controls only and excluded clinical populations. However, between the healthy controls, some studies included both musicians and non-musicians (Matthews et al., 2020; Park et al., 2014; Zhou et al., 2022), which could also influence the results due to the impact of musicianship on neural correlates of music processing (Hyde et al., 2009; Palomar-García et al., 2017).

Secondly, another limitation of this meta-analysis is related to the sub-analyses. Particularly, within each analysis we included studies from both theoretical approaches without considering the divergence between them. For example, in the analysis of brain activity evoked by pleasant music, we included contrasts such as "joy > fear," "like > dislike," "major > minor," "pleasant > unpleasant." To this respect, future meta-analyses in the field should differentiate between discrete and dimensional approaches (e.g., investigating whether there are differences between "joy > fear" and "pleasant > unpleasant" in the neural correlates). Likewise, within the sub-analyses of pleasant and unpleasant processing we considered emotions varying in terms of hedonic valence but also in arousal, which could be a limitation of this study and should be considered in future research. For example, within the label of unpleasant emotions we considered studies focused on fear or sadness, but both emotions differ both in terms of valence and arousal. Looking toward future meta-analyses, it could be interesting to investigate altered brain activations during music listening in patients suffering from disordered emotional reactivity, such as in depression or anxiety.

5. Conclusions

The present study showed significant clusters of activations in numerous cortical and subcortical regions during music-evoked emotions, replicating results obtained in prior meta-analyses (Koelsch, 2014, 2020). Likewise, this meta-analysis was the first to systematically compare the neural correlates of pleasant and unpleasant emotions induced by music stimuli. The results obtained in this study showed that pleasant and unpleasant music specifically activated different brain regions. Particularly, unpleasant music activated the amygdala and the anterior cingulate cortex, whereas pleasant music activated the striatum and the thalamus. Taken together, these findings provide useful information about the brain areas involved in music listening. Moreover, from a more clinical viewpoint, these results could open the avenue for the development of standardized protocols using music as a tool to induce and regulate emotions, especially in affective or neurodegenerative disorders characterized by anomalies in emotional processing, reactivity, and regulation, such as depression, anxiety or dementia.

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TABLES

Table 1. Contrasts included in the meta-analysis

Study	Modality	Nr. of Subjects	Con

Aubé et al., 2015	fMRI	47	Fear
			Hap
			Mus
Altenmüller et al., 2014	fMRI	18	Stim
Berthold-Losleben et al., 2018	fMRI	32 (16 females)	Posi
Bogert et al., 2016	fMRI	56 (34 females)	Mair
Brattico et al., 2011	fMRI	15 (6 females)	Sad
			Hap
Brattico et al., 2016	fMRI	29 (15 females)	Like
			Disli
			Hap
			Sad
Bravo et al., 2020	fMRI	16 (8 females)	Cons
			Diss
			Diss
Blood et al., 1999	PET	10 (5 females)	Posi
			Nega
			Posi
			Nega
Blood & Zatorre, 2001	fMRI	10 (5 females)	Posi
			Nega
			Incr
			Decr
			Posi
			Nega
			Posi
			Nega
Chapin et al., 2010	fMRI	14 (9 females)	Emo
			Emo
Daly et al., 2019	fMRI	21	Gene
			Gene
			Clas
			Clas
Engel et al., 2022	fMRI	21	Sam
Flores-Gutiérrez et al., 2007	fMRI	6	Plea
			Unp
			Exci
			Calr
Keller et al., 2013	fMRI	21	Mus
Koelsch & Skouras, 2014	fMRI	20	Joy
Koelsch et al., 2021	fMRI	24 (13 females)	Joy
Koelsch et al., 2022	fMRI	33	Posi
			Func
Koelsch et al., 2013	fMRI	18	Joy
			Fear
			Inter
			Emo
Koelsch et al., 2018	fMRI	24	GLM
			GLM
			GLM
			GLM

			ECM
			ECM
			ECM
			ECM
			PPI
			PPI
			PPI
Lepping et al., 2016	fMRI	20	Posi
			Nega
Menon & Levitin, 2005	fMRI	13 (7 females)	Scra
Mueller et al., 2011	fMRI	20 (7 females)	Loca
Mueller et al., 2015	fMRI	23 (13 females)	Corr
Okuya et al., 2017	fMRI	20 (2 females)	Hap
			Sad
			Fear
Salimpoor et al., 2013	fMRI	19 (10 females)	Mus
			Mus
			Emo
Tabei, 2015	fMRI	17 (10 females)	Felt
Trost et al., 2012	fMRI	16 (9 females)	Mus
			Corr
			Corr
			Corr
			Corr
			Corr
			Corr
			Corr
			Corr
Zhang et al., 2012	PET	10 males	Decr
			Incr
Koelsch et al., 2006	fMRI	11 (5 females)	Unp
			Plea
Sakurai et al., 2021	fMRI	30	Liste
Kornysheva et al., 2010	fMRI	18	Beau
Lehne et al., 2014	fMRI	25	Posi
			Tens
			Tens
Martínez-Molina et al., 2016	fMRI	45	Mus
Matthews et al., 2020	fMRI	54	Med
Mizuno & Sugishita, 2007	fMRI	18	Majo
			Mino
			Majo
			Mino
Park et al., 2013	fMRI	12	Hap
			Fear
Petrini et al., 2011	fMRI	16	Aud
Plailly et al., 2007	fMRI	13	Fam
			Unfa
Shany et al., 2019	fMRI	40 (for fMRI 31 in Ligeti; 28 in Glass, and 28 in Mussorgsky)	Mus
Sievers et al., 2021	fMRI	20 (11 females)	Mus
Skouras et al., 2014	fMRI	32	Joy

			Joy
Taruffi et al., 2021	fMRI	24	Emp
Wong et al., 2011	fMRI	22	Inte
			Con
Zhou et al., 2022	fMRI	41	Regi
			Regi
Demorest et al., 2010	fMRI	16 (8 females)	Cult
			Cult
Guo et al., 2021	fMRI	49	Chin
			Chin
			Wes
			Wes
Jeong et al., 2011	fMRI	15	Hap
			Sad
Khalfa et al., 2005	fMRI	13 (5 females)	Mino
			Mod
Kim et al., 2017	fMRI	23 (13 females)	Com
			Com
			Inte
Kim et al., 2019	fMRI	Experiment I 16 (14 females)	Part
			Part
			Part
			Part
			Join
			Inte
Kim et al., 2019	fMRI	23 (13 females, experiment II)	Part
			Part
			Part
			Part
			Join
			Inte
			PPI
Kleipzig et al., 2020	fMRI	16 (12 females)	Mus
			Mus
Liu et al., 2018	fMRI	48 (25 females)	Fast
			Med
Mitterschiffhaler et al., 2007	fMRI	16 (10 females)	Hap
			Sad
			Sad
Oetken et al., 2017	fMRI	20 (11 females)	Mus
Park et al., 2014	fMRI	24	Simi
Sachs et al., 2020	fMRI	40 (21 females)	Who
Salimpoor et al., 2011	PET and fMRI	10	PET
			fMR
Singer et al., 2016	fMRI	29 for Ligeti; 26 for Glass	Dyn
Suzuki et al., 2008	PET	13	Beau
			Ugly
			Mino
Taruffi et al., 2017	fMRI	24 (12 females)	ECM
			ECM
Mutschler et al., 2010	fMRI	19	Pian

Koelsch et al., 2008	fMRI	20 (10 females)	Irreg

Note : In those cases where the number of women was not included in the article, the number is not included in this table either.

Table 2. Peak coordinates and anatomical structures activated by listening to music

Cluster	**Brain Region**	**ALE**	**Z - Value**	**x**	**y**	**z**	**Brodmann Area**
1	L Superior Temporal Gyrus	0.078	8.4	-50	-18	4	22
	L Superior Temporal Gyrus	0.073	8.3	-50	-12	-2	22
	L Transverse Temporal Gyrus	0.047	6.0	-40	-28	12	41
	L Superior Temporal Gyrus	0.045	5.7	-60	-38	14	22
	L Supramarginal Gyrus	0.024	3.4	-42	-4	-18	21
2	R Superior Temporal Gyrus	0.081	9.0	52	-18	6	13
	R Superior Temporal Gyrus	0.053	6.4	56	-2	-4	22
3	R Amygdala	0.071	8.0	20	-8	-14	-
	R Caudate	0.044	5.7	12	6	0	-
	R Putamen	0.038	5.0	28	12	10	-
	R Parahippocampal Gyrus	0.034	4.6	14	-26	-8	-
	R Substantia Nigra	0.026	3.6	4	-34	-12	-
	L Thalamus	0.025	3.5	-6	-30	-4	-
4	L Amygdala	0.055	6.9	-22	-12	-18	-
	L Parahippocampal Gyrus	0.045	5.7	-26	-20	-14	28
	L Lentiform Nucleus	0.029	4.0	-20	-2	6	-
	L Lentiform Nucleus	0.027	3.8	-18	-2	0	-
	L Caudate	0.026	3.6	-16	0	14	-
5	L Caudate	0.046	5.8	-12	10	-2	-
6	L Insula	0.034	4.6	-34	4	12	13
	L Claustrum	0.031	4.2	-30	14	12	-
	L Insula	0.024	3.4	-36	22	12	13
7	L Cingulate Gyrus	0.030	4.1	2	20	36	32
	L Cingulate Gyrus	0.029	4.0	0	14	40	32
8	R Anterior Cingulate	0.046	5.9	6	52	-8	-
9	L Anterior Cingulate	0.035	4.7	-2	36	-10	24

Table 3. Peak coordinates and anatomical structures while listening to unpleasant > pleasant music

Cluster	Brain Region	ALE	Z - Value	x	y	z	Brodmann Area
1	R Amygdala	0.026	5.7	20	-6	-16	-
2	L Anterior Cingulate	0.022	5.1	-2	36	-8	24
3	L Parahippocampal Gyrus	0.020	4.8	-20	-14	-18	28
4	R Anterior Cingulate	0.024	5.5	6	52	-6	32
5	R Parahippocampal Gyrus.	0.016	4.1	22	-26	-16	35
	R Hippocampus	0.015	3.9	30	-24	-18	-

Table 4. Peak coordinates and anatomical structures while listening to pleasant > unpleasant music

Cluster	**Brain Region**	**ALE**	**Z - Value**	**x**	**y**	**z**	**Brodmann Area**
1	L Superior Temporal Gyrus	0.029	5.8	-52	-18	8	22

	L Superior Temporal Gyrus	0.027	5.4	-60	-12	6	22
2	R Superior Temporal Gyrus	0.039	7.0	50	-20	8	13
3	R Parahippocampal Gyrus	0.019	4.3	24	-14	-16	28
	R Hippocampus	0.018	4.1	32	-18	-16	-
4	R Caudate	0.024	5.0	12	8	-2	-
5	L Thalamus	0.020	4.4	2	-18	6	-
6	R Lentiform Nucleus	0.022	4.7	28	12	8	-

FOOTNOTES

We included some studies that use clinical populations, but in the ALE analysis we only considered the control group (healthy population).

FIGURE CAPTION

Figure 1. Flow diagram of article selection following PRISMA guidelines.

Figure 2. Flowchart illustrating all important steps of the meta-analysis following the guidelines by Mueller et al., 2018.

Figure 3. Results from ALE meta-analysis of brain regions active during listening to unpleasant and pleasant music. Radiological convention in coronal slices: R (right) and L (left). Gradient of the activation peaks represented according to their ALE value.

Figure 4. Results from ALE meta-analysis of brain regions active during listening to pleasant (compared to unpleasant) music (green) and unpleasant (compared to pleasant) music (red). Radiological convention in coronal slices: R (right) and L (left). Gradient of the activation peaks represented according to their ALE value.

FUNDING

The author(s) disclosed receipt of the following financial support for the research, authorship and/or publication of this article: This work was supported by the Universitat Jaume I [grant number UJI-B2019-34], AEI [grant number PID2020-114633GB-100] and by the University of Münster [postdoc grant for NF-S].

We acknowledge support from the Open Access Publication Fund of the University of Münster.

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