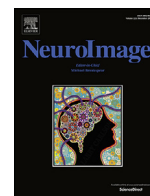


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A coordinate-based meta-analysis of music-evoked emotions

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ABSTRACT

Since the publication of the first neuroscience study investigating emotion with music about two decades ago, the number of functional neuroimaging studies published on this topic has increased each year. This research interest is in part due to the ubiquity of music across cultures, and to music's power to evoke a diverse range of intensely felt emotions. To support a better understanding of the brain correlates of music-evoked emotions this article reports a coordinate-based meta-analysis of neuroimaging studies ($n = 47$ studies with $n = 944$ subjects). The studies employed a range of diverse experimental approaches (e.g., using music to evoke joy, sadness, fear, tension, frissons, surprise, unpleasantness, or feelings of beauty). The results of an activation likelihood estimation (ALE) indicate large clusters in a range of structures, including amygdala, anterior hippocampus, auditory cortex, and numerous structures of the reward network (ventral and dorsal striatum, anterior cingulate cortex, orbitofrontal cortex, secondary somatosensory cortex). The results underline the rewarding nature of music, the role of the auditory cortex as an emotional hub, and the role of the hippocampus in attachment-related emotions and social bonding.

1. Introduction

Music appears to be part of human nature, as evidenced by the observation that every known culture has music. In most musical traditions, the fundamental structural principles of music are tactus (or "beat") and scale (i.e., an organization of pitches in ascending or descending order). Tactus and scale immediately afford that several individuals produce sounds together in synchrony and harmony. Engaging in the synchronization of movements while making music promotes cooperation and is a potent elicitor of social bonding, associated with emotions that are often intensely pleasurable and moving. Likewise, merely listening to music can elicit strong emotions, and using music to regulate emotions (e.g. to reduce stress and to promote positive emotions) has been reported to be the most important personal use of music across different cultures (Boer & Fischer, 2012).

The power to evoke emotions makes music a highly valuable tool for the investigation of emotions. In fact, given the ubiquity of music across cultures, and thus most probably throughout human history, our understanding of emotions would remain incomplete without a proper understanding of music-evoked emotions (Koelsch, 2018). Neuroscience has used music to investigate emotions for about two decades now, and the number of studies published per year on this topic has increased constantly. These studies have provided new insights into the neural correlates of human emotions: A previous meta-analysis (Koelsch, 2014) revealed two main findings: *First*, brain structures involved in music-

evoked emotions with positive valence comprised the entire reward network, consisting of the ventral striatum (including the nucleus accumbens, NAc), dorsal striatum (head of the caudate nucleus), amygdala, anterior cingulate cortex (ACC), orbitofrontal cortex (OFC), insula, mediodorsal thalamus (MD), and secondary somatosensory cortex (SII). This network was also observed in a meta-analysis on monetary, food, and erotic rewards (Sescousse et al., 2013). Thus, the observation of that network in studies on music and emotion underlined the pleasurable nature of music, and showed that music can activate the entire brain circuitry involved in the affective processing of primary and secondary rewards. *Second*, in addition to the reward network, the anterior hippocampus was implicated in music-evoked emotions (bilaterally). This stays in contrast to functional neuroimaging studies on reward (Sescousse et al., 2013), and indicated that music-evoked emotions are not only related to rewards. Instead, it was suggested that the anterior hippocampus plays a role in attachment-related emotions associated with the promotion of social bonding with music (Koelsch, 2014; Koelsch et al., 2015). However, given the dominance of research investigating the hippocampus with regard to cognitive functions (such as learning, memory, and spatial navigation), rather than emotions, a major question of the current meta-analysis is whether that result would be corroborated with a more substantial number of studies.

To date, only one meta-analysis on music-evoked emotions is available (Koelsch, 2014). However, the number of studies published since then on this topic is larger than the number of studies included in that

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meta-analysis. This shows the great interest in the field, and motivates a new meta-analysis. Moreover, since then, two errors in the software used to compute that meta-analysis (GingerALE) have been corrected (Eickhoff et al., 2017). The current meta-analysis thus had the aim to test the hypotheses that brain structures involved in music-evoked emotions include (i) the reward network (with ventral and dorsal striatum, amygdala, ACC, OFC, insula, MD, and SII), as well as (ii) the anterior hippocampal formation.

2. Methods

A coordinate-based activation likelihood estimation (ALE) meta-analysis was computed. ALE determines the likelihood of a voxel for being a source of activation within a set of studies across the whole brain. The analysis was performed following the ten methodological recommendations by Müller et al., 2018; see also the step-by-step flowchart in Fig. 1).

2.1. Search method and study selection

A search using the search term: {"music" AND "emotion" AND ["fMRI" OR "functional Magnetic Resonance Imaging" OR "PET" OR "Positron Emission Tomography"]} with no date boundaries (cutoff date: 6th September 2019) was performed with the following databases: PubMed (www.ncbi.nlm.nih.gov/pubmed), ISI web of knowledge (Claviate Analytics, Philadelphia, PA, U.S.A.), and Scopus (Elsevier, Amsterdam, Netherlands). This search returned 199 studies in ISI, 224 studies in Scopus, and 196 in PubMed.

Criteria for study inclusion were whole-brain analysis, provision of stereotaxic coordinates (MNI or Talairach space), use of a music stimulus, and at least one measure assessing the subjective feeling component evoked by that stimulus. None of the contrasts included music with lyrics (so that any observed effects can be attributed to music, and not merely to the lyrics of songs), and none of the contrasts included a comparison of music against a non-auditory (e.g., rest) condition (so that any effects observed in the auditory cortex cannot merely be due to the contrast of sound with no-sound). In addition, an inclusion criterion was added for studies using a decoding analysis: Even if such studies did not include a direct comparison of music against music, they were included if they included a crossmodal decoding or classification for an emotion parameter (such as valence). The reason is that such results cannot merely be due to the contrast of sound with no-sound. Finally, studies were excluded if subjects (or a subgroup of subjects) were part of another study, to avoid that inclusion of multiple contrasts from the same set of subjects creates dependence across contrast maps.

Functional connectivity results were included only if they were modulated by music-evoked emotions (i.e., only PPI- or emotion-specific FC results were included). Contrasts were included independent of their direction (e.g., both positive and negative correlations with chills intensity), independent of their emotion (e.g., joy, fear, sadness, tension), and independent of the neuroimaging technique (e.g., fMRI, dopamine-specific PET) because the current meta-analysis aimed at identifying brain structures that show activity changes during music-evoked emotions in general, rather than brain structures that show activation or deactivation (or availability of a specific neurotransmitter) for a specific emotion. This approach was motivated by the previous meta-analysis on this topic (Koelsch, 2014), and justified by the fact that the structures of the greater limbic system often have complex receptor-architectonics, with different inhibitory and excitatory receptors being colocalized within the same voxel. Hence, the same brain structure might show signal changes due to inhibitory synaptic processes in one emotion condition, and due to excitatory processes in another. Emotion-specific meta-analyses might be computed in the future, when more studies on particular music-evoked emotions are available.

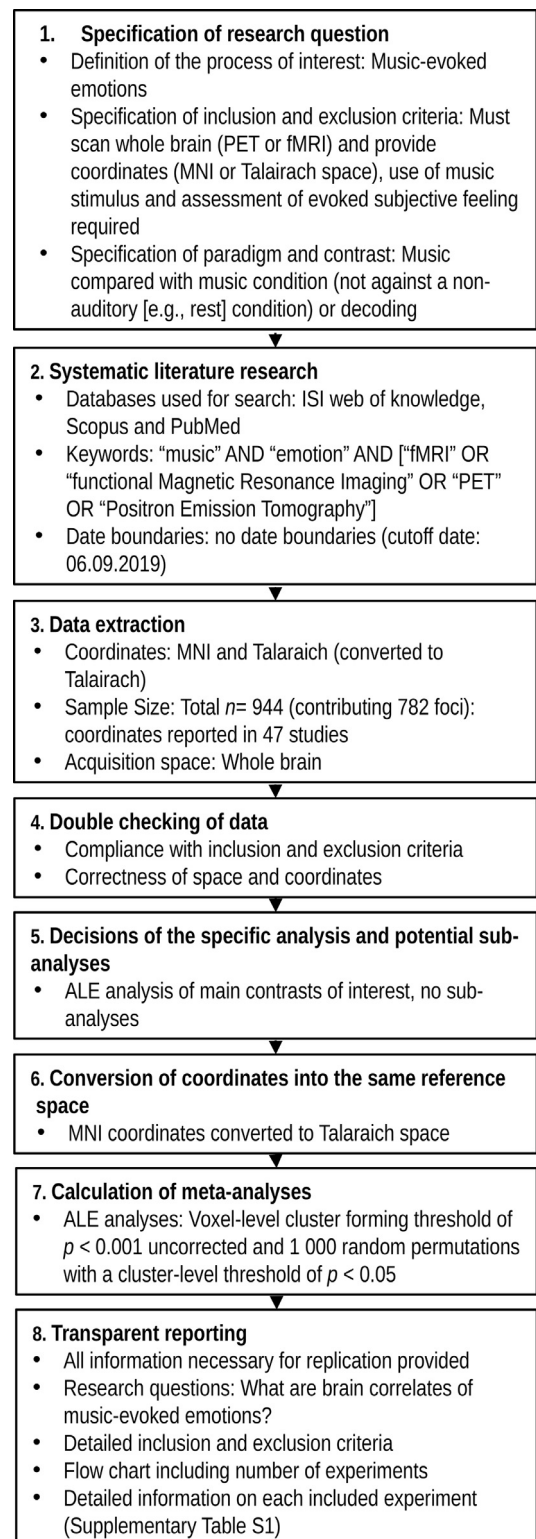


Fig. 1. Meta-analysis flowchart. Flowchart diagram as recommended in the best practice guidelines for conducting neuroimaging meta-analyses by Müller et al. (2018), reporting all important steps of the meta-analysis.

2.2. Data analysis

For the selected studies and contrasts, information was obtained about reference space, sample size, and coordinates of activations. This information was double-checked by an independent researcher, who also double-checked compatibility of studies and contrasts with inclu-

sion and exclusion criteria. All coordinates were transformed into Talairach space (where necessary) using the ICBM (International Consortium for Brain Mapping) transformation (Lancaster et al., 2007). Coordinates of contrasts were prepared for a pooled analysis, i.e., the coordinates from all relevant contrasts of one study with one sample were entered as one experiment (Müller et al., 2018). Then, a random-effects ALE analysis was performed using GingerALE 3.0.2 (Eickhoff et al., 2017; Eickhoff et al., 2009; Eickhoff et al., 2012; Laird et al., 2005; Turkeltaub et al., 2012). A cluster-level FWE correction was applied with a cluster-level threshold of $p < 0.05$ and a voxel-level cluster forming threshold of $p < 0.001$ (1000 thresholding permutations), as recommended by Müller et al. (2018). The resulting peak coordinates are reported in Talairach space, but to assess anatomical probabilities, the coordinates were transformed to MNI space using the tal2icbm transformation (Lancaster et al., 2007) and then entered in the Anatomy toolbox v. 2.2c for SPM12 (Eickhoff et al., 2005).

3. Results

Study and contrast selection resulted in 47 experiments (Table 1) with 944 subjects and 782 foci. The ALE results of these experiments (FWE-corrected at the cluster-level with $p < 0.05$ and a voxel-level cluster forming threshold of $p < 0.001$, see Methods) indicated eight clusters with 23 peaks (Table 2; the 3D-images containing the ALE results are provided in the Supplementary Materials). The contrasts contributing to each of the clusters are listed in Supplementary Table S1.

The largest cluster (Cluster #1) included peaks in the right anterior hippocampus and amygdala (Fig. 2a), as well as the ventral striatum (including the nucleus accumbens) and the dorsal striatum bilaterally (head of the nucleus caudatus, Fig. 2b). This cluster also encompassed the right bed nucleus of the stria terminalis (BNST) and the ventral pallidum bilaterally (although no separate peaks were indicated within these structures). Clusters #2 and #3 encompassed the left and right superior temporal gyrus (STG), with local maxima in the transverse gyri, corresponding to primary auditory cortex bilaterally (Fig. 2c & d). In both hemispheres, these clusters also encompassed voxels (and in the left hemisphere a separate peak) located superiorly of the lateral sulcus in the parietal operculum (POP), corresponding to secondary somatosensory cortex (SII). Cluster #4 comprised of peaks in the left amygdala and the adjacent anterior hippocampal formation (Fig. 2a). Clusters #5, #6, and #7 (Fig. 2e) revealed peaks in the medial orbitofrontal cortex (ventromedial prefrontal cortex), the frontopolar (area Fp2 / area 10) and anterior cingulate cortex (areas p24, p32 and s32 according to Palomero-Gallagher et al., 2019), as well as peaks at the border between the middle and posterior cingulate cortex (areas 24d and 23c according to Palomero-Gallagher et al., 2009). Finally, Cluster #8 had a peak in the inferior colliculus, and extended to the medial geniculate body (MGB).

4. Discussion

The present ALE analysis indicates large clusters encompassing the amygdala and the anterior hippocampus, numerous structures of the reward network (ventral and dorsal striatum, anterior cingulate cortex, orbitofrontal cortex, secondary somatosensory cortex), and the auditory cortex. This corroborates the prominent role of these structures in music-evoked emotions.

4.1. Hippocampus

While the role of other limbic- and paralimbic structures in emotions is well established, the hippocampal formation is usually discussed with regard to its cognitive functions such as learning, memory, spatial orientation, navigation and exploration. However, the contrasts contributing to the hippocampal clusters (see Supplementary Table S1) reveal that such cognitive functions alone cannot explain the hippocampal activations. For example, increasing reward

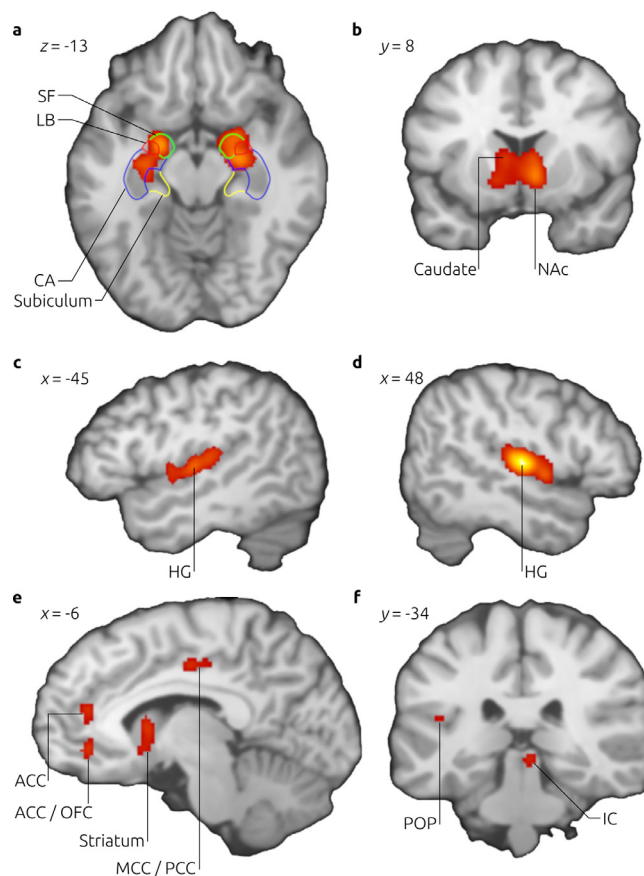


Fig. 2. ALE meta-analysis results. Clusters of significant activity changes were found bilaterally in the amygdala (including both the superficial amygdala (SF) and the laterobasal amygdala (LB)) and the cornu ammonis (CA) of the hippocampus (panel a), the ventral striatum (including the nucleus accumbens (NAC)) and the dorsal striatum (caudate nucleus) bilaterally (panel b), auditory cortex including and surrounding Heschl's gyrus (HG) in the left (panel c) and right (panel d) hemisphere, medial orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), and middle / posterior cingulate cortex (MCC/PCC) in the medial wall (panel e), and in the right inferior colliculus (IC, panel f). The cluster in the left auditory cortex extended into the parietal operculum (POP), where it showed a separate local maximum (panel f). Note that, owing to the different experimental paradigms used in these studies, limbic and paralimbic brain areas that have not been indicated in this meta-analysis may nevertheless contribute to music-evoked emotions. Outlines of anatomical structures in panel a are adapted from probability maps according to Eickhoff et al. (2005); the SF is shown in green, the LB is shown in red, the CA is shown in blue and the subiculum is shown in yellow. Coordinates refer to Talairach space, images are shown in neurological convention.

value of music evokes increasing functional connectivity between the (right) hippocampus and the (right) NAC, even when the music is controlled for familiarity (Salimpoor et al., 2013). One study (Mitterschiffthaler et al., 2007) used sad-sounding music, and sad-sounding music often evokes nostalgia (Vuoskoski et al., 2012; Taruffi & Koelsch, 2014; Eerola et al., 2016), and thus likely also autobiographical memory. However, that study (Mitterschiffthaler et al., 2007) observed activation in the right hippocampus only, while autobiographical memory is associated with a clear left-hemispheric lateralization of hippocampus activation (Spreng et al., 2009; Pehrs et al., 2018). Notably, no such left-lateralization is apparent in the present data (if anything, cluster size and z-values were larger in the right hippocampus). Thus, it is unlikely that the hippocampal clusters observed in the present results are associated merely with autobiographical memory or familiarity.

Table 1
Studies and contrasts included in the meta-analysis.

Study	Modality	Nr. of subjects	Contrast	Nr. of foci
Blood et al., 1999	PET	10	Positive correlations with dissonance	3
			Negative correlations with dissonance	5
Blood & Zatorre, 2001	PET	10	Positive correlations with chills intensity	10
			Negative correlations with chills intensity	7
			Increases in rCBF for subject-selected music minus control music	10
			Decreases in rCBF for subject-selected music minus control music	7
			Positive correlations with pleasantness	9
			Negative correlations with ratings of pleasantness	6
			Positive correlations with ratings of emotional intensity	8
			Negative correlations with ratings of emotional intensity	7
Menon & Levitin, 2005	fMRI	13	Unpleasant > pleasant	3
Khalfa et al., 2005	fMRI	13	Minor - major	3
Koelsch et al., 2006	fMRI	11	Pleasant > unpleasant	3
			Unpleasant > pleasant	3
Mitterschiffthaler et al., 2007	fMRI	16	Happy > neutral	11
			Sad > neutral	7
Eldar et al., 2007	fMRI	14	Negative combination effect	10
			Positive combination effect	11
Mizuno & Sugishita, 2007	fMRI	18	Major - neutral	8
			Minor - neutral	5
			Major - minor	6
			Minor - major	3
Koelsch et al., 2008	fMRI	11	Irregular > regular	4
Suzuki et al., 2008	PET	13	Consonance vs. dissonance	1
			Dissonance vs. consonance	3
			Minor vs. major	1
Green et al., 2008	fMRI	21	Minor - major	4
Chapin et al., 2010	fMRI	13	Emotional arousal	2
			Emotional arousal X experience	9
Salimpoor et al., 2011	PET	10	Pleasure - neutral	7
	fMRI	10	Pleasure > neutral	2
Mueller et al., 2011	fMRI	20	Pleasant > unpleasant	7
Caria et al., 2011		14	Happy favorite music > happy standard	20
Brattico et al., 2011	fMRI	15	Sad > happy	3
			Happy > sad	3
Trost et al., 2012	fMRI	16	Positive correlations with arousal ratings	13
			Negative correlations with arousal ratings	3
			Positive correlations with valence ratings	11
			Negative correlations with valence ratings	3
Salimpoor et al., 2013	fMRI	19	Music purchased vs. music not purchased	8
			Emotion-specific functional connectivity (increase in reward value)	39
Koelsch et al., 2013	fMRI	18	Joy > fear	4
			Fear > joy	1
			Interaction contrast of emotion (joy vs. fear) X time	12
			Emotion-specific functional connectivity (joy > fear)	30
Lehne et al., 2014	fMRI	25	Positive correlation with tension	1
			Tension (versions with dynamics) > tension (versions without dynamics)	2
			Tension increase > tension decrease	8
Keller et al., 2013	fMRI	21	Music vs. scrambled music X trait anhedonia	12
Aust et al., 2013	fMRI	28	Pleasant > neutral	10
			Unpleasant > neutral	7
Altenmüller et al., 2014	fMRI	18	Positive pieces > less positive pieces	9
Koelsch & Skouras, 2014	fMRI	20	ECM contrast joy > fear	26
Gebauer et al., 2014	fMRI	39	ASD > NT: group difference for happy vs. sad music	3
			Main effect of emotional vs. neutral music	13
			Main effect of happy vs. sad music	11
Skouras et al., 2014	fMRI	16	Joy > fear	4
Trost et al., 2014	fMRI	18	Consonant vs. dissonant music epochs	7
Halko et al., 2015	fMRI	22	Parametric responses to expected value during Liked music as compared with disliked music	5
Mueller et al., 2015	fMRI	23	Correlation with pleasantness	16
Tabei, 2015	fMRI	17	Felt emotion > passive listening	3
McPherson et al., 2016	fMRI	12	Negative improvisation > positive improvisation	17
			Positive improvisation > negative improvisation	3
Brattico et al., 2016	fMRI	29	Like > dislike	26
Lepping et al., 2016	fMRI	20	Positive > negative valence	6
Bogert et al., 2016	fMRI	56	Main effect of emotion	7
Singer et al., 2016	fMRI	26	Dynamic common activation, parcels encompassed in network 10	37

(continued on next page)

Table 1 (continued)

Study	Modality	Nr. of subjects	Contrast	Nr. of foci
Huang et al., 2016	fMRI	18	Popular music > notes clip	12
Martinez-Molina et al., 2016	fMRI	45	Artistic music > notes clip	1
Okuya et al., 2017	fMRI	20	Pleasure ratings as a parametric effect	7
			Correlation between BOLD signals and felt happiness rating	
			Correlation between BOLD signals and felt sadness ratings	1
			Correlation between BOLD signals and felt fear ratings	19
Kim et al., 2017a	fMRI	20	Searchlight analysis based on between-modal valence differences	9
Oetken et al., 2017	fMRI	20	Musically induced mood (happy vs. sad vs. neutral) X self-evaluation vs. lexical decision making	4
Kim et al., 2017b	fMRI	23	Effect of dissonance	7
			Intersubject correlation between rating contrast and BOLD contrasts	1
			Common effect of dissonance	1
Taruffi et al., 2017	fMRI	24	ECM contrasts sad > happy	7
			ECM contrasts happy > sad	1
Freeman et al., 2017	fMRI	16	Main effect of task (music > scrambled music)	7
			Main effect of task (scrambled music > music)	4
			Music vs. scrambled music X cannabis without cannabidiol compared with placebo	7
Koelsch et al., 2018a	fMRI	24	GLM comparisons between emotion conditions (joy, fear, neutral)	12
			ECM comparisons between emotion conditions (joy, fear, neutral)	11
			PPI results with seeds in primary auditory cortex	18
			PPI results with seeds in planum polare	20
			PPI results with seeds in planum temporale	25
Liu et al., 2018	fMRI	48	Musician - non-musician	1
			Fast - slow	2
			Medium - slow	6
Berthold-Losleben et al., 2018	fMRI	32	Positive > neutral auditory stimulation	12
Daly et al., 2019	fMRI	21	BOLD co-variation with reported felt affect (but not with movement) during generated music listening tasks	19
			BOLD co-variation with reported felt affect (but not with movement) during classical music listening tasks	12

Abbreviations: ASD: Autism spectrum disorder; ECM: Eigenvector centrality mapping; GLM: General linear model; NT: Neurotypical; PPI: Psychophysiological interaction; rCBF: regional cerebral blood flow.

Table 2.

List of peak coordinates and anatomical structures.

Anatomical structure	Cluster nr.	Coordinate (Talairach)	z-value
R anterior hippocampus (CA2, 21%)	1	24 -14 -10	6.4
R amygdala		20 -4 -10	6.2
R ventral striatum / NAc		8 8 -2	5.7
R dorsal striatum / head of CN		8 4 6	5.5
L ventral striatum / NAc		-12 10 -4	4.4
L dorsal striatum / head of CN		-8 6 6	4.3
L STG / auditory cortex (TE 1.2, 49%)	2	-50 -6 2	6.1
L STG / auditory cortex (TE 1.0, 30%)		-48 -16 4	6.1
L parietal operculum / SII (OP1, 36%)		-42 -28 12	5.6
R STG / auditory cortex (TE 1.0, 39%)	3	48 -16 6	7.9
R STG / auditory cortex (TE 1.2, 53%)		50 -4 2	5.6
L amygdala	4	-18 -6 -12	6.9
L anterior hippocampus (CA2, 8%)		-28 -16 -10	5.3
L hippocampal formation (DG, 17%)		-26 -22 -10	5.1
Pre-genual ACC	5	-8 38 14	4.4
Area s32 (19%)		-8 38 -6	4.3
PCC (area 23c/d)	6	-2 -24 40	4.6
MCC (area 24)		-4 -16 38	4.2
Area Fp2 (67%)	7	6 48 2	4.7
Area p24		10 38 4	3.6
Area p32		6 36 -2	3.5
Inferior colliculus	8	6 -32 -8	4.2
Medial geniculate body		10 -28 -6	4.1

Abbreviations: CA: cornu ammonis; CN: caudate nucleus; DG: dentate gyrus; L: left; MCC: middle cingulate cortex; NAc: nucleus accumbens; PCC: posterior cingulate cortex; R: right; SII: secondary somatosensory cortex; STG: superior temporal gyrus. Where available, anatomical probabilities, as determined with the SPM Anatomy Toolbox (Eickhoff et al., 2005), are provided in brackets.

In animal research, the role of the hippocampus in emotion is well established. The ventral hippocampus in rodents (corresponding to the anterior hippocampus in humans) is implicated in anxiety and anxiety-related behaviors (e.g., lesions of the ventral hippocampus reduce expression of fear and have anxiolytic effects; [Bannerman et al., 2014](#); [Strange et al., 2014](#)). In addition, the ventral hippocampus projects to anterior and ventromedial hypothalamic nuclei which are involved in reproductive and social agonistic behaviors (in addition to their role in defensive responses; [Strange et al., 2014](#)). The hippocampus also projects to the paraventricular nucleus of the hypothalamus, which controls the release of oxytocin, a hormone critical for the development of maternal behavior and pair bonding ([Strange & Yebra, 2015](#)). Notably, in humans, oxytocin also appears to be released during singing in a choir ([Kreutz, 2014](#); [Keeler et al., 2015](#)). These findings point to the notion that the hippocampus, beyond its role in anxiety and fear-conditioning, plays a role in social bonding and associated attachment-related emotions. In humans, such emotions include joy, happiness, and being moved when social attachments are experienced, or sadness when social attachments are severed.

In research with humans, the notion that the hippocampus plays a role in emotions is still not common. Meta-analytic data and reviews on specific emotions do not find involvement of the hippocampus in fear ([Diekhof et al., 2011](#)), empathy for pain ([Shamay-Tsoory, 2011](#)), emotion regulation ([Etkin et al., 2015](#); [Frank et al., 2014](#)), cognitive reappraisal of emotion ([Buhle et al., 2014](#)), or reward ([Sescousse et al., 2013](#)). However, in a meta-analysis of neuroimaging studies on brain activation to emotional stimuli in general (independent of specific emotions), peaks in the bilateral hippocampi were observed for both negative and positive emotion stimuli ([Stevens & Hamann, 2012](#); [Lindquist et al., 2015](#)). Moreover, a meta-analytic review on the brain basis of emotion ([Lindquist et al., 2012](#)) reported increased activity in the right hippocampus for the perception of emotions (in face, body or voice), independent of emotional qualia, and in the left hippocampus when participants perceived fear or sadness. Thus, the finding that music evokes activity changes in both left and right hippocampus, associated with both positive and negative emotions (**Supplementary Table S1**), is well in agreement with animal research, and with two meta-analyses investigating emotion independent of specific emotions.

The scarcity of hippocampal activations in human emotion research, and thus the scarcity of information about the functional role of the hippocampus in emotions, may be due to a tendency in affective neuroscience to focus on individual emotions such as fear or reward, rather than emotions associated with social attachments and social bonding. Such emotions are easily elicited with music because music promotes synchronization of movements, and movement synchronization to a beat with other individuals facilitates social bonding, including increased mutual trust and cooperation ([Tarr et al., 2014](#)). At the same time, such synchronization is associated with positive emotional effects ([Tarr et al., 2014](#); [Trost et al., 2017](#)), and possibly with activation of the endogenous opioid system ([Tarr et al., 2014](#); [Bernatzky et al., 2011](#)), i.e. with release of endogenous opioids including endorphins. The emotional effects of the release of such opioids include pleasantness, relaxation, as well as reduction of stress, anxiety, and pain ([Bernatzky et al., 2011](#)). Endorphins also support behaviours associated with social bonding (such as laughter, play, and synchronized movement). The hippocampus produces endogenous opioids and releases them into several brain areas such as the NAc and other structures of the reward system ([Lathe, 2001](#)). In addition, the hippocampus can initiate the release of endorphins from the hypothalamus (a major production site of endogenous opioids; [Lathe, 2001](#)). Because experiments on music and emotion often involve synchronization (even if synchronization is covert, or unintentional), they are often also social bonding experiments. Therefore, it is tempting to speculate that the activity changes in the anterior hippocampus (as observed in the present meta-analysis) 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, as well as changes in hypothalamo-pituitary-adrenal axis activity ([Koelsch & Skouras, 2014](#); [Koelsch et al., 2016](#)). Given the scarce knowledge about the neural correlates of social bonding in humans, music thus appears to be a highly useful tool for a more systematic investigation of this topic, for example with regard to the capacity of music to facilitate the emergence of trust, sympathy, as well as compassion, and the role that the hippocampus plays in these emotions.

However, none of the studies included in the present meta-analysis assessed social bonding nor social attachment (let alone release of endogenous opioids or oxytocin), leaving room for several alternative explanations regarding the hippocampal clusters observed in the present results: (1) Although it is unlikely that these activations were purely due to autobiographical memory processes (as argued above), it is well possible that such processes nevertheless contributed, at least in part, to activity changes in the hippocampus. For example, it has been argued that music likely elicits emotional memories and, hence, activity in the hippocampus associated with memory retrieval ([Trost & Frühholz, 2015](#)). It is also possible that hippocampal activations reflect the encoding of the emotional experience elicited by the experimental musical stimulus itself, or the encoding of preferred musical stimuli. (2) Likewise, “episodic simulation”, e.g. inferring others’ mental states through simulation could have contributed to the (left) hippocampal clusters. For example, the hippocampus appears to be involved in episodic simulation during empathy ([Pehrs et al., 2018](#)), and the hippocampus has been suggested to play a facilitative role in the processing of emotions pertaining to others’ mental states, possibly associated with an “ongoing recall and/or prospective simulation as a means to generate and sustain the emotion” ([Immordino-Yang & Singh, 2013](#)). (3) Another interesting possibility is that hippocampal activations were in part associated with the exploration of the musical stimuli, similar to (right anterior) hippocampal activations during the exploration of visual displays ([Ryals et al., 2015](#)). Such processes likely involve neural loops including hippocampus, nucleus accumbens (NAc), globus pallidus, and the ventral tegmental area ([Shohamy & Adcock, 2010](#)), with the NAc motivating “epistemic foraging” ([Friston et al., 2017](#); [Cheung et al., 2019](#)). The NAc also motivates to resolve uncertainty (discussed in more detail in the next section), and the hippocampus has been implicated in the encoding of predictability during active inference ([Rigoli et al., 2019](#)), which involves recruitment of learned priors. Interestingly, a recent study showed that in a context of high predictability (i.e., when listeners are certain about their prediction for the next chord), harmonies elicit pleasure when they are surprising ([Cheung et al., 2019](#)). On the other hand, in a context of low predictability (i.e. high uncertainty) harmonies elicit pleasure when they are not surprising ([Cheung et al., 2019](#); [Gold et al., 2019b](#)). Such pleasure (emerging from an interaction between uncertainty and surprise) was reflected in activity changes in the anterior hippocampus bilaterally. Hence, future studies could also shed further light on the role of the hippocampus in the encoding of predictability, and in the generation of emotions elicited by the interaction between predictability and surprise.

4.2. Ventral striatum and pallidum

The present analysis yielded local maxima in both the left and the right ventral striatum (including the NAc) and the ventral pallidum bilaterally. Both NAc and ventral pallidum host “hedonic hotspots” ([Berridge et al., 2009](#)), and 8 out of 10 of the contrasts that contributed to the activations in these areas (**Supplementary Table S1**) used music stimuli associated with “positive valence” ([Trost et al., 2012](#)), “pleasantness” ([Menon & Levitin, 2005](#); [Keller et al., 2013](#); [Mueller et al., 2015](#)), “liking / wanting” ([Salimpoor et al., 2013](#)), “reward” ([Salimpoor et al., 2013](#)) and “chills” ([Blood & Zatorre, 2001](#)). Thus, the present results clearly underline that the rewarding nature of music is associated with

activity in the ventral striatum and ventral pallidum. Consistent with this notion, individuals with specific musical anhedonia show reduced activity in the NAc in response to music, along with decreased functional connectivity between the right auditory cortex and the NAc (Martinez-Molina et al., 2016). Moreover, in individuals with trait anhedonia music evokes reduced reactivity and connectivity of mesolimbic and paralimbic reward pathways (Keller et al., 2013).

NAc activation in response to music involves dopaminergic activity: dopamine availability increases in the ventral striatum during the experience of music-evoked chills (Salimpoor et al., 2011), and administration of levodopa (a dopamine precursor) increases the hedonic experience and music-related motivational responses (Ferreri et al., 2019). Interestingly, after administration of naltrexone, a μ -opioid antagonist, both positive and negative emotions to music are attenuated (Mallik et al., 2017), indicating that, in addition to dopamine, endogenous opioids are associated with experiencing emotions in music.

Notably, the NAc is part of an emotion network that processes reward and pleasure. This network, as reported by Sescousse et al. (2013), also includes the dorsal striatum, amygdala, orbitofrontal (ventromedial prefrontal) cortex, cingulate cortex, the medio-dorsal thalamus (MD), insular cortex, and secondary somatosensory cortex (SII). The present analysis indicated clusters in all of these structures except MD and insula. Thus, not only the ventral striatum, but the reward network at large is activated by music, underlining the role of music for pleasure. Interestingly, it has been claimed that the reward networks associated with money, food, and erotic rewards differ slightly from each other, owing to inherent differences between rewards and between the contexts in which these rewards are obtained (e.g., erotic rewards involving the extrastriate body area and the hypothalamus; Sescousse et al., 2013). Perhaps the reward network associated with music is specialized for social rewards, e.g. when NAc activity is driven by hippocampal innervation associated with social bonding. The idea that such a network for social rewards might include less activation of MD and insula compared to other reward networks is consistent with recent meta-analytic data showing that prosocial (altruistic) behaviour activates a reward network including the NAc, ACC, and OFC, but not MD and insula (Cutler & Campbell-Meiklejohn, 2019).

Finally, another interesting role of the nucleus accumbens in musical emotions is the motivation of epistemic foraging and obtaining epistemic value by resolving uncertainty. For example, NAc activation was observed for musical reward prediction errors (Gold et al., 2019a) and musical surprise (Shany et al., 2019). Interestingly, the NAc (along with the dorsal striatum) is activated during chords with high uncertainty (Cheung et al., 2019), i.e. when listeners are motivated to hear the next chord to resolve uncertainty, consistent with the role of the NAc in motivating behaviour aimed at obtaining rewards, and consistent with the notion of the role for dopamine in the encoding and control of precision of information that engenders action (Friston et al., 2012).

4.3. Amygdala

The contrasts contributing to the local maxima in the amygdala (Supplementary Table S1) evoked negative as well as positive emotions. Negative emotions included “fear” (Eldar et al., 2007; Okuya et al., 2017), “less pleasantness” (Blood & Zatorre, 2001), or “unpleasantness” (Koelsch et al., 2006), while positive emotions included “pleasantness” (Mueller et al., 2011; Mueller et al., 2015), and “joy” (Koelsch et al., 2013). This finding is compatible with the emerging view that the amygdala plays a role in both negative and positive emotions (Lindquist et al., 2015), owing to its role as an emotional coordination structure that (i) detects emotional signals from conspecifics (perhaps the superficial amygdaloid nuclei are specifically involved in this function; Bzdok et al., 2012), (ii) receives information about threats or potential rewards from other structures such as the thalamus, auditory cortex, hippocampus and OFC (especially in the laterobasal complex; LeDoux, 2000), (iii) initiates and terminates activity in different emotion systems (e.g., in the face

of threat, activity in pleasure networks is downregulated and activity in flight- or fight-systems upregulated), thereby (iv) coordinating neural activity in different emotion-structures and emotion-networks. This role of the amygdala as a “conductor of the emotion orchestra in the brain” (Koelsch et al., 2015) is compatible with its high functional and anatomical centrality (i.e., the amygdala has both functional and anatomical connections to several emotional hubs in the brain; Pessoa, 2018). Part of this role of the amygdala is the regulation of peripheral arousal, consistent with the well-established role of the central nucleus of the amygdala (which belongs to the centro-medial amygdaloid nuclei group) in arousal regulation (Singer et al., 2016; Bzdok et al., 2012). In addition to regulating arousal during music listening (Singer et al., 2016), amygdala activity appears to increase when musical events evoke a sudden increase in tension (Koelsch et al., 2008; Lehne et al., 2014). However, such events are often unexpected tones or chords, thus an interesting alternative explanation of these studies (Koelsch et al., 2008; Lehne et al., 2014) is that amygdala and hippocampus modulate the attentional gain in response to prediction errors (such as unexpected chords in Koelsch et al., 2018b).

4.4. Auditory cortex

Large clusters were also yielded in the auditory cortex. Several of the contrasts contributing to these clusters used acoustical features that differed between music stimuli as regressors of no interest, thus at least some of the activations were not simply due to acoustical differences (e.g., Koelsch et al., 2013; Koelsch & Skouras, 2014). This supports the idea that the auditory cortex plays an important role in emotions, beyond the traditional notion that sensory cortices have merely perceptual functions. This notion was already established in early work on emotion circuits in the brain, showing that fear conditioning to acoustic stimuli involves projections from the auditory cortex to the amygdala (LeDoux, 2000). On the other hand, increasing reward value of music (as measured by the amount of money participants were willing to spend on the music they heard) is correlated with increasing functional connectivity between the (right) auditory cortex and the ventral striatum/nucleus accumbens (Salimpoor et al., 2013). Functional connectivity between the auditory cortex and the nucleus accumbens is particularly strong in individuals with greater-than-average reward sensitivity to music, whereas individuals with *specific musical anhedonia* show reduced functional connectivity between these structures (Martinez-Molina et al., 2016). More recently, it was found that auditory core, belt, and parabelt regions have influential positions even within wider-ranging emotion networks, driving emotion-specific functional connectivity with a number of limbic/paralimbic regions, including (beyond the ventral striatum) OFC, ACC, parahippocampal cortex and insular cortex (Koelsch et al., 2018a).

Notably, other structures of the auditory pathway, particularly the inferior colliculus and the auditory thalamus, are also involved in emotional reactions to acoustic stimuli, which has led to the notion of an *auditory-limbic pathway* including the auditory brainstem and thalamus, the amygdala, and the auditory cortex (Strait et al., 2009; Koelsch, 2014). Besides the auditory cortex, the amygdala, and the thalamus (medial geniculate body), the present results also yield a meta-analytic activation of the (right) inferior colliculus (IC), thus showing large parts of the auditory-limbic pathway to be involved in music-evoked emotions. By virtue of its projections into the autonomic nervous system and the somatic motor system, the IC generates coordinated visceromotor activity in response to relatively simple acoustical features such as dissonance (see also activation of the IC in response to dissonance in the study by Kim et al., 2017b), and in response to biologically coded signals (such as affective vocalizations of conspecifics) as well as learned auditory signals with emotional valence (such as conditioned auditory stimuli; see e.g. Müller-Ribeiro et al., 2016).

4.5. Secondary somatosensory cortex

Interestingly, the present data also indicated a local maximum in the (left) secondary somatosensory cortex (SII). SII is located in the parietal operculum (POP), in four cytoarchitecturally separate fields that mainly cover the upper bank of the Sylvian fissure, extending medially into the superior-posterior insula, and laterally into the inferior parietal lobule (Eickhoff et al., 2006). Thus, activations of the superior-posterior insula in functional neuroimaging experiments are often labeled as insular activations (and activations of the superior bank of the posterior Sylvian fissure as auditory activations), rather than activations of SII. SII is sensitive for pain, touch, pressure, vibration, temperature, and vestibular information; it responds to various complex stimuli, including input from other sensory modalities (but not simply pure somatosensory stimuli) and, in contrast to primary somatosensory cortex, is also activated when viewing other people being touched (reviewed in Keysers et al., 2010). The POP has been suggested as the neural substrate of the subjective feeling of emotions, synthesizing information from limbic structures (such as hippocampus and MD), paralimbic structures (such as OFC and insula), and neocortical structures (such as primary somatosensory cortex) into an *emotion percept* (Koelsch et al., 2015). Thus, such an emotion percept is synthesized from intero-, extero-, and proprioceptive information (and can be modified by cognitive appraisal; reviewed in Koelsch et al., 2015). Future studies could be mindful of the fact that activations within the superior bank of the posterior Sylvian fissure, and of the outermost part of the posterior-superior insula, can be activations of SII associated with the representation of emotion percepts.

4.6. Limitations

A general limitation of coordinate-based meta-analyses is that only those activations can be detected which were elicited in previous studies; this depends on which emotions were investigated and which experimental paradigms were used. Thus, other experimental approaches might lead to a different meta-analytic activation pattern. However, the present results indicate brain structures that are activated reliably across studies, and if a structure does not occur in the present meta-analysis, this does not indicate that this structure cannot be activated by music-evoked emotions. For example, no cluster was observed in the (anterior) insula in the present meta-analysis, despite the well-established role of the insula in emotions, e.g. with regard to its interoceptive function (thus contributing to the feeling component of emotion) and its role in the regulation of autonomic activity. Correspondingly, previous studies on music-evoked emotions reported a correlation of regional cerebral blood flow in the insula with the intensity of chills (Blood & Zatorre, 2001), or increased blood oxygenation in the insula during music evoking feelings of “vitality” associated with high arousal and high valence (Trost et al., 2012). Perhaps no insular cluster was identified in the present meta-analysis because several of the other studies included in this analysis aimed at matching arousal levels between experimental conditions.

5. Conclusions

The present results show large clusters of significant activity changes bilaterally in the anterior hippocampal formation, the amygdala, the ventral and dorsal striatum, and the auditory cortex. The results are consistent with the main results of a previous meta-analysis (Koelsch, 2014), and indicate that hippocampal activations were not only due to cognitive, but rather emotional processes. It is suggested that these emotional processes in the hippocampus are associated with attachment-related emotions and social bonding promoted by music, in particular by motoric and emotional synchronization. Moreover, several structures of the reward network were observed, underlining the rewarding and thus pleasurable nature of music. Finally, large clusters were indicated in the auditory cortex, supporting the emerging role of the auditory cortex as

an emotional hub, beyond the traditional view that the auditory cortex merely accomplishes sensory processing. Future studies might test these hypotheses further, also using regions of interest as identified in this study (the 3D-images containing the ALE results are provided in the Supplementary Materials).

6. Credit author statement

A credit author statement does not apply because this is an article of a sole author.

7. Data availability statement

The 3D-images (NIFTI file format) containing the ALE results are provided in the Supplementary Materials. The data that support the findings of this study are available from the author upon reasonable request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117350.

References

- Altenmüller, E., Siggel, S., Mohammadi, B., Samii, A., Münte, T.F., 2014. Play it again, Sam: brain correlates of emotional music recognition. *Front. Psychol.* 5, 114.
- Aust, S., Filip, K., Koelsch, S., Grimm, S., Bajbouj, M., 2013. Music in depression: neural correlates of emotional experiences in remitted depression. *World J. Psychiatry* 3 (2), 8–17.
- Bannerman, D.M., Sprengel, R., Sanderson, D.J., McHugh, S.B., Rawlins, J.N.P., Monyer, H., Seeburg, P.H., 2014. Hippocampal synaptic plasticity, spatial memory and anxiety. *Nat. Rev. Neurosci.* 15 (3), 181–192.
- Bernatzky, G., Presch, M., Anderson, M., Panksepp, J., 2011. Emotional foundations of music as a non-pharmacological pain management tool in modern medicine. *Neurosci. Biobehav. Rev.* 35 (9), 1989–1999.
- Berridge, K.C., Robinson, T.E., Aldridge, J.W., 2009. Dissecting components of reward: liking, wanting, and learning. *Current Opin. Pharmacol.* 9 (1), 65–73.
- Berthold-Losleben, M., Habel, U., Brehl, A.-K., Freiherr, J., Losleben, K., Schneider, F., Amunts, K., Kohn, N., 2018. Implicit affective rivalry: A behavioral and fMRI study combining olfactory and auditory stimulation. *Front. Behav. Neurosci.* 12, 313.
- Blood, A.J., Zatorre, R., Bermudez, P., Evans, A.C., 1999. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nat. Neurosci.* 2 (4), 382–387.
- Blood, A.J., Zatorre, R.J., 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci.* 98 (20), 11818.
- Boer, D., Fischer, R., 2012. Towards a holistic model of functions of music listening across cultures: A culturally decentred qualitative approach. *Psychol. Music* 40 (2), 179–200.
- Bogert, B., Numminen-Kontti, T., Gold, B., Sams, M., Numminen, J., Burunat, I., Lampinen, J., Brattico, E., 2016. Hidden sources of joy, fear, and sadness: explicit versus implicit neural processing of musical emotions. *Neuropsychologia* 89, 393–402.
- Brattico, E., Alluri, V., Bogert, B., Jacobsen, T., Vartiainen, N., Nieminen, S., Tervaniemi, M., 2011. A functional MRI study of happy and sad emotions in music with and without lyrics. *Front. Psychol.* 2, 1–16.
- Brattico, E., Bogert, B., Alluri, V., Tervaniemi, M., Eerola, T., 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.
- Buhle, J.T., Silvers, J.A., Wager, T.D., Lopez, R., Onyemekwu, C., Kober, H., Weber, J., Ochsner, K.N., 2014. Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cereb. Cortex* 24 (11), 2981–2990.
- Bzdok, D., Laird, A.R., Zilles, K., Fox, P.T., Eickhoff, S.B., 2012. An investigation of the structural, connective, and functional subspecialization in the human amygdala. *Hum. Brain Mapp.* 34, 3247–3266.
- Caria, A., Venuti, P., de Falco, S., 2011. Functional and dysfunctional brain circuits underlying emotional processing of music in autism spectrum disorders. *Cereb. Cortex* 21 (12), 2838–2849.
- Chapin, H., Jantzen, K., Kelso, J.S., Steinberg, F., Large, E., 2010. Dynamic emotional and neural responses to music depend on performance expression and listener experience. *PLoS One* 5 (12), e13812.

- Cheung, V.K., Harrison, P.M., Meyer, L., Pearce, M.T., Haynes, J.-D., Koelsch, S., 2019. Uncertainty and surprise jointly predict musical pleasure and amygdala, hippocampus, and auditory cortex activity. *Current Biol.* 101, 364–369.
- Cutler, J., Campbell-Meiklejohn, D., 2019. A comparative fMRI meta-analysis of altruistic and strategic decisions to give. *NeuroImage* 184, 227–241.
- Daly, I., Williams, D., Hwang, F., Kirke, A., Miranda, E.R., Nasuto, S.J., 2019. Electroencephalography reflects the activity of sub-cortical brain regions during approach-withdrawal behaviour while listening to music. *Sci. Rep.* 9 (1), 9415.
- Diekhof, E.K., Geier, K., Falkai, P., Gruber, O., 2011. Fear is only as deep as the mind allows: a coordinate-based meta-analysis of neuroimaging studies on the regulation of negative affect. *NeuroImage* 58 (1), 275–285.
- Eerola, T., Vuoskoski, J.K., Kautiainen, H., 2016. Being moved by unfamiliar sad music is associated with high empathy. *Front. Psychol.* 7, 1176.
- Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. *NeuroImage* 59 (3), 2349–2361.
- Eickhoff, S.B., Laird, A.R., Fox, P.M., Lancaster, J.L., Fox, P.T., 2017. Implementation errors in the GingerALE software: description and recommendations. *Hum. Brain Mapp.* 38 (1), 7–11.
- Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Hum. Brain Mapp.* 30 (9), 2907–2926.
- Eickhoff, S.B., Schleicher, A., Zilles, K., Amunts, K., 2006. The human parietal operculum. I. cytoarchitectonic mapping of subdivisions. *Cereb. Cortex* 16 (2), 254.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage* 25 (4), 1325–1335.
- Eldar, E., Ganor, O., Admon, R., Bleich, A., Hendler, T., 2007. Feeling the real world: limbic response to music depends on related content. *Cereb. Cortex* 17 (12), 2828–2840.
- Etkin, A., Büchel, C., Gross, J.J., 2015. The neural bases of emotion regulation. *Nat. Rev. Neurosci.* 16 (11), 693.
- Ferreri, L., Mas-Herrero, E., Zatorre, R.J., Ripollés, P., Gomez-Andres, A., Alicart, H., Olivé, G., Marco-Pallarés, J., Antonijóan, R.M., Valle, M., et al., 2019. Dopamine modulates the reward experiences elicited by music. *Proc. Natl. Acad. Sci.* 116 (9), 3793–3798.
- Frank, D., Dewitt, M., Hudgens-Haney, M., Schaeffer, D., Ball, B., Schwarz, N., Hussein, A., Smart, L., Sabatinelli, D., 2014. Emotion regulation: quantitative meta-analysis of functional activation and deactivation. *Neurosci. Biobehav. Rev.* 45, 202–211.
- Freeman, T.P., Pope, R.A., Wall, M.B., Bisby, J.A., Luijten, M., Hindocha, C., Mokrysz, C., Lawn, W., Moss, A., Bloomfield, M.A., et al., 2017. Cannabis dampens the effects of music in brain regions sensitive to reward and emotion. *Int. J. Neuropsychopharmacol.* 21 (1), 21–32.
- Friston, K.J., Rosch, R., Parr, T., Price, C., Bowman, H., 2017. Deep temporal models and active inference. *Neurosci. Biobehav. Rev.* 77, 388–402.
- Friston, K.J., Shiner, T., FitzGerald, T., Galea, J.M., Adams, R., Brown, H., Dolan, R.J., Moran, R., Stephan, K.E., Bestmann, S., 2012. Dopamine, affordance and active inference. *PLoS Computat. Biol.* 8 (1), e1002327.
- Gebauer, L., Skewes, J., Westphael, G., Heaton, P., Vuust, P., 2014. Intact brain processing of musical emotions in autism spectrum disorder, but more cognitive load and arousal in happy vs. sad music. *Front. Neurosci.* 8.
- Gold, B.P., Mas-Herrero, E., Zeighami, Y., Benovoy, M., Dagher, A., Zatorre, R.J., 2019a. Musical reward prediction errors engage the nucleus accumbens and motivate learning. *Proc. Natl. Acad. Sci.* 116 (8), 3310–3315.
- Gold, B.P., Pearce, M.T., Mas-Herrero, E., Dagher, A., Zatorre, R.J., 2019b. Predictability and uncertainty in the pleasure of music: a reward for learning? *J. Neurosci.* (pp. 0428–19).
- Green, A.C., Bærentsen, K.B., Stødkilde-Jørgensen, H., Wallentin, M., Roepstorff, A., Vuust, P., 2008. Music in minor activates limbic structures: a relationship with dissonance? *Neuroreport* 19 (7), 711–715.
- Halko, M.-L., Mäkelä, T., Nummenmaa, L., Hlushchuk, Y., Schürmann, M., 2015. Hedonic context modulates risky choices and reward responses in amygdala and dorsal striatum. *J. Neurosci. Psychol. Econ.* 8 (2), 100.
- Huang, P., Huang, H., Luo, Q., Mo, L., 2016. The difference between aesthetic appreciation of artistic and popular music: Evidence from an fMRI study. *PLoS One* 11 (11), e0165377.
- Immordino-Yang, M.H., Singh, V., 2013. Hippocampal contributions to the processing of social emotions. *Hum. Brain Mapp.* 34 (4), 945–955.
- Keeler, J.R., Roth, E.A., Neuser, B.L., Spitsbergen, J.M., Waters, D.J.M., Vianney, J.-M., et al., 2015. The neurochemistry and social flow of singing: bonding and oxytocin. *Front. Hum. Neurosci.* 9, 518.
- Keller, J., Young, C.B., Kelley, E., Prater, K., Levitin, D.J., Menon, V., 2013. Trait anhedonia is associated with reduced reactivity and connectivity of mesolimbic and paralimbic reward pathways. *J. Psychiatric Res.* 47 (10), 1319–1328.
- Keysers, C., Kaas, J.H., Gazzola, V., 2010. Somatosensation in social perception. *Nat. Rev. Neurosci.* 11 (6), 417–428.
- Khalifa, S., Schon, D., Anton, J.L., Liégeois-Chauvel, C., 2005. Brain regions involved in the recognition of happiness and sadness in music. *Neuroreport* 16 (18), 1981–1984.
- Kim, J., Shinkareva, S.V., Wedell, D.H., 2017a. Representations of modality-general valence for videos and music derived from fMRI data. *NeuroImage* 148, 42–54.
- Kim, S.-G., Lepsien, J., Fritz, T.H., Mildner, T., Mueller, K., 2017b. Dissonance encoding in human inferior colliculus covaries with individual differences in dislike of dissonant music. *Sci. Rep.* 7 (1), 5726.
- Koelsch, S., 2014. Brain correlates of music-evoked emotions. *Nat. Rev. Neurosci.* 15 (3), 170–180.
- Koelsch, S., 2018. Investigating the neural encoding of emotion with music. *Neuron* 98 (6), 1075–1079.
- Koelsch, S., Boehlig, A., Hohenadel, M., Nitsche, I., Bauer, K., Sack, U., 2016. The impact of acute stress on hormones and cytokines, and how their recovery is affected by music-evoked positive mood. *Sci. Rep.* 6.
- Koelsch, S., Fritz, T., Cramon, D.Y., Müller, K., Friederici, A.D., 2006. Investigating emotion with music: An fMRI study. *Hum. Brain Mapp.* 27 (3), 239–250.
- Koelsch, S., Fritz, T., Schlaug, G., 2008. Amygdala activity can be modulated by unexpected chord functions during music listening. *NeuroReport* 19 (18), 1815–1819.
- Koelsch, S., Jacobs, A., Liebal, K., Klann-Delius, G., von Scheve, C., Menninghaus, W., Gebauer, G., 2015. The quartet theory of human emotions: An integrative and neuro-functional model. *Phys. Life Rev.* 13, 1–27.
- Koelsch, S., 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 (7), 3485–3498.
- Koelsch, S., Skouras, S., Fritz, T., Herrera, P., Bonhage, C., Küssner, M.B., Jacobs, A.M., 2013. The roles of superficial amygdala and auditory cortex in music-evoked fear and joy. *NeuroImage* 81, 49–60.
- Koelsch, S., Skouras, S., Lohmann, G., 2018a. The auditory cortex hosts network nodes influential for emotion processing: An fMRI study on music-evoked fear and joy. *PLoS one* 13 (1), e0190057.
- Koelsch, S., Vuust, P., Friston, K., 2018b. Predictive processes and the peculiar case of music. *Trends Cognit. Sci.* 23 (1), 63–77.
- Kreutz, G., 2014. Does singing facilitate social bonding. *Music Med.* 6 (2), 51–60.
- Laird, A.R., Fox, P.M., Price, C.J., Glahn, D.C., Uecker, A.M., Lancaster, J.L., Turkeltaub, P.E., Kochunov, P., Fox, P.T., 2005. ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Hum. Brain Mapp.* 25 (1), 155–164.
- Lancaster, J.L., Tordesillas-Gutiérrez, D., Martínez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between mni and talairach coordinates analyzed using the icbm-152 brain template. *Hum. Brain Mapp.* 28 (11), 1194–1205.
- Lathe, R., 2001. Hormones and the hippocampus. *J. Endocrinol.* 169 (2), 205–231.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Ann. Rev. Neurosci.* 23, 155–184.
- Lehne, M., Rohrmeier, M., Koelsch, S., 2014. Tension-related activity in the orbitofrontal cortex and amygdala: an fMRI study with music. *Soc. Cognit. Affect. Neurosci.* 9 (10), 1515–1523.
- Lepping, R.J., Atchley, R.A., Chryssikou, E., Martin, L.E., Clair, A.A., Ingram, R.E., Simmons, W.K., Savage, C.R., 2016. Neural processing of emotional musical and nonmusical stimuli in depression. *PLoS One* 11 (6), e0156859.
- Lindquist, K.A., Satpute, A.B., Wager, T.D., Weber, J., Barrett, L.F., 2015. The brain basis of positive and negative affect: evidence from a meta-analysis of the human neuroimaging literature. *Cereb. Cortex* 26 (5), 1910–1922.
- Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Barrett, L.F., 2012. The brain basis of emotion: a meta-analytic review. *Behav. Brain Sci.* 35 (3), 121.
- Liu, Y., Liu, G., Wei, D., Li, Q., Yuan, G., Wu, S., Wang, G., Zhao, X., 2018. Effects of musical tempo on musicians' and non-musicians' emotional experience when listening to music. *Front. Psychol.* 9.
- Mallik, A., Chanda, M.L., Levitin, D.J., 2017. Anhedonia to music and μ -opioids: Evidence from the administration of naltrexone. *Sci. Rep.* 7, 41952.
- Martinez-Molina, N., Mas-Herrero, E., Rodriguez-Fornells, A., Zatorre, R.J., Marco-Pallarés, J., 2016. Neural correlates of specific musical anhedonia. *Proc. Natl. Acad. Sci.* 113 (46), E7337–E7345.
- McPherson, M.J., Barrett, F.S., Lopez-Gonzalez, M., Jiradejvong, P., Limb, C.J., 2016. Emotional intent modulates the neural substrates of creativity: an fMRI study of emotionally targeted improvisation in jazz musicians. *Sci. Rep.* 6, 18460.
- Menon, V., Levitin, D.J., 2005. The rewards of music listening: response and physiological connectivity of the mesolimbic system. *NeuroImage* 28 (1), 175–184.
- Mitterschiffthaler, M.T., Fu, C.H., Dalton, J.A., Andrew, C.M., Williams, S.C., 2007. A functional MRI study of happy and sad affective states evoked by classical music. *Hum. Brain Mapp.* 28, 1150–1162.
- Mizuno, T., Sugishita, M., 2007. Neural correlates underlying perception of tonality-related emotional contents. *Neuroreport* 18 (16), 1651–1655.
- Mueller, K., Fritz, T., Mildner, T., Richter, M., Schulze, K., Lepsien, J., Schroeter, M.L., Möller, H.E., 2015. Investigating the dynamics of the brain response to music: A central role of the ventral striatum/nucleus accumbens. *NeuroImage* 116, 68–79.
- Mueller, K., Mildner, T., Fritz, T., Lepsien, J., Schwarzbauer, C., Schroeter, M.L., Möller, H.E., 2011. Investigating brain response to music: A comparison of different fMRI acquisition schemes. *NeuroImage* 54 (1), 337–343.
- Müller, V.I., Cieslik, E.C., Laird, A.R., Fox, P.T., Radua, J., Mataix-Cols, D., Tench, C.R., Yarkoni, T., Nichols, T.E., Turkeltaub, P.E., et al., 2018. Ten simple rules for neuroimaging meta-analysis. *Neurosci. Biobehav. Rev.* 84, 151–161.
- Müller-Ribeiro, F.C., Goodchild, A.K., McMullan, S., Fontes, M.A., Dampney, R.A., 2016. Coordinated autonomic and respiratory responses evoked by alerting stimuli: role of the midbrain colliculi. *Respir. Physiol. Neurobiol.* 226, 87–93.
- Oetken, S., Pauly, K.D., Gur, R.C., Schneider, F., Habel, U., Pohl, A., 2017. Don't worry, be happy-neural correlates of the influence of musically induced mood on self-evaluation. *Neuropsychologia* 100, 26–34.
- Okuya, T., Date, T., Fukino, M., Iwakawa, M., Sasabe, K., Nagao, K., Moriizumi, Y., Akiyama, I., Watanabe, Y., 2017. Investigating the type and strength of emotion with music: An fMRI study. *Acoust. Sci. Technol.* 38 (3), 120–127.
- Palomero-Gallagher, N., Hoffstaedter, F., Mohlberg, H., Eickhoff, S.B., Amunts, K., Zilles, K., 2019. Human pregenual anterior cingulate cortex: structural, functional, and connective heterogeneity. *Cereb. Cortex* 29 (6), 2552–2574. doi:10.1093/cercor/bhy124.
- Palomero-Gallagher, N., Vogt, B.A., Schleicher, A., Mayberg, H.S., Zilles, K., 2009. Receptor architecture of human cingulate cortex: Evaluation of the four-region neurobiological model. *Hum. Brain Mapp.* 30 (8), 2336–2355.

- Pehrs, C., Zaki, J., Taruffi, L., Kuchinke, L., Koelsch, S., 2018. Hippocampal-temporopolar connectivity contributes to episodic simulation during social cognition. *Sci. Rep.* 8 (1), 9409.
- Pessoa, L., 2018. Emotion and the interactive brain: Insights from comparative neuroanatomy and complex systems. *Emot. Rev.* 10 (3), 204–216.
- Rigoli, F., Michely, J., Friston, K.J., Dolan, R.J., 2019. The role of the hippocampus in weighting expectations during inference under uncertainty. *Cortex* 115, 1–14.
- Ryals, A.J., Wang, J.X., Polnaszek, K.L., Voss, J.L., 2015. Hippocampal contribution to implicit configuration memory expressed via eye movements during scene exploration. *Hippocampus* 25 (9), 1028–1041.
- Salimpoor, V.N., Benovoy, M., Larcher, K., Dagher, A., Zatorre, R.J., 2011. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nat. Neurosci.* 14, 257–262.
- Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A., Zatorre, R.J., 2013. Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science* 340, 216–219.
- Sescousse, G., Caldú, X., Segura, B., Dreher, J.-C., 2013. Processing of primary and secondary rewards: A quantitative meta-analysis and review of human functional neuroimaging studies. *Neurosci. Biobehav. Rev.*
- Shamay-Tsoory, S.G., 2011. The neural bases for empathy. *The Neurosci.* 17 (1), 18–24.
- Shany, O., Singer, N., Gold, B.P., Jacoby, N., Tarrasch, R., Hendler, T., Granot, R., 2019. Surprise-related activation in the nucleus accumbens interacts with music-induced pleasantness. *Soc. Cognit. Affect. Neurosci.* 14 (4), 459–470.
- Shohamy, D., Adcock, R.A., 2010. Dopamine and adaptive memory. *Trends Cognit. Sci.* 14 (10), 464–472.
- Singer, N., Jacoby, N., Lin, T., Raz, G., Shpigelman, L., Gilam, G., Granot, R.Y., Hendler, T., 2016. Common modulation of limbic network activation underlies musical emotions as they unfold. *Neuroimage* 141, 517–529.
- Skouras, S., Gray, M., Critchley, H., Koelsch, S., 2014. Superficial amygdala and hippocampal activity during affective music listening observed at 3 t but not 1.5 t fMRI. *NeuroImage* 101, 364–369.
- Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cognit. Neurosci.* 21 (3), 489–510.
- Stevens, J.S., Hamann, S., 2012. Sex differences in brain activation to emotional stimuli: a meta-analysis of neuroimaging studies. *Neuropsychologia* 50 (7), 1578–1593.
- Strait, D.L., Kraus, N., Skoe, E., Ashley, R., 2009. Musical experience and neural efficiency – effects of training on subcortical processing of vocal expressions of emotion. *Eur. J. Neurosci.* 29 (3), 661–668.
- Strange, B.A., Witter, M.P., Lein, E.S., Moser, E.I., 2014. Functional organization of the hippocampal longitudinal axis. *Nat. Rev. Neurosci.* 15 (10), 655–669.
- Strange, B.A., Yebra, M., 2015. The multi-instrumentalist hippocampus. *Phys. Life Rev.* 13, 85.
- Suzuki, M., Okamura, N., Kawachi, Y., Tashiro, M., Arao, H., Hoshishiba, T., Gyoba, J., Yanai, K., 2008. Discrete cortical regions associated with the musical beauty of major and minor chords. *Cognit. Affect. Behav. Neurosci.* 8 (2), 126–131.
- Tabei, K., 2015. Inferior frontal gyrus activation underlies the perception of emotions, while precuneus activation underlies the feeling of emotions during music listening. *Behav. Neurol.* 2015.
- Tarr, B., Launay, J., Dunbar, R.I., 2014. Music and social bonding: "self-other" merging and neurohormonal mechanisms. *Front. Psychol.* 5, 1096.
- Taruffi, L., Koelsch, S., 2014. The paradox of music-evoked sadness: An online survey. *PLoS One* 9 (10), e110490.
- Taruffi, L., Pehrs, C., Skouras, S., Koelsch, S., 2017. Effects of sad and happy music on mind-wandering and the default mode network. *Sci. Rep.* 7 (1), 14396.
- Trost, W., Ethofer, T., Zentner, M., Vuilleumier, P., 2012. Mapping aesthetic musical emotions in the brain. *Cereb. Cortex* 22 (12), 2769–2783.
- Trost, W., Frühholz, S., 2015. The hippocampus in an integral part of the temporal limbic system during emotional processing. *Phys. Life Rev.*
- Trost, W., Frühholz, S., Schön, D., Labbé, C., Pichon, S., Grandjean, D., Vuilleumier, P., 2014. Getting the beat: entrainment of brain activity by musical rhythm and pleasantness. *NeuroImage* 103, 55–64.
- Trost, W., Labbé, C., Grandjean, D., 2017. Rhythmic entrainment as a musical affect induction mechanism. *Neuropsychologia* 96, 96–110.
- Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Hum. Brain Mapp.* 33 (1), 1–13.
- Vuoskoski, J.K., Thompson, W.F., McIlwain, D., Eerola, T., 2012. Who enjoys listening to sad music and why. *Music Percept. Interdiscip. J.* 29 (3), 311–317.