Revisiting top-down and bottom-up brain processes: a systematic review and ALE meta-analysis of musical studies.

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Abstract

The most remarkable feature of the human brain is perhaps its ability to constantly integrate information from the environment with internal representations to decide the best action. The integration of top-down and bottom-up processes during complex multi-modal human activities, however, is yet to be understood. Music provides an excellent model for understanding this since music listening leads to the urge to move, and music making entails both playing and listening at the same time (i.e. audio-motor coupling). Here, we conducted activation likelihood estimation (ALE) meta-analyses of 130 neuroimaging studies of music perception, production and imagery, with 2660 foci, 139 experiments, and 2516 participants. We found that music perception relies on auditory cortices, music production involves sensorimotor cortices, and music imagery recruits cingulum. This indicates that the brain requires distinct structures to process information which is made available either by the environment (i.e. bottom-up, music perception) or by internal representations (i.e. top-down, music production and imagery).

1. Introduction.

One of the key features of the human brain is the ability to constantly integrate information and coordinate a variety of different tasks. Indeed, a successful existence depends on the brain's capacity to combine external stimuli with internal representations to ultimately select the best response to the ever-changing environment[1]. The processes which regulate such needs have often been framed in the notorious "top-down/bottom-up" dichotomy, a concept that has been redefined by predictive coding theories.

Throughout the years, key examples of both top-down and bottom-up processes have been revealed. On the one hand, it has been shown that environmental stimuli activate different brain cortices, coherently with the chosen sensory modality[2] (e.g. visual inputs activate visual brain regions, while auditory stimuli trigger auditory cortices). According to the predictive coding theory, bottom-up processing is represented as a series of loops formed by ascending and descending connections between neighbouring levels in a hierarchically organized system (feedforward-feedback). This system is reliable and fast, with a semi-hardwired architecture sufficiently stable to allow for rapid processing of stimuli, and that can be re-shaped by training. On the other hand, top-down mechanisms have been described in diverse manners including anatomical (connections between levels of hierarchy), cognitive (hypothesis-driven), *gestaltist* (modulation of bottom-up), and dynamic (entrainment of neuronal populations by oscillatory activity)[3]; all suggesting that the system allows individuals to predict future events and stimuli. Notably, the term top-down should always be challenged when used[4]. According to the predictive coding theory, top-down processes can be seen as influences that allow the semi-hardwired network to be flexible and ensure efficient and reliable sensory processing. In other words, the system takes as much new information as possible (perception) to construct predictions about the environment to rapidly apply it in a behaviour (action). Taking this in consideration, it is clear that bottom-up and top-down mechanisms are not opposites, and that ascending and descending connections are involved in both processes.

Advanced experimental designs and techniques allowed researchers to conduct investigations on the interaction between top-down and bottom-up processes, which is of crucial importance to gain complete insights into the complexity of the human brain. Although decades of neuroscience have highly advanced our knowledge of such systems, the integration of such mechanisms during complex multi-modal human activities is yet to be understood.

In this context, music is an ideal example of constant integration of multi-modal top-down and bottom-up mechanisms[5], as it requires a successful audio-motor coupling[6]. Thus, how the brain processes music may represent a privileged tool to gain insights into such central topics. Indeed, music is built upon several concurrent bottom-up processes such as perception of sounds and rhythms. Moreover, it also comprises a number of top-down mechanisms such as music production and music imagery, the latter being the abstract mental manipulation of musical sounds[7]. On the neural level, previous studies investigating such processes have provided a wide array of underlying active brain areas, spanning from auditory and sensorimotor cortices[8] to cerebellum[9], cingulum[10], basal ganglia[11], hippocampus[12], and amygdala[13]. In light of this, music may offer an ideal

opportunity to investigate similarities and differences between top-down and bottom-up processes in complex multi-modal brain functioning.

A large number of high-quality studies on music neuroscience already exists. However, these works are often scattered and have mainly explored independent features of the brain understanding of music, lacking a comprehensive picture able to describe the complexity underlying music perception, production, imagination and creation. Indeed, to fully benefit from decades of studies on the musical brain, neuroscience urges meta-analytic efforts to ensure reliability and provide a comprehensive understanding of how the brain processes multi-modal human activities such as music.

Thus, for the first time, we have performed a coordinate-based meta-analysis of a wide range of functional magnetic resonance imaging (fMRI) studies using state-of-the-art methods such as activation likelihood estimation (ALE)[14], to investigate the neural mechanisms underlying music perception, production and imagery.

2. Results.

A total of 1417 articles were identified through database searching, and after removing duplicates, 1210 articles were initially screened by title and abstract. A total of 303 articles were assessed for eligibility in the full-text screening stage. From these, 130 fulfilled criteria and were included in both qualitative and quantitative synthesis (ALE meta-analysis) (**Supplementary Figure 1**).

2.1. Characteristics of studies.

The characteristics of all studies included in the final meta-analysis are shown in **Table 1** and a summary is found in the **Supplementary Information** (p.6).

Insert Table 1

2.2. MRI Quality.

MRI quality of the included studies in the meta-analysis was assessed by a set of guidelines for the standardized reporting of MRI studies[15,16]. All studies reported their MRI design, software package and image acquisition, processing and analyses. Overall, good MRI practices were performed in the included studies (**Supplementary Table 1** and **Supplementary Table 2**).

2.3. Primary outcomes: ALE meta-analyses.

The first ALE meta-analysis included all foci extracted from the included studies (2660 foci, 139 experiments and 2516 subjects). Significant peak clusters resulted in the following areas (alphabetical order): amygdala, anterior cingulate cortex, caudate, cerebellum, hippocampus, inferior frontal gyrus, insula, middle frontal gyrus, parahippocampal gyrus, precentral gyrus (primary motor cortex), putamen, superior parietal lobule, superior temporal gyrus (primary auditory cortex), thalamus, and transverse temporal gyrus. Such results suggest an extensive network involved in music cognition, including the cortex, basal ganglia, brainstem, and cerebellum (**Figure 1**, **Table 2**).

2.3.1. Music perception.

The music perception ALE meta-analysis included 1898 foci, 105 experiments and 2035 subjects. Significant peak clusters resulted in the following areas: (1) left superior temporal gyrus (primary auditory cortex, x=-54, y=-16, z=2), extending to limbic areas such as the anterior cingulate cortex, amygdala, hippocampus and insula; basal ganglia including caudate, putamen and globus pallidus; cerebellum (culmen); and brainstem (red nucleus); and (2) right superior temporal gyrus (primary auditory cortex, x=52, y=-20, z=4), extending to insula, frontal areas (inferior, middle and superior frontal gyri), and putamen. Such results show consistency of cortical and subcortical areas presumably involved in bottom-up processing of music (**Figure 1**, **Table 2**).

2.3.2. Music production.

The music production ALE meta-analysis included 499 foci, 19 experiments and 292 subjects. Significant peak clusters resulted in the following areas: (1) right precentral gyrus (primary motor cortex, x=54, y=4, z=32), extending to the superior temporal gyrus, middle temporal gyrus,

transverse temporal gyrus, inferior frontal gyrus and insula; (2) left precentral gyrus (x=-48, y=0, z=42), extending to postcentral gyrus (primary somatosensory cortex), superior temporal gyrus, middle temporal gyrus, middle frontal gyrus, inferior parietal lobule and anterior cingulate gyrus; (3) left medial frontal gyrus (premotor cortex, x=-10, y=-10, z=52), extending to the anterior cingulate gyrus, superior frontal gyrus and precentral gyrus; and (4) left superior temporal gyrus (x=-42, y=-28, z=6), extending to the transverse temporal gyrus, insula and postcentral gyrus. These results evidence not only the obvious involvement of the somatomotor system, but also limbic and executive cognitive functions while playing music (**Figure 1**, **Table 2**).

2.3.3. Music imagery.

The music imagery ALE meta-analysis included 263 foci, 15 experiments and 189 subjects. Significant peak clusters resulted in the following areas: (1) left medial frontal gyrus (Brodmann area 6, x=0, y=6, z=58), extending to the cingulate gyrus and the superior frontal gyrus; (2) the left superior parietal lobe (Brodmann area 7, x=-34, y=-58, z=56), including the angular gyrus, the inferior parietal lobule, supramarginal gyrus, and the intraparietal sulcus; and (3) left thalamus (ventral posterior lateral nucleus, x=-14, y=-14, z=8), extending to the claustrum, basal ganglia, the insula, and auditory cortex. These results show that music imagination recruits motor areas involved in the generation of movements such as the premotor cortex and supplementary motor area; areas of the basal ganglia which are also involved in facilitation of movements; and parietal areas involved in perceptual-motor coordination and theory-of-mind (**Figure 1**, **Table 2**).

Insert Figure 1

Insert Table 2

2.4. Contrast analyses.

A subsequent contrast ALE meta-analysis was conducted to compare the primary outcomes, by means of conjunction and subtraction. The purpose of this analysis was to identify common and distinct brain activity between music perception, production and imagery (**Figure 2**, **Supplementary Table 3**).

Insert Figure 2

2.4.1. Music perception vs music production.

Clusters identified as likely to be active during both music perception and production (conjunction) include the right superior temporal gyrus (BA42), left superior temporal gyrus (BA41), left superior temporal gyrus (BA22), insula, post-central gyrus, claustrum and inferior frontal gyrus (BA9). The contrast analysis (subtraction) yielded areas specific to perception (perception-production) and production (production-perception). Areas more likely to be active in music perception are the primary auditory cortices in both hemispheres and the left anterior cingulate gyrus. Conversely, areas more likely to be active in music production include the motor and somatosensory primary cortices, inferior frontal gyrus, prefrontal cortices, basal ganglia, thalamus, and cerebellum.

2.4.2. Music production vs music imagery.

Clusters that are presumably active during both music production and music imagery (conjunction) include the superior frontal gyrus, medial frontal gyrus, anterior cingulate cortex, inferior parietal lobule, and insula. The contrast analysis (subtraction) resulted in areas either specific to music production (production-imagery) or to music imagery (imagery-production). Areas more likely to be active in music production include the insula, motor and somatosensory cortices, brainstem, thalamus, superior temporal gyrus (Brodmann areas 22 and 41), and putamen. Areas more likely to be active while imagining music include the inferior parietal lobule, superior parietal lobule, angular gyrus, middle frontal gyrus, medial frontal gyrus and precentral gyrus.

2.4.3. Music imagery vs music perception.

Clusters likely active during both music imagery and music perception (conjunction) include the insula, superior temporal gyrus, thalamus, putamen, caudate, and claustrum. The contrast analysis (subtraction) resulted in areas either specific to music imagery (imagery-perception) or to music perception (perception-imagery). Areas more related to music imagery include the inferior and superior parietal lobe, the inferior, medial and middle frontal gyri, and areas of the cingulate cortex. Finally, areas more likely to be active during music perception include the superior and transverse temporal gyrus, insula, caudate, putamen, amygdala, hippocampus and middle frontal gyrus.

2.5. Subgroup analyses.

Subgroup analyses were conducted independently for every primary outcome to identify specific brain regions related to specific musical features such as pitch, rhythm, timbre, tonality, structure, melody, harmony, familiarity, emotion, creativity, and musicianship.

2.5.1. Music perception subgroup analysis.

In terms of musical features, harmony subgroup resulted in areas of the insula, superior temporal gyrus extending to the middle and inferior frontal gyri, and motor areas such as precentral gyrus and medial frontal gyrus (primary and secondary motor cortices, respectively). Melody subgroup showed bilateral auditory cortices, insula, middle temporal gyrus, middle frontal gyrus, and posterior cingulate cortex extending to precuneus. The rhythm subgroup showed areas in the middle temporal gyrus (BA22), middle and medial frontal gyrus, left superior temporal gyrus, precentral gyrus, putamen, cerebellum, inferior parietal lobule and insula. The timbre subgroup analysis yielded areas located across the auditory cortices on both hemispheres including planum polare, planum temporale and Heschl's gyrus. Tonality subgroup analysis resulted in areas of the inferior frontal gyrus and the insula.

In the music emotion subgroup, cortical and subcortical structures related to different functional processes such as perception in the auditory cortex (Heschl's gyrus) were found; limbic areas such as amygdala, insula and hippocampus; motor nuclei of the basal ganglia; and cognitive-related areas such as prefrontal cortices. In terms of valence, positive valence such as joy, arousal, pleasure, power and wonder appear to activate not only primary auditory cortices but also basal ganglia, brainstem, hypothalamus, insula, and hippocampus; negative valence such as sadness and nostalgia seem to activate limbic areas such as the hippocampus, amygdala and insula; cognitive

areas such as prefrontal cortex and inferior frontal gyrus; and putamen and globus pallidus in the basal ganglia.

Music familiarity was assessed by subgroup results from familiar and unfamiliar music. Familiar music showed areas of the primary auditory cortices, bilaterally. These clusters extended to motor areas of putamen, caudate and thalamus; limbic areas of insula, hippocampus and prefrontal cortex. Unfamiliar music adds to these areas the amygdala and premotor areas. Interestingly, motor areas of the basal ganglia were less prominent in unfamiliar music when compared to familiar music.

In terms of musicianship, both musician and non-musician subgroups resulted in areas of the auditory cortices, primary and secondary motor cortices, insula, and inferior frontal gyrus. Interestingly, the non-musician subgroup showed additional areas such as putamen and caudate in basal ganglia, cerebellum, parahippocampal gyrus, and thalamus, suggesting that non-musicians activate a more extensive motor network while listening to music than trained musicians who probably use less resources to process music (**Figure 3**, **Supplementary Table 4**).

Insert Figure 3

2.5.2. Music production subgroup analysis.

In terms of musical features, harmony subgroup resulted in areas of the motor cortex and premotor cortex, auditory cortex and insula. Melody subgroup resulted in temporal areas extending to the insula. Pitch subgroup showed areas in the transverse and superior temporal gyri, medial frontal gyrus and pre-post central gyri. Rhythm subgroup included areas of the somatosensory cortex, superior frontal gyrus and insula, extending to the basal ganglia.

Creativity while producing music was assessed by pooling studies on improvisation and showed that creating new music activates areas of the medial globus pallidus and medial frontal gyrus, while playing learnt music activates areas of the primary auditory and motor cortices, premotor cortex and cerebellum.

Producing familiar music activates the premotor and motor cortex, auditory cortex, inferior parietal, and culmen in the cerebellum. Conversely, unfamiliar music production recruits premotor areas, somatosensory cortex, precuneus, basal ganglia and insula.

In terms of musicianship, music production of trained musicians activates areas of the primary auditory cortex, insula and premotor cortex, while non-musicians show activity of primary auditory cortex, insula, cingulate cortex and inferior frontal gyrus while producing music (**Figure 4**, **Supplementary Table 5**).

Insert Figure 4

2.5.3. Music imagery subgroup analysis.

In terms of musical features, imagining melodies activates the inferior frontal gyrus, bilaterally, and the premotor cortex. Pitch imagination engages the precuneus and the inferior parietal lobule.

Finally, timbre imagination activates the primary auditory cortex, bilaterally, the posterior cingulate cortex and premotor cortex.

Imagining familiar music engages the superior parietal lobule, premotor and motor cortices, thalamus and culmen. Conversely, the imagery of unfamiliar music recruits the inferior parietal lobe, middle temporal gyrus and the premotor cortex.

When imagining music, trained musicians recruit premotor cortices, prefrontal cortex, the inferior and superior parietal lobules extending to the angular gyrus and precuneus. Non-musicians, in turn, activate the premotor cortex and the superior parietal lobule while imagining music (**Figure 5**, **Supplementary Table 6**).

Insert Figure 5

2.6. Meta-analytic connectivity modelling (MACM).

MACM was performed to functionally segregate the behavioural contribution of each music-related region-of-interest (ROI) resulted from the primary outcome (n=10). The ROIs were imported into the BrainMap database separately, to identify studies reporting activation within each ROI boundary (summary in **Supplementary Information** (p.43); **Supplementary Table 7** for MACM, and **Supplementary Table 8** for functional characterization).

3. Discussion

In the current work, we have conducted ALE meta-analyses of neuroimaging studies with a total of 2660 foci, 139 experiments, and 2516 subjects, to realise a comprehensive picture of the top-down and bottom-up mechanisms required by music processing. Our main results, whose robustness is guaranteed by the large numbers of studies included in the analyses, provide a complex and appetising picture of the brain activity underlying music processing. Indeed, while music perception mainly relies on auditory cortices, music production involves sensorimotor cortices. Further, music imagery presents a higher recruitment of cingulate brain regions. Finally, our primary outcomes were complemented with a number of subgroup and meta-analytic connectivity analyses, describing in full the complexity of the brain mechanisms underlying music processing.

3.1. Characteristics of included studies.

The publications included in this comprehensive systematic review and meta-analysis reported a clear research question, inclusion and exclusion criteria for participants, description of methods and explicit results. In line with reproducibility efforts, the included studies used state-of-the-art techniques and computational MRI tools important for the support of standardization of neuroimaging studies. However, some works lacked important demographic data such as the years of education, age of musical training onset, and current time of musical practice, which may have an effect on behavioural tasks and neuroimaging data.

3.2. Music perception

Temporal lobe areas

As expected, the main result concerning music perception involved temporal regions and especially auditory cortices. Indeed, we found convergence in various temporal lobe areas assumed to be related to auditory feature processing as well as semantic and conceptual aspects of music. Namely, primary auditory regions of the Heschl's gyrus (BA41), planum temporale (BA41), posteriorly the planum polare (BA38), as well as secondary auditory areas within the superior temporal gyrus (BA21), middle temporal gyrus (BA38) and the Wernicke's area (BA22). Activation of both primary and secondary areas may reflect hierarchical computation of auditory processing including lower-level extraction followed by alignment to preconstructed predictions. Middle temporal gyrus (BA21) as well as frontal regions within BA47, which were also observed, may be seen in light of lexical-semantic and conceptual aspects[17] of music.

Audio-motor coupling

We also found convergence in motor-associated areas, assumingly related to temporal processing, inherent audio-motor coupling and entrainment. These include areas within the basal ganglia (caudate, putamen, globus pallidus and thalamus), sensorimotor areas (premotor cortex) and the cerebellum (lobule III). As music unfolds over time and does so at a specific periodicity (rhythm, beat, metre), it is not surprising to see brain activation in areas related to temporal processing in the motor domain[18]. Furthermore, previous studies have proposed significant connectivity within the fronto-temporal-cerebellar network during the perceptual analysis of music listening[19,20]. In

concordance with neuroimaging results, electroencephalography (EEG) studies have found synchronised neural activity in the gamma-band within this network, in response to rhythmic expectancy[21,22]. Additionally, specific neuronal firing patterns were found in those areas with respect to time comprehension[23]. These include ramping spike activity, which refers to a consistent increase or decrease in neuronal firing rate, spectral responses and network-produced ensemble patterns[24]. In relation to the lentiform nucleus, the putamen has been proposed to be important for internal beat perception[25] and for generation of internalised groupings or chunking of action representations[26].

Limbic system

Further, our ALE analysis outlined the convergence areas within the reward system (limbic and paralimbic system) with undeniable processing of emotional features of music as well as aesthetic expression. The universality of musically evoked reward and emotion has gained immense interest within music cognition research, with studies investigating emotional connection to the predictability[27] with respect to tension[28], temporal complexity and harmonic consonance/dissonance[29] and the previously mentioned entrainment, to list a few. In line with previous studies, our results show significant results localised in the hippocampus, amygdala, insula as well as the cingulate gyrus (BA24).

Executive functions

Finally, our results about music perception showed a smaller but relevant recruitment of areas commonly related to executive functions. These areas include frontal regions within the superior frontal gyrus (BA10) as well as the dorsolateral prefrontal cortex (BA9, BA46). Due to the multidimensional nature of a musical stimulus (pitch, timbre etc.), it is not surprising to see extensive functional activation in areas responsible for attentional processes and executive function. For instance, voxel-based lesion studies have outlined the superior frontal gyrus likely related to multitasking[27] and working memory[30].

3.3. Music production

Playing an instrument or engaging in music production requires extremely intricate motor control functions as well as the ability to internalise and portray emotional meaning. Accordingly, and unsurprisingly, with regards to our music production analysis, we found convergence in areas related to motor planning and execution. Namely, areas within the precentral gyrus, (BA6, BA2 and BA4), middle frontal gyrus (BA6, premotor cortex (PMC), putamen as well as cerebellar structures (culmen, fastigum and declive). Aside from their obvious motor function in relation to instrument playing, these areas are also likely to be involved in various sensory-motor coupling. Previous studies have repeatedly outlined the PMC and the planum temporale to be the crucial players in various sensorimotor transformations[31]. In relation to music, the rostral dPMC has been recruited during increasingly more complex rhythms[32] and saliency[33]. This means that the PMC could be responsible for modifying motor sequences to reflect auditory sequential patterns in a predictive and anticipatory manner. Furthermore, we found a prominent activation of the cerebellum commonly associated with motor command adjustments and motor learning[34]. With regard to music, previous studies have also shown the cerebellum engagement in tasks related to production

and perception of singing[35] and highlighted its supervision role in fine-grained movements on the musical instrument[36].

Limbic areas

Aside from motor dexterity crucial for the technical component of instrument playing, the performance must engage the listener with loaded emotional content. Although with reduced strength compared to motor areas, our results point to a number of regions involved in the processing and conveyance of emotional material including the anterior cingulate gyrus, insula and the fastigum of the cerebellum. Previous findings of neuroanatomical studies have outlined the temporal lobe having strong connectivity with the anterior cingulate gyrus[37]. Further, for an appropriate emotional response the anterior cingulate has shown to require specific sensory information[31]. Thus, the anterior cingulate gyrus may be crucial for top-down control of emotional meaning and bottom-up processing of emotional content. In complement, numerous neuroimaging studies have outlined the activation of cingulate gyrus during musical performance[38,39]. Interestingly, an emerging body of research is suggesting a role of the cerebellum in cognition and emotion with reciprocal connections to various limbic system regions. The fastigial nucleus in particular has been shown to have extensive topographic connections with non-motor systems including the limbic system encompassing areas such as the anterior cingulate gyrus[40].

3.4. Music imagery

Temporal cortex and cingulate gyrus

The main results from our ALE analysis show music imagery to recruit cingulate regions, inferior frontal gyrus (BA47) and multiple auditory areas relevant to feature processing, working memory and conceptual and/or semantic facets of the experience. With regards to the cingulate gyrus, previous studies highlighted multiple roles involving this particular brain structure. For example, it has been shown to be involved in prediction error responses and supervision processes[41], which could be coherent with our findings related to imagery of musical information. Along this line, several works proposed cingulum as a key structure for learning and memory[42], which could also be relevant for our findings since musical imagery implies retrieval of musical information that was previously learned. Another key function of cingulate brain regions relates to the limbic system and emotion formation and processing[43]. However, with regards to imagery, this latter evidence may be less relevant. In relation to temporal areas, foci convergence was found within a large portion of the Wernicke's area (BA22, BA40, BA39) and insula, with no primary auditory cortex activation. This result is generally mirrored in imagery studies in the auditory and language domain[44] which define regions adjacent to the primary cortex imperative to auditory imagery.

Motor-associated areas

Furthermore, we found convergence in motor-associated areas within BA6 and the basal ganglia as well as the superior and inferior parietal lobule within BA7. As previously mentioned, neuroimaging studies on rhythm, metre and beat have outlined the medial frontal gyrus, superior frontal gyrus along with the basal ganglia in the context of temporal feature processing and inherent audio-motor coupling[45]. In relation to imagery, activation within the SMA is particularly

interesting, being repeatedly found in various imagery domains including visual imagery[46]. Furthermore, such region was also found in relation to imagination in hallucination studies[47]. Within our results, the SMA was specific to imagery suggesting its distinct role in mental manipulation and generation of internalised representations also during music.

3.5. Comparison between music perception, production, and imagery.

A direct comparison of music perception, production and imagery for each of the respective pairs revealed several indications of music processing specificity likely resulting from a bidirectional organisation of the brain. Crucially, the general trend reveals that despite some activation overlap, the three processes engage distinct brain regions at varying proportions of activation across all contrast analyses. For instance, both music imagery and music production, when contrasted with music perception, showed a unique and broad activation of left superior and inferior parietal lobule (BA7). Previously, studies outlined these areas to be key for top-down or goal directed attentional orienting[48], and specific to imagery, the superior parietal lobule has been named a potential candidate for top-down generation and maintenance of domain-unspecific mental images[49]. The presence of these areas in both domains, further substantiates this claim and is highly suggestive of its marked function of top-down processes within the hierarchical system. Furthermore, when contrasting music perception with music production and vice versa, the right primary auditory area showed specificity to the perception contrast, indicative of a preference for bottom-up retrieval of information from the environment. However, this should be interpreted with some caution due to inter-subject variability with regard to localisation of the primary auditory cortex[50].

3.6. Limitations and future perspectives.

Although our meta-analyses comprise a large number of studies and thus arguably provide reliable results, some limitations should be mentioned. First, by definition meta-analyses rely on the combination of the data from previous studies and therefore are highly dependent on the quality of such studies. In our case, we utilised studies that possessed high-quality standards, making feasible data extraction and conduction of statistical analysis. However, we should highlight that a thorough description of the methods and an even stronger focus on the description of the experimental settings would be highly beneficial for the field and thus we encourage future studies to further increase their already high-level quality. Second, we relied on the assumptions of the GingerALE method that was used in our study. Therefore, the accuracy of our findings necessarily relies on the statistical estimation of coordinate-based anatomic foci (input) which were treated as spatial probability distributions centred at the given coordinates. As conceivable, we could not control the heterogeneity of the methods used in the studies included in the meta-analysis (ranging from preprocessing software, statistical thresholds, smoothing, and participants' characteristics) and we acknowledge that this fact could represent a potential confounder for our analyses. As in traditional meta-analyses, we have assessed the publication bias[51] and revealed that the cluster obtained from the primary outcome presented an FSN = 86, which is greater than the required minimum of 39. Importantly, this outcome proves a robust convergence of the foci emerged from our analyses (further information is reported in **Supplementary Table 9**).

With regard to future perspectives, we believe that the neuroscientific community would benefit from designing new ad-hoc studies to directly investigate the relationship between brain activity and different features of music processing such as music perception, production and imagination. Although our results provide a robust picture of the brain networks recruited by those different processes, carefully designed experiments which systematically modulate and compare stimuli and conditions would further refine the knowledge on this broad and complex topic.

4. Conclusions.

In the present work, we have conducted a series of meta-analyses on decades of studies investigating the brain activity underlying music processing. We have shed new light on how the brain processes and combines top-down and bottom-up mechanisms during complex multi-modal human activities such as music. The outcomes of our synthesis highlighted three main concurrent music procedures, known as music perception (bottom-up), music production and imagery (top-down). Strikingly, our results showed that the brain relied on different structures and mechanisms to process similar musical information. Indeed, while music perception mainly relies on auditory cortices, music production involves cerebellum and sensorimotor cortices. Differently, music imagery shows a key recruitment of cingulate regions. Taken together, our findings provide robust evidence that the brain requires different structures to process similar information which is made available either by the environment (i.e. bottom-up, music perception) or by internal representations (i.e. top-down, music production and imagery).

5. Methods and Materials.

5.1. Search strategy, screening, and extraction.

This comprehensive systematic review and meta-analysis followed procedures from the Cochrane Handbook for Systematic Reviews[52], and from the Center for Reviews and Dissemination (https://www.york.ac.uk/crd/). The review protocol was pre-registered in PROSPERO (CRD42019140177), and was carried out in accordance with the PRISMA statement[53]. A systematic literature search was conducted in PubMed, Scopus and PsycInfo for articles published up to February 26th, 2021. The search strategy for music perception, production and imagery was developed using keywords and MeSH terms (details in **Supplementary Information**). An additional manual search of references from individual studies was conducted in order to find other applicable sources.

To ensure concurrence between the research question and data extracted, the following inclusion criteria was established: (1) healthy adults (18-80 age range); (2) studies investigating music listening, music playing, or music imagery, with no restrictions on music genre, parameter, or instrument; (3) using fMRI or PET; (4) whole-brain analyses; and (5) results reported in stereotactic coordinates either Talairach or Montreal Neurological Institute (MNI) three-dimensional-coordinate system. Studies were excluded using the following criteria: (1) review articles with no original experimental data, (2) populations with any form of disorder or disability; (3) paediatric population; (4) auditory stimuli not related to music; (5) functional connectivity analyses; (6) region-of-interest (ROI) analyses.

Two reviewers (AP and VPN) independently screened by title and abstract and selected articles for full-text review and data extraction. Screening and data extraction were performed using the Covidence tool[54]. Any disagreements that arose between the reviewers were resolved through discussion.

The following variables were extracted from each study: first author, year of publication, number of participants, age, sex, musical feature, year of education, year of musical training, age of onset of musical training, training hours per week, and MRI acquisition, processing, and analysis parameters. The main outcome to extract was coordinates resulting from functional brain activity related to music perception, production and/or imagination. If any of these points were not reported in the original article, authors were contacted to retrieve this information. Nine authors were contacted, with 3 positive answers.

5.2. Quality assessment of MRI studies.

A set of guidelines used for the standardization of reporting MRI results was utilized to assess the quality of the included studies[15,16]. Such guidelines dictate a more consistent and coherent policy for the reporting of MRI methods to ensure that methods can be understood and replicated.

5.3. Activation Likelihood Estimation (ALE) and meta-analytic connectivity modelling (MACM).

All meta-analyses were performed using the activation likelihood estimation (ALE) method, implemented in GingerALE software v3.0.2[55], from the BrainMap[55] platform. Reported significant

coordinates (foci) were extracted from each study. If necessary, coordinates were converted from Talairach coordinates to MNI space using the Lancaster transform (icbm2tal) incorporated in GingerALE[14,56]. The ALE method extracts the coordinates from the included studies and tests for anatomical consistency and concordance between the studies. The coordinates are weighted according to the size of the sample (number of subjects), and these weightings contribute to form estimates of anatomic likelihood estimation for each intracerebral voxel on a standardized map. This method treats anatomic foci not as single points, but as spatial probability distributions centred at the given coordinates. Thus, the algorithm tests the correlation between the spatial locations of the foci across MRI studies investigating the same construct and assesses them against a null-distribution of random spatial association between experiments[46]. Statistical significance of the ALE scores was determined by a permutation test using cluster-level inference at $p < 0.05$ (FWE). Clusters with small volume should be interpreted with caution, as we did not impose any minimum cluster size of supra-threshold voxels.

The primary outcome was brain functional activity related to music, pooling all studies together, to examine comprehensively the brain regions associated with music perception, music production, and music imagery. Then, the resulting ALE maps from each group were tested for similarity (conjunction) and difference (subtraction) in a contrast analysis to identify common and distinct brain areas recruited while listening, playing and/or imagining music. Additionally, we conducted a series of subgroup analyses to identify brain regions related to specific musical features. Such subgroup analyses were conducted independently for each primary outcome and included: pitch, rhythm, timbre, tonality, structure, melody, harmony, familiarity, emotion, creativity, and musicianship.

Meta-analytic connectivity modelling (MACM) was conducted to identify patterns of co-activation from regions-of-interest (ROI) resulting from the primary outcomes, aiming to functionally segregate each region's putative contribution to behavioural domains and paradigm classes[57,58]. Such analyses were performed using Sleuth[59] and GingerALE from the BrainMap database. Then, ALE meta-analyses were performed over all foci resulted after the search in Sleuth to identify regions of significant convergence. Sleuth search was performed for each music-related ROI independently and included the experiment level search criteria of "context: normal mapping" and "activations: activation only". Functional characterization of music-related clusters was based on the "Behavioral Domain" (BD) meta-data categories in the BrianMap database which include action, perception, emotion, cognition and interoception.

All meta-analytic results (ALE maps) were visualized using Mango[60] on the MNI152 1mm standard brain, and resulting coordinates were cross-referenced to the Harvard-Oxford Cortical and Subcortical Atlas and the Juelich Histological Atlas via NeuroVault[61] and FSLeyes[62], respectively.

5.4. Fail-Safe N analysis (FSN).

Coordinate-based meta-analyses such as ALE can be subject to different forms of publication bias which may impact results and invalidate findings (e.g., the "file drawer problem"). The Fail-Safe N analysis (FSN)[51] assesses the robustness of results against potential publication bias. This method refers to the amount of contra-evidence that can be added to a meta-analysis before the results

change and can be obtained for each cluster that survives thresholding in an ALE meta-analysis. It is estimated that a 95% confidence interval for the number of studies that report no local maxima varies from 5 to 30 per 100 published studies of normal human brain mapping. Using the upper bound and the fact that the present meta-analysis consists of 130 studies, an estimate for the number of unpublished experiments is 39. Therefore, the minimum FSN was defined as 39. A higher FSN indicates more stable results and hence a higher robustness. Such analyses were performed only on primary outcomes.

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Authors' contributions.

VPN and AP designed the meta-analysis. VPN and AP conducted the screening of the studies and data extraction. LB performed the sensitivity analysis. VPN and AP wrote the first draft of the manuscript and prepared the initial versions of the figures and tables. LB edited and wrote paragraphs in the Introduction and Discussion. VPN prepared the final figures and tables. PV contributed to financially supporting the study and commented the final versions of the manuscript. VPN finalized the paper for submission and all authors edited the manuscript and approved its final version.

Conflict of interest.

There is no actual or potential financial and other conflict of interest related to this manuscript.

Data availability.

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Figure legends.

Figure 1. Anatomic likelihood estimation meta-analytic results for studies of music perception, production and imagery, at cluster level inference $p < 0.05$ (FWE). The primary outcome included ALE meta-analysis of all included foci, and music perception, music production, and music imagery, independently. Z, peak Z-value.

Figure 2. Conjunction analyses comparing foci for music perception, production and imagery, at cluster level inference $p < 0.05$ (FWE). Contrast analyses were performed for music perception, production and imagery fMRI studies, and were tested for similarity (conjunction) and difference (subtraction), to illustrate common and/or distinct areas between the domains.

Figure 3. Musical feature subgroup meta-analyses for music perception, at cluster level inference $p < 0.05$ (FWE). Z, peak Z-value.

Figure 4. Musical feature subgroup meta-analyses for music production, at cluster level inference $p < 0.05$ (FWE). Z, peak Z-value.

Figure 5. Musical feature subgroup meta-analyses for music imagery, at cluster level inference $p < 0.05$ (FWE). Z, peak Z-value.

Table 1. Characteristics of the studies included in meta-analysis.

												Age		Education (years)		Onset (years)		Training (hr/week)	
	Author	Year	Domain	n	Method	Feature	Familiarity	Males	Females	Total	Musicians	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD
1	Agustus	2018	Perception	20	fMRI	melody	Y	10	10	20	Y	66.6	-	-	-	-	-	-	-
2	Alluri	2012	Perception	11	fMRI	timbre, key, rhythm	N	6	5	11	Y	23.2	3.7	16.1	6	9.1	3.4	2.5	1.2
3	Alluri	2013	Perception	11	fMRI	non-specific	Y	7	4	11	N	26.4	5	-	-	-	--	-	-
4	Alonso	2016	Perception	22	fMRI	melody	N	11	11	22	N	24.09	5.45	-	-	-	-	-	-
5	Alttenmüller	2014	Production	18	fMRI	emotion +	N	14	4	18	N	28.7	8.7	8.4	5.7	-	-	-	-
6	Angulo-Perkins	2014	Perception	53	fMRI	non-specific	N	29	24	53	B	28	8	-	-	-	-	-	-
7	Armony	2015	Imagery	47	fMRI	non-specific	N	27	20	47	B	26.4	-	-	-	-	-	-	-
8	Bangert	2006	Imagery	14	fMRI	non-specific	N	6	8	14	Y	-	-	-	-	-	-	-	-
9	Barrett	2016	Perception	12	fMRI	emotion +	Y	4	8	12	N	22.4	-	-	-	-	-	-	-
10	Barrett	2018	Perception	25	fMRI	tonality	Y	-	-	-	N	-	-	-	-	-	-	-	-
11	Barrett	2020	Perception	1	fMRI	creativity	N	0	1	1	Y	44	-	-	-	-	-	-	-
12	Bastepe-Gray	2020	Perception	7	fMRI	non-specific	Y	7	0	7	Y	22.8	2.1	6.3	1.5	-	-	10	2.5
13	Baumann	2007	Imagery	7	fMRI	non-specific	N	1	6	7	B	25.7	3.2	0	0	-	-	-	-
14	Bengtsson	2006	Imagery	11	fMRI	rhythm and melody	Y	11	0	11	Y	33	-	-	-	5.7	1.4	-	-
15	Bengtsson	2007	Perception	11	fMRI	structure/ creativity	Y	11	0	11	Y	32.6	6	-	-	5.7	1.4	-	-
16	Bengtsson	2009	Perception	17	fMRI	rhythm+ beat +metre	N	14	3	17	N	23.6	-	-	-	-	-	-	-
17	Bianco	2016	Perception	29	fMRI	harmony	N	12	17	29	Y	24.7	2.9	17.2	4.8	7.3	3.08	-	-
18	Bishop	2013	Perception	12	fMRI	rhythm+ beat +metre	Y	6	6	12	N	21.2	3	-	-	-	-	-	-
19	Blood	1999	Perception	10	PET	emotion +	N	5	5	10	N	-	-	-	-	-	-	-	-
20	Bodner	2001	Perception	7	fMRI	rhythm+ beat +metre	Y	7	-	-	N	-	-	-	-	-	-	-	-
21	Bogert	2016	Production	56	fMRI	emotion- non-specific	N	-	-	-	N	28.2	8.21	5	-	-	-	2	-
22	Brattico	2016	Production	29	fMRI	emotion +	Y	14	15	29	B	23.9	3.1	-	-	-	-	-	-
23	Bravo	2017a	Perception	12	fMRI	harmony	N	5	7	12	N	29	5.16	-	-	-	-	-	-
24	Bravo	2017b	Imagery + Production	14	fMRI	harmony	N	7	7	14	N	30.45	3.05	-	-	-	-	-	-
25	Bravo	2020	Perception	16	fMRI	harmony	N	8	8	16	N	29	5.16	-	-	-	-	-	-
26	Brown	2004	Perception	10	PET	non-specific	N	5	5	10	N	33.8	-	-	-	-	-	-	-
27	Brown	2007	Perception	11	fMRI	melody	N	5	6	11	N	24.6	-	-	-	12.3	-	-	-
28	Chapin	2010	Perception	14	fMRI	emotion - non-specific	N	5	9	14	N	-	-	-	-	-	-	-	-
29	Chen	2008a	Perception	12	fMRI	rhythm+beat+metre	N	-	-	12	N	24	-	-	-	-	-	-	-
30	Chen	2008b	Perception	24	fMRI	rhythm+ beat +metre	N	12	12	24	N	23.83	-	-	-	-	-	-	-
31	Chiang	2018	Perception	20	fMRI	structure- normal	N	12	8	20	Y	-	-	-	-	-	-	-	-
32	Danielsen	2014	Perception	19	fMRI	rhythm+ beat +metre	N	11	8	19	N	35.2	6.2	-	-	-	-	-	-
33	Demorest	2009	Production	16	fMRI	memory	N	8	8	16	N	28.6	-	-	-	-	-	-	-
34	Donnay	2014	Perception	11	fMRI	harmony	N	11	0	11	Y	38.8	11	-	-	-		-	-
35	Engel	2011	Perception	22	fMRI	creativity	N	22	0	0	Y	-	-	12.8	6.8	-	-	7.4	5.8
36	Escoffier	2013	Perception	16	fMRI	emotion-non-specific	N	9	7	16	N	21.7	1.9	-	-	-	-	-	-
37	Fedorenko	2012	Production	12	fMRI	structure- normal	N	6	6	12	N	-	-	-	-	-	-	-	-
38	Flores-Gutiérrez	2007	Perception	19	fMRI	emotion + and -	N	11	8	19	N	25	3.05	-	-	-	-	-	-
39	Fujisawa	2011	Perception	12	fMRI	harmony	Y	12	0	12	N	-	-	-	-	-	-	-	-
40	González-García	2016	Perception	11	fMRI	harmony	Y	0	11	11	Y	-	-	-	-	-	-	-	-
41	Grahn	2007	Perception	27	fMRI	rhythm+ beat +metre	N	8	19	27	B	24.5	-	-	-	-	-	-	-
42	Grahn	2009a	Perception	35	fMRI	rhythm+ beat +metre	N	23	12	35	N	29.9	7.2	-	-	-	-	-	-
43	Grahn	2009b	Perception	36	fMRI	rhythm+ beat +metre	N	21	15	36	N	29	-	-	-	-	-	-	-
44	Grahn	2013	Perception	24	fMRI	rhythm+ beat +metre	N	11	13	24	B	27	-	-	-	-	-	-	-
45	Green	2008	Perception	21	fMRI	harmony	N	-	-	-	N	27.3	-	-	-	-	-	-	-
46	Green	2012	Perception	21	fMRI	familiarity	N	9	12	21	N	27.3	-	-	-	-	-	-	-
47	Green	2018	Perception	22	fMRI	familiarity	N	17	5	22	N	-	-	-	-	-	-	-	-
48	Halpern	1999	Perception	8	fMRI	melody	N	3	5	8	B	-	-	-	-	-	-	-	-
49	Halpern	2004	Perception	10	fMRI	timbre	N	5	5	10	Y	-	-	5	-	-	-	-	-
50	Herdener	2014	Perception	22	fMRI	rhythm+ beat +metre	N	-	-	22	B	-	-	5	-	-	-	-	-
51	Herholtz	2012	Perception	10	fMRI	non-specific	Y	5	5	10	N	27	-	-	-	-	-	-	-
52	Huang	2016	Perception	18	fMRI	non-specific	Y	18	0	18	N	-	-	-	-	-	-	-	-
53	Janata	2002a	Perception	8	fMRI	tonality	Y	-	-	8	N	-	-	-	-	-	-	-	-
54	Janata	2002b	Perception	12	fMRI	melody	N	5	7	12	Y	28.5	-	8.3	3.5	-	-	-	-
55	Janata	2009	Production	13	fMRI	memory	N	2	11	13	Y	20	-	-	-	-	-	-	
56	Jeong	2011	Perception	15	fMRI	emotion + and -	N	5	10	15	N	22.8	3.4	-	-	-	-	-	-
57	Jungblut	2012	Perception	30	fMRI	rhythm+ beat +metre	N	17	13	30	N	26.3	-	-	-	-	-	-	-
58	Khalfa	2005	Perception	13	fMRI	emotion non-specific	N	8	5	13	N	28	-	-	-	-	-	-	-

59	Kleber	2007	Perception	16	fMRI	non-specific	Y	5	11	16	Y	31.06	8.27	14.06	7.59	-	-	25.73	7.26
60	Kleider-Offutt	2019	Perception	28	fMRI	non-specific	N	11	17	28	N	21.4	-	-	-	-	-	-	-
61	Koelsch	2003	Perception	11	fMRI	emotion + and -	N	5	6	11	N	24.6	-	-	-	-	-	-	-
62	Koelsch	2014	Perception	20	fMRI	emotion +	N	10	10	20	N	25.55	4.8	-	-	-	-	-	-
63	Koelsch	2018	Imagery	24	fMRI	emotion + and -	Y	12	12	24	N	23.39	3.3	-	-	-	-	-	-
64	Kornysheva	2010	Perception	18	fMRI	rhythm+ beat +metre	N	17	11	18	N	25.1	-	-	-	-	-	-	-
65	Langheim	2002	Perception	6	fMRI	non-specific	Y	2	4	6	Y	27	-	-	-	-	-	-	-
66	Leaver	2009	Production	20	fMRI	non-specific	N	10	10	20	N	24.7	-	-	-	-	-	-	-
67	Lee	2011	Production + Perception	12	fMRI	melody	N	7	5	12	N	20.4	-	5.7	-	-	-	-	-
68	Lehne	2013	Perception	25	fMRI	tension, loudness	N	22	13	25	N	23.9	3.6	6.4	3.6	-	-	-	-
69	Levitin	2005	Perception	13	fMRI	structure	N	6	7	13	Y	-	-	-	-	-	-	-	-
70	Levitin	2016	Production + Perception	1	fMRI	non-specific	Y	1	0	1	Y	55	-	-	-	-	-	-	-
71	Li	2019	Production	31	fMRI	rhythm+ beat +metre	N	15	16	31	N	-	-	7	-	-	-	-	-
72	Limb	2006	Imagery	24	fMRI	rhythm+ beat +metre	N	18	6	24	B	-		-	-	-	-	-	-
73	Limb	2008	Production	6	fMRI	creativity	N	6	0	6	B	34.2	10.4	-	-	-	-	-	-
74	Liu	2018	Production	12	fMRI	creativity	N	12	0	12	B	30.3	-	9.8	4.3	-	-	-	-
75	Matthews	2020	Perception	51	fMRI	rhythm+ beat +metre	N	30	21	51	B	-	-	-	-	-	-	-	-
76	Meister	2004	Imagery + Perception	12	fMRI	learnt	Y	2	10	12	Y	26.6	-	-	-	-	-	-	-
77	Merrill	2012	Imagery	21	fMRI	non-specific	N	14	7	21	N	24.2	2.4	-	-	-	-	-	-
78	Mizuno	2007	Imagery	18	fMRI	tonality	N	10	8	10	N	23.1	2.8	12.4	5.8	-	-	-	-
79	Montag	2011	Perception	33	fMRI	emotion +	Y	6	27	33	N	23.55	5.04	-	-	-	-	-	-
80	Morrison	2003	Perception	6	fMRI	non-specific	N	2	4	6	B	38.3	-	-	-	-	-	-	-
81	Mueller	2015	Perception	23	fMRI	emotion +	N	10	13	23	N	25.9	2.9	-	-	-	-	-	-
82	Ohnishi	2001	Perception	28	fMRI	non-specific	N	14	14	28	B	-	-	-	-	-	-	-	-
83	Park	2013	Perception	12	fMRI	emotion +	N	5	7	12	Y	20.33	2.14	13.2	3.6	-	-	-	-
84	Park	2014	Production	24	fMRI	emotion -	N	20	14	24	B	-	-	-	-	-	-	-	-
85	Parsons	2005	Perception	8	PET	learnt	Y	3	5	8	Y	-	-	-	-	-	-	-	-
86	Pereira	2011	Imagery	27	fMRI	familiarity	N	9	18	27	N	32	-	-	-	-	-	-	-
87	Peretz	2009	Imagery	9	fMRI	familiarity	Y	0	9	9	N	-	-	-	-	-	-	-	-
88	Petrini	2011	Perception	16	fMRI	emotion non-specific	N	8	8	16	N	21.75	-	-	-	-	-	-	-
89	Pfordresher	2014	Perception	20	fRMI	melody	Y	4	16	20	Y	24	-	13.4	-	-	-	-	-
90	Ragert	2014	Perception	17	fMRI	melody	N	9	8	17	Y	26.12	4.2	16.44	5.92	-	-	-	-
91	Reiterer	2008	Perception	17	fMRI	timbre	N	8	9	17	N	25.2	-	-	-	-	-	-	-
92	Rogalsky	2011	Imagery	20	fMRI	melody	Y	9	11	20	N	22.6	-	3.5	-	-	-	-	-
93	Sammler	2010	Imagery	12	fMRI	familiarity	Y	6	6	12	N	29	-	-	-	-	-	-	-
94	Schmithorst	2005	Perception	15	fMRI	melody	Y	4	11	15	N	37.8	15.2	-	-	-	-	-	-
95	Schön	2010	Perception	10	fMRI	non-specific	N	2	8	10	N	24	-	3	-	-	-	-	-
96	Schwenzer	2011	Perception	16	fMRI	pitch	N	8	8	16	N	-	-	-	-	-	-	-	-
97	Shany	2019	Perception	40	fMRI	emotion +	N	18	22	40	B	25.5	3.6	6	-	-	-	-	-
98	Sikka	2015	Perception	40	fMRI	familiarity	N	0	40	40	N	-	-	-	-	-	-	-	-
99	Singer	2016	Perception	40	fMRI	emotion non-specific	N	18	22	40	B	25.5	3.6	12.3	4.7	-	-	-	-
100	Skouras	2014	Production	32	fMRI	emotion non-specific	Y	14	18	32	N	22.93	2.75	3.62	5.04	-	-	-	-
101	Spada	2014	Production	20	fMRI	melody + harmony	N	6	14	20	Y	30.29	7.02	21	6.86	12	-	-	-
102	Tabei	2015	Perception	17	fMRI	emotion non-specific	N	7	10	17	N	21.4	2	-	-	-	-	-	-
103	Tachibana	2010	Imagery + Production	12	fMRI	pitch	N	7	5	12	N	24	-	9.1	5.4	-	-	-	-
104	Taruffi	2017	Perception	24	fMRI	emotion + and -	N	12	12	24	N	25.3	-	-	-	-	-	-	-
105	Tervaniemi	2000	Perception	30	PET	harmony	N	30	0	30	N	26.2	-	-	-	-	-	-	-
106	Tervaniemi	2006	Perception	17	fMRI	timbre	N	9	8	17	N	25.1	-	-	-	-	-	-	-
107	Thaut	2008	Perception	12	fMRI	rhythm+ beat +metre	N	9	3	12	Y	26.1	1.8	-	-	-	-	7	-
108	Tillmann	2003	Perception	15	fMRI	tonality	Y	6	9	15	Y	19.4	-	8.2	2.54	-	-	-	-
109	Tillmann	2006	Perception	20	fMRI	timbre/familiarity	Y	9	11	20	Y	25.1	-	4.5	5.3	-	-	-	-
110	Toiviainen	2014	Perception	15	fMRI	various	N	10	5	15	N	25.7	5.2	-	-	-	-	-	-
111	Trost	2012	Perception	15	fMRI	emotion + and -	N	8	7	15	N	28.8	9.9	-	-	-	-	-	-
112	Trost	2014	Production	18	fMRI	harmony	Y	7	11	18	N	25.8	7.5	5	-	-	-	-	-
113	Tsai	2010	Perception	12	fMRI	rhythm+ beat +metre	Y	2	10	12	N	-	-	-	-	-	-	-	-
114	Tsai	2012	Perception	15	fMRI	rhythm+timbre	N	12	3	15	Y	22	-	6.4	3.1	-	-	-	-
115	Tsai	2018	Perception	14	fMRI	pitch	N	3	11	14	N	-	-	-	-	-	-	-	-
116	Tsai	2019	Production	16	fMRI	pitch/harmony	Y	5	11	16	N	22.44	1.58	-	-	-	-	-	-
117	Uhlig	2013	Perception	17	fMRI	melody	Y	9	8	17	Y	26.12	4.2	16.44	5.92	-	-	-	-
118	Villarreal	2013	Perception	24	fMRI	rhythm+creativity	N	9	15	24	N	21.9	1.6	-	-	-	-	-	-
119	Vuust	2011	Perception	18	fMRI	rhythm	N	14	4	18	Y	29	1	-	-	8	-	7	-

120	Wallmark	2018	Perception	15	fMRI	emotion	N	7	8	15	N	19.1	0.72	-	-	-	-	-	-
121	Watanabe	2008	Perception	18	fMRI	memory	N	12	6	18	N	22.4	0.4	-	-	-	-	-	-
122	Whitehead	2018	Perception	24	fMRI	melody	N	13	11	24	N	25.5	-	4.2	4.73	-	-	-	-
123	Wilson	2010	Perception	26	fMRI	melody	Y	11	15	26	B	31.7	12.4	-	-	-	-	-	-
124	Yoo	2001	Perception	12	fMRI	pitch	N	8	4	12	N	29.9	5.8	-	-	-	-	-	-
125	Zarate	2008	Perception	24	fMRI	pitch	Y	12	12	24	B	-	-	10	3.39	-	-	-	-
126	Zarate	2010	Perception	9	fMRI	pitch	Y	3	6	9	Y	23	3.93	11	4.28	-	-	-	-
127	Zatorre	1994	Perception	12	PET/fMRI	melody	N	6	6	12	N	-	-	-	-	-	-	-	-
128	Zatorre	1996	Perception	12	PET	melody	N	6	6	12	N	22	-	-	-	-	-	-	-
129	Zatorre	2010	Perception	12	fMRI	melody	Y	5	7	12	Y	23	-	16	-	-	-	-	-
130	Zvyagintsev	2013	Perception	15	fMRI	melody	N	8	7	15	N	25.1	5.7	-	-	-	-	-	-

Y, yes; N, no; B, both.

Table 2. Anatomic likelihood estimation meta-analytic results for music perception, production and imagery at cluster level inference p < 0.05 (FWE).

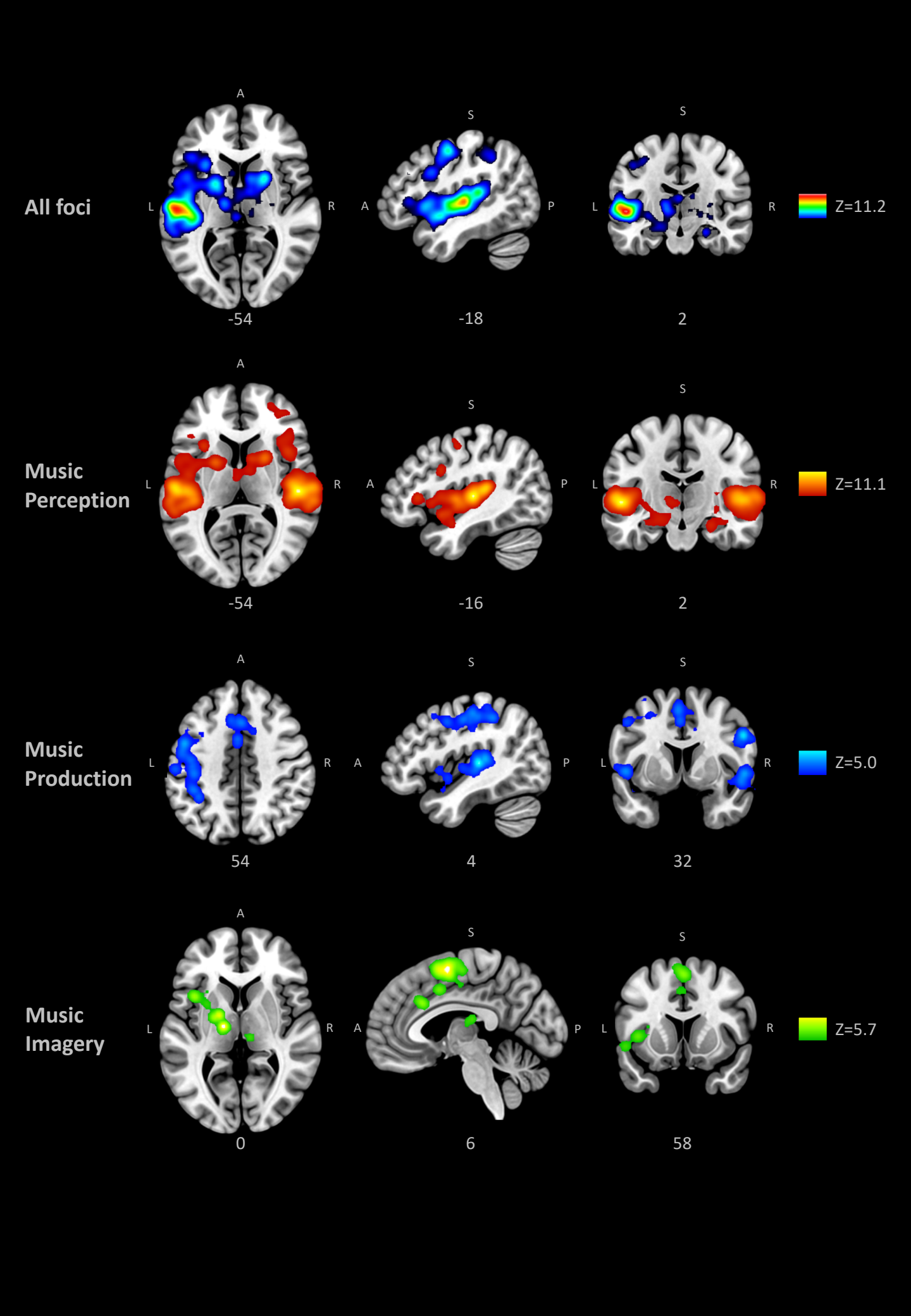
Cluster number	Volume (mm^3)	MNI coordinates x	y	z	ALE	P	Z	Label (Side region BA)
a. All foci: 2660 foci, 139 experiments, 2516 subjects.								
1	130424	-54	-18	2	1E-01	3E-29	11.2	L Superior Temporal Gyrus BA41
		-42	-32	12	8E-02	4E-17	8.3	L Transverse Temporal Gyrus BA41
		-50	-6	48	7E-02	9E-14	7.4	L Precentral Gyrus BA4
		-50	0	-8	6E-02	1E-11	6.7	L Superior Temporal Gyrus BA22
		-54	-42	20	6E-02	3E-11	6.6	L Superior Temporal Gyrus BA13
		22	8	6	6E-02	5E-10	6.1	R Putamen
		-22	4	6	6E-02	6E-10	6.1	L Putamen
		-62	-34	12	6E-02	7E-10	6.1	L Superior Temporal Gyrus BA22
		-50	12	-2	5E-02	4E-09	5.8	L Insula BA13
		-32	18	10	5E-02	1E-07	5.1	L Insula BA13
		-42	-46	42	5E-02	2E-07	5.1	L Inferior Parietal Lobule BA40
		-4	-26	0	5E-02	4E-07	5.0	L Thalamus
		-32	24	0	4E-02	6E-07	4.8	L Insula BA13
		-36	-52	42	4E-02	2E-06	4.7	L Inferior Parietal Lobule BA40
		-30	22	4	4E-02	2E-06	4.7	L Insula BA13
		-14	-14	8	4E-02	3E-06	4.6	L Thalamus
		24	6	-4	4E-02	7E-06	4.4	R Putamen
		-8	10	0	4E-02	8E-06	4.3	L Caudate
		-48	10	30	4E-02	8E-06	4.3	L Inferior Frontal Gyrus BA9
		-18	-4	-8	4E-02	1E-05	4.2	L Putamen
		-20	-4	-18	4E-02	4E-05	4.0	L Parahippocampal Gyrus
		-42	26	4	4E-02	4E-05	3.9	L Inferior Frontal Gyrus BA13
		-54	8	14	3E-02	7E-05	3.8	L Inferior Frontal Gyrus BA44
		24	-14	-18	3E-02	2E-04	3.6	R Parahippocampal Gyrus BA28
		14	-4	10	3E-02	2E-04	3.6	R Thalamus
		0	-18	16	3E-02	2E-04	3.6	L Thalamus
		-20	-12	-14	3E-02	6E-04	3.2	L Amygdala
		-34	-58	58	3E-02	7E-04	3.2	L Superior Parietal Lobule BA7
		-40	-28	46	3E-02	7E-04	3.2	L Inferior Parietal Lobule BA40
		-28	-6	50	3E-02	8E-04	3.2	L Middle Frontal Gyrus BA6
		-32	-14	-2	3E-02	1E-03	3.1	L Putamen
		-36	-20	54	3E-02	1E-03	3.1	L Precentral Gyrus BA4
		-30	0	50	3E-02	1E-03	3.0	L Middle Frontal Gyrus BA6
		8	-24	0	3E-02	2E-03	2.9	R Thalamus
		-42	-2	-18	3E-02	2E-03	2.9	L Sub-Gyral BA21
		-54	4	22	3E-02	2E-03	2.9	L Inferior Frontal Gyrus BA9
		-34	4	48	3E-02	2E-03	2.8	L Middle Frontal Gyrus BA6
		26	-26	-16	3E-02	3E-03	2.7	R Parahippocampal Gyrus BA35
		-18	10	-12	2E-02	4E-03	2.6	L Putamen
		30	-2	-20	2E-02	6E-03	2.5	R Amygdala
		2	12	-8	2E-02	7E-03	2.5	L Anterior Cingulate BA25
		-30	-20	-16	2E-02	7E-03	2.4	L Hippocampus
		12	-16	16	2E-02	7E-03	2.4	R Thalamus
		6	-36	-8	2E-02	1E-02	2.3	R Cerebellum
		-42	26	28	2E-02	1E-02	2.2	L Middle Frontal Gyrus BA9
		30	-16	-4	2E-02	1E-02	2.2	R Putamen
		20	-16	-2	2E-02	2E-02	2.2	R Thalamus
		32	-10	-20	2E-02	2E-02	2.2	R Hippocampus
		34	-18	-14	2E-02	2E-02	2.1	R Hippocampus
		38	-20	-14	2E-02	2E-02	2.1	R Hippocampus
		30	-16	8	2E-02	2E-02	2.0	R Putamen
b. Music perception: 1898 foci, 105 experiments, 2035 subjects.								
1	100608	-54	-16	2	1E-01	1E-28	11.0	L Superior Temporal Gyrus BA22
		-40	-30	12	7E-02	4E-14	7.5	L Transverse Temporal Gyrus BA41
		-48	-34	12	6E-02	7E-12	6.8	L Superior Temporal Gyrus BA41
		22	8	6	6E-02	6E-11	6.4	R Putamen
		-22	4	6	5E-02	1E-09	6.0	L Putamen
		-32	18	10	4E-02	3E-07	5.0	L Insula BA13
		-50	14	-2	4E-02	3E-07	5.0	L Insula BA13
		-8	10	0	4E-02	7E-07	4.8	L Caudate Head
		10	6	4	4E-02	8E-07	4.8	R Caudate Body

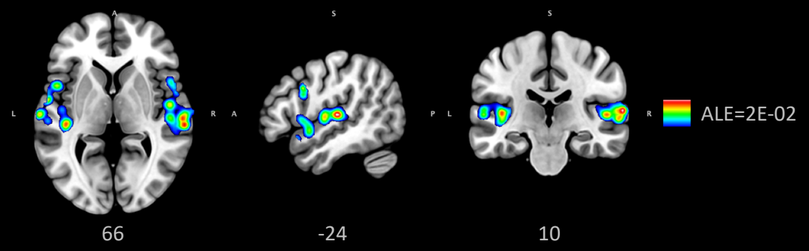
		-30	24	0	3E-02	6E-06	4.4	L Insula BA13
		-4	-26	0	3E-02	1E-05	4.3	L Thalamus
		-18	-4	-18	3E-02	2E-05	4.2	L Parahippocampal Gyrus BA28
		24	-14	-18	3E-02	2E-05	4.1	R Parahippocampal Gyrus BA28
		-42	26	4	3E-02	4E-05	3.9	L Inferior Frontal Gyrus BA13
		-54	6	12	3E-02	7E-05	3.8	L Precentral Gyrus BA6
		-20	-12	-14	3E-02	1E-04	3.7	L Amygdala
		-18	-2	-8	3E-02	1E-04	3.6	L Lateral Globus Pallidus
		-16	-28	-14	3E-02	3E-04	3.4	L Parahippocampal Gyrus BA35
		-26	-32	-12	3E-02	3E-04	3.4	L Parahippocampal Gyrus BA36
		-42	-4	-18	2E-02	8E-04	3.1	L Sub-Gyral BA21
		-18	10	-12	2E-02	9E-04	3.1	L Putamen
		-10	-18	2	2E-02	9E-04	3.1	L Thalamus
		8	-24	-2	2E-02	1E-03	3.1	R Thalamus
		-36	2	10	2E-02	1E-03	3.1	L Insula BA13
		-10	-12	12	2E-02	1E-03	3.0	L Thalamus
		-8	40	-6	2E-02	1E-03	3.0	L Anterior Cingulate BA24
		2	12	-8	2E-02	2E-03	3.0	L Anterior Cingulate BA25
		-30	-20	-16	2E-02	2E-03	2.9	L Hippocampus
		12	-16	16	2E-02	3E-03	2.8	R Thalamus
		-2	-10	8	2E-02	3E-03	2.8	L Thalamus
		12	0	-10	2E-02	3E-03	2.8	R Medial Globus Pallidus
		26	-26	-14	2E-02	3E-03	2.7	R Parahippocampal Gyrus BA28
		8	32	-10	2E-02	3E-03	2.7	R Anterior Cingulate BA24
		-2	-4	6	2E-02	4E-03	2.7	L Thalamus
		32	-10	-20	2E-02	4E-03	2.6	R Amygdala
		30	-2	-20	2E-02	4E-03	2.6	R Amygdala
		-24	26	-10	2E-02	5E-03	2.6	L Claustrum
		0	-18	16	2E-02	5E-03	2.5	L Thalamus
		20	0	-16	2E-02	6E-03	2.5	R Parahippocampal Gyrus BA28
		38	-20	-16	2E-02	6E-03	2.5	R Hippocampus
		34	-18	-14	2E-02	6E-03	2.5	R Hippocampus
		-32	-16	-2	2E-02	6E-03	2.5	L Putamen
		-16	-42	-12	2E-02	7E-03	2.5	L Cerebellum. Culmen
		30	-16	-4	2E-02	8E-03	2.4	R Lateral Globus Pallidus
		18	-6	22	2E-02	8E-03	2.4	R Caudate Body
		-36	-4	-20	2E-02	9E-03	2.4	L Amygdala
		0	28	-10	2E-02	1E-02	2.3	L Anterior Cingulate BA24
		-2	26	-6	2E-02	1E-02	2.3	L Anterior Cingulate BA24
		-36	-32	-12	2E-02	1E-02	2.3	L Hippocampus
		-44	6	-24	2E-02	1E-02	2.2	L Superior Temporal Gyrus BA38
		-62	-6	-22	2E-02	2E-02	2.1	L Middle Temporal Gyrus BA21
		-54	2	24	2E-02	3E-02	1.9	L Inferior Frontal Gyrus BA9
		0	-22	-12	2E-02	3E-02	1.9	L Brainstem. Red Nucleus
		4	38	-16	2E-02	3E-02	1.9	R Anterior Cingulate BA32
2	58704	52	-20	4	1E-01	7E-27	10.7	R Superior Temporal Gyrus BA22
		54	-4	-4	8E-02	3E-17	8.4	R Superior Temporal Gyrus BA22
		64	-30	10	5E-02	2E-10	6.2	R Superior Temporal Gyrus BA42
		48	14	-4	4E-02	2E-07	5.1	R Insula BA13
		42	12	6	3E-02	8E-06	4.3	R Insula BA13
		42	26	2	3E-02	1E-05	4.3	R Inferior Frontal Gyrus BA13
		42	20	34	3E-02	7E-05	3.8	R Precentral Gyrus BA9
		48	10	26	3E-02	8E-05	3.8	R Inferior Frontal Gyrus BA9
		40	48	12	3E-02	3E-04	3.4	R Middle Frontal Gyrus BA10
		54	10	-16	2E-02	1E-03	3.1	R Superior Temporal Gyrus BA38
		38	50	20	2E-02	2E-03	2.9	R Middle Frontal Gyrus BA10
		38	10	-18	2E-02	2E-03	2.9	R Inferior Frontal Gyrus BA13
		38	10	-18	2E-02	2E-03	2.9	R Inferior Frontal Gyrus BA13
		40	38	30	2E-02	2E-03	2.9	R Middle Frontal Gyrus BA9
		42	6	-14	2E-02	2E-03	2.9	R Extra-Nuclear BA13
		28	54	8	2E-02	3E-03	2.8	R Superior Frontal Gyrus BA10
		48	42	6	2E-02	1E-02	2.3	R Inferior Frontal Gyrus BA46
		36	40	22	2E-02	1E-02	2.3	R Middle Frontal Gyrus BA9
		48	-32	24	2E-02	1E-02	2.3	R Insula BA13
		24	58	0	2E-02	2E-02	2.1	R Superior Frontal Gyrus BA10
		30	-16	10	2E-02	2E-02	2.0	R Putamen

c. Music production: 499 foci, 19 experiments, 292 subjects.								
1	29056	54	4	32	2E-02	3E-07	5.0	R Precentral Gyrus BA6
		66	-24	10	2E-02	7E-07	4.8	R Superior Temporal Gyrus BA42
		50	-20	6	2E-02	7E-07	4.8	R Superior Temporal Gyrus BA13
		64	-26	4	2E-02	7E-07	4.8	R Superior Temporal Gyrus BA22
		62	-22	2	2E-02	4E-06	4.5	R Superior Temporal Gyrus BA41
		54	6	-2	2E-02	1E-05	4.2	R Superior Temporal Gyrus BA22
		50	-10	4	2E-02	2E-05	4.1	R Insula BA13
		64	-28	14	2E-02	2E-05	4.1	R Superior Temporal Gyrus BA42
		68	-16	8	2E-02	4E-05	3.9	R Transverse Temporal Gyrus BA42
		58	-36	8	2E-02	6E-05	3.9	R Middle Temporal Gyrus BA22
		52	10	24	2E-02	8E-05	3.8	R Inferior Frontal Gyrus BA9
		52	-42	12	2E-02	1E-04	3.7	R Superior Temporal Gyrus BA22
		58	-10	22	1E-02	3E-04	3.4	R Precentral Gyrus BA4
		48	16	-16	1E-02	3E-04	3.4	R Inferior Frontal Gyrus BA47
		38	0	18	1E-02	7E-04	3.2	R Insula BA13
		54	-28	18	1E-02	3E-03	2.8	R Superior Temporal Gyrus BA41
		38	-2	2	9E-03	6E-03	2.5	R Claustrum
		40	-34	16	9E-03	6E-03	2.5	R Superior Temporal Gyrus BA41
		52	-12	20	8E-03	1E-02	2.2	R Insula BA13
		56	8	14	8E-03	2E-02	2.1	R Inferior Frontal Gyrus BA44
		64	6	-16	7E-03	3E-02	1.9	R Superior Temporal Gyrus BA21
2	26056	-48	0	42	2E-02	8E-07	4.8	L Precentral Gyrus BA6
		-40	-40	46	2E-02	5E-06	4.4	L Inferior Parietal Lobule BA40
		-36	-46	48	2E-02	7E-06	4.3	L Inferior Parietal Lobule BA40
		-40	-26	46	2E-02	1E-05	4.2	L Inferior Parietal Lobule BA40
		-62	-34	14	2E-02	2E-05	4.1	L Superior Temporal Gyrus BA22
		-60	-44	20	2E-02	2E-05	4.1	L Superior Temporal Gyrus BA13
		-58	-56	20	2E-02	4E-05	4.0	L Superior Temporal Gyrus BA22
		-44	-22	50	2E-02	5E-05	3.9	L Postcentral Gyrus BA2
		-52	-46	22	2E-02	9E-05	3.8	L Superior Temporal Gyrus BA13
		-44	-14	44	2E-02	1E-04	3.6	L Precentral Gyrus BA4
		-56	-22	44	1E-02	3E-04	3.4	L Postcentral Gyrus BA3
		-56	-50	12	1E-02	4E-04	3.4	L Superior Temporal Gyrus BA22
		-52	-16	38	1E-02	4E-04	3.3	L Postcentral Gyrus BA2
		-52	-36	28	1E-02	2E-03	3.0	L Inferior Parietal Lobule BA40
		-28	4	50	1E-02	5E-03	2.6	L Middle Frontal Gyrus BA6
		-46	12	48	1E-02	5E-03	2.6	L Middle Frontal Gyrus BA6
		-38	2	48	9E-03	8E-03	2.4	L Middle Frontal Gyrus BA6
		-28	-34	56	8E-03	2E-02	2.1	L Sub-Gyral BA40
		-30	-26	60	8E-03	2E-02	2.1	L Precentral Gyrus BA4
		-32	-32	62	7E-03	2E-02	2.1	L Postcentral Gyrus BA40
		-34	4	62	7E-03	2E-02	2.0	L Middle Frontal Gyrus BA6
		-48	-46	4	7E-03	2E-02	2.0	L Middle Temporal Gyrus BA22
		-34	8	42	7E-03	2E-02	2.0	L Middle Frontal Gyrus BA6
		-18	6	48	6E-03	4E-02	1.7	L Cingulate Gyrus BA24
3	18000	-10	-10	52	2E-02	1E-06	4.7	L Medial Frontal Gyrus BA6
		0	20	40	2E-02	7E-06	4.3	L Cingulate Gyrus BA32
		0	-4	58	2E-02	9E-06	4.3	L Medial Frontal Gyrus BA6
		-4	4	54	2E-02	2E-05	4.1	L Medial Frontal Gyrus BA6
		-2	12	62	2E-02	5E-05	3.9	L Superior Frontal Gyrus BA6
		-2	2	46	2E-02	5E-05	3.9	L Cingulate Gyrus BA24
		-8	18	48	2E-02	8E-05	3.8	L Medial Frontal Gyrus BA32
		12	10	38	1E-02	8E-04	3.1	R Cingulate Gyrus BA24
		10	22	54	1E-02	2E-03	2.9	R Superior Frontal Gyrus BA8
		6	14	62	1E-02	4E-03	2.7	R Superior Frontal Gyrus BA6
		8	34	28	9E-03	6E-03	2.5	R Cingulate Gyrus BA32
		2	-12	68	7E-03	2E-02	2.1	L Medial Frontal Gyrus BA6
		-6	-14	66	7E-03	2E-02	2.0	L Medial Frontal Gyrus BA6
		-10	-14	64	7E-03	2E-02	2.0	L Precentral Gyrus BA6
4	16584	-42	-28	6	3E-02	3E-09	5.8	L Superior Temporal Gyrus BA41
		-58	-4	0	2E-02	2E-06	4.6	L Superior Temporal Gyrus BA22
		-50	8	0	2E-02	5E-06	4.4	L Insula
		-66	-18	2	2E-02	2E-05	4.1	L Superior Temporal Gyrus BA22
		-58	-22	10	2E-02	5E-05	3.9	L Transverse Temporal Gyrus BA41
		-60	-16	8	2E-02	5E-05	3.9	L Transverse Temporal Gyrus BA42

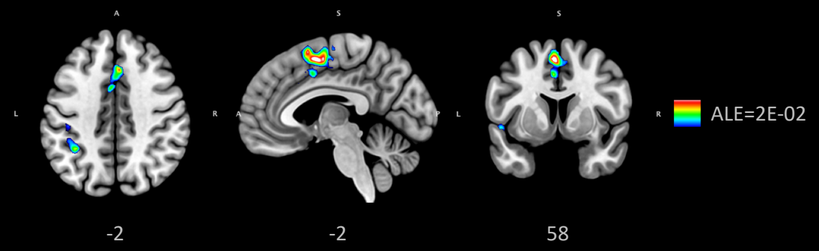
		-58	-24	6	2E-02	7E-05	3.8	L Superior Temporal Gyrus BA41
		-48	0	-6	1E-02	2E-04	3.6	L Superior Temporal Gyrus BA22
		-46	-14	2	1E-02	2E-03	2.8	L Insula BA13
		-44	4	-18	7E-03	2E-02	2.0	L Superior Temporal Gyrus BA38
		-54	-18	20	7E-03	2E-02	2.0	L Postcentral Gyrus BA43
d. Music imagery: 263 foci, 15 experiments, 189 subjects.								
1	14704	0	6	58	2E-02	6E-09	5.7	L Medial Frontal Gyrus BA6
		-2	0	62	2E-02	1E-07	5.2	L Medial Frontal Gyrus BA6
		4	24	42	1E-02	1E-04	3.7	R Cingulate Gyrus BA32
		-4	22	30	1E-02	2E-04	3.6	L Cingulate Gyrus BA32
		-4	8	42	1E-02	7E-04	3.2	L Cingulate Gyrus BA24
		0	20	62	7E-03	7E-03	2.5	L Superior Frontal Gyrus BA6
		4	20	62	7E-03	7E-03	2.4	R Superior Frontal Gyrus BA6
		-4	-12	46	6E-03	2E-02	2.1	L Cingulate Gyrus BA24
2	12824	-34	-58	56	2E-02	1E-07	5.1	L Superior Parietal Lobule BA7
		-32	-54	42	2E-02	2E-07	5.1	L Angular Gyrus BA39
		-40	-64	52	2E-02	8E-06	4.3	L Inferior Parietal Lobule BA7
		-32	-52	32	1E-02	4E-04	3.4	L Middle Temporal Gyrus BA39
		-40	-36	32	8E-03	4E-03	2.6	L Supramarginal Gyrus BA40
		-44	-30	42	7E-03	6E-03	2.5	L Inferior Parietal Lobule BA40
3	12424	-14	-14	8	2E-02	2E-07	5.1	L Thalamus
		-18	-4	6	2E-02	2E-05	4.2	L Thalamus
		-40	14	2	1E-02	2E-04	3.5	L Insula BA13
		-2	-18	14	1E-02	1E-03	3.0	L Thalamus
		-56	22	-4	9E-03	1E-03	3.0	L Inferior Frontal Gyrus BA47
		-50	14	-6	9E-03	2E-03	2.9	L Superior Temporal Gyrus BA22
		-50	6	-6	8E-03	5E-03	2.6	L Superior Temporal Gyrus BA22
		-30	16	12	7E-03	7E-03	2.5	L Claustrum
		-28	18	8	7E-03	7E-03	2.5	L Claustrum
		-30	6	2	7E-03	7E-03	2.5	L Thalamus
		8	-22	6	7E-03	8E-03	2.4	R Thalamus
		-48	30	-16	6E-03	2E-02	2.1	L Inferior Frontal Gyrus BA47

ALE, anatomic likelihood estimation; P, p-value; Z, peak z-value; R, right; L, left; BA, Brodmann area.

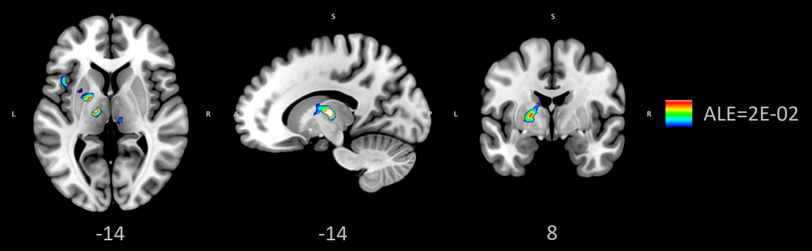

All foci
A
L
R
-54
S
A
P
-18
S
L
R
2
Z=11.2
Music Perception
A
L
R
-54
S
A
P
-16
S
L
R
2
Z=11.1
Music Production
A
L
R
54
S
A
P
4
S
L
R
32
Z=5.0
Music Imagery
A
L
R
0
S
A
P
6
S
L
R
58
Z=5.7



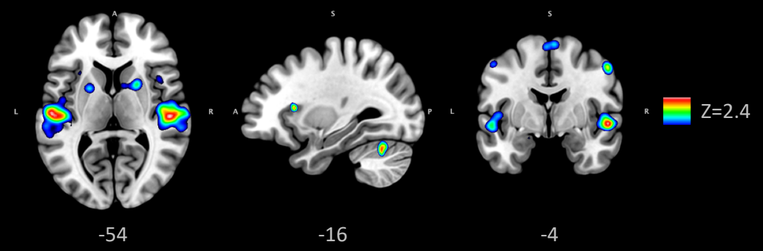
Perception + Production



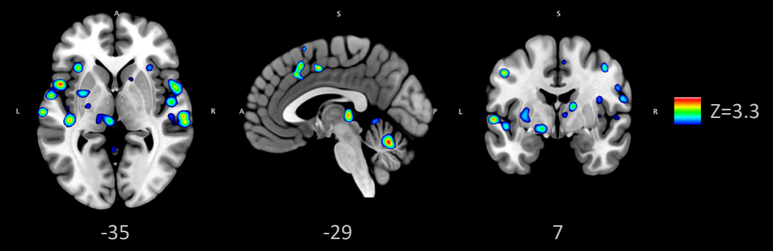
Production + Imagery



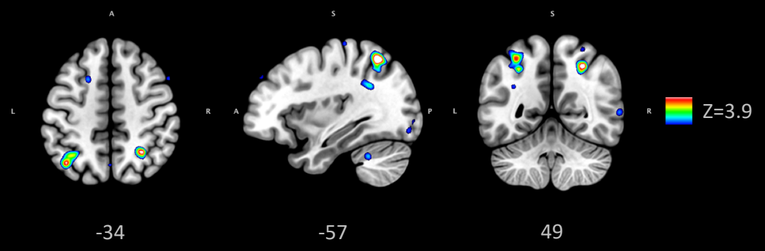
Imagery + Perception



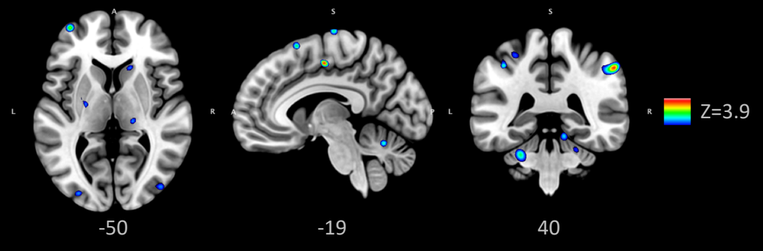
Perception - Production



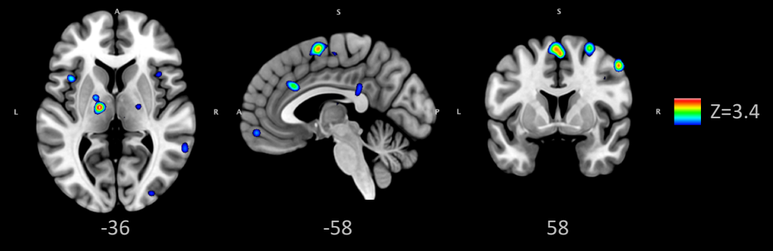
Production - Imagery



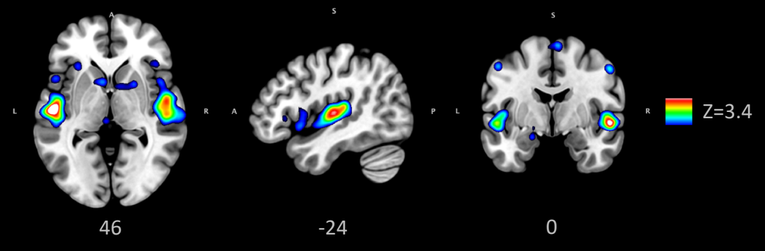
Imagery - Perception



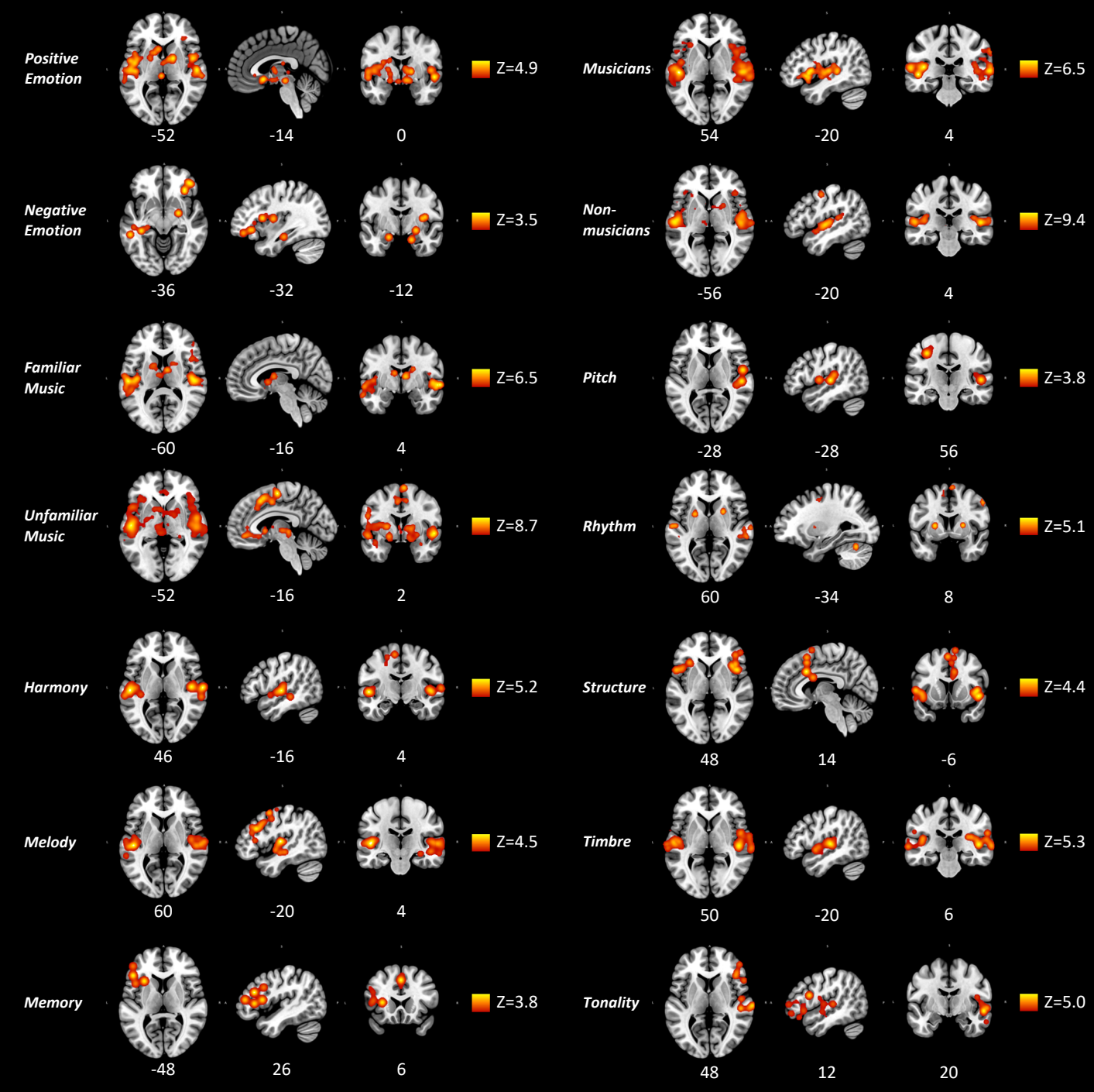
Production - Perception

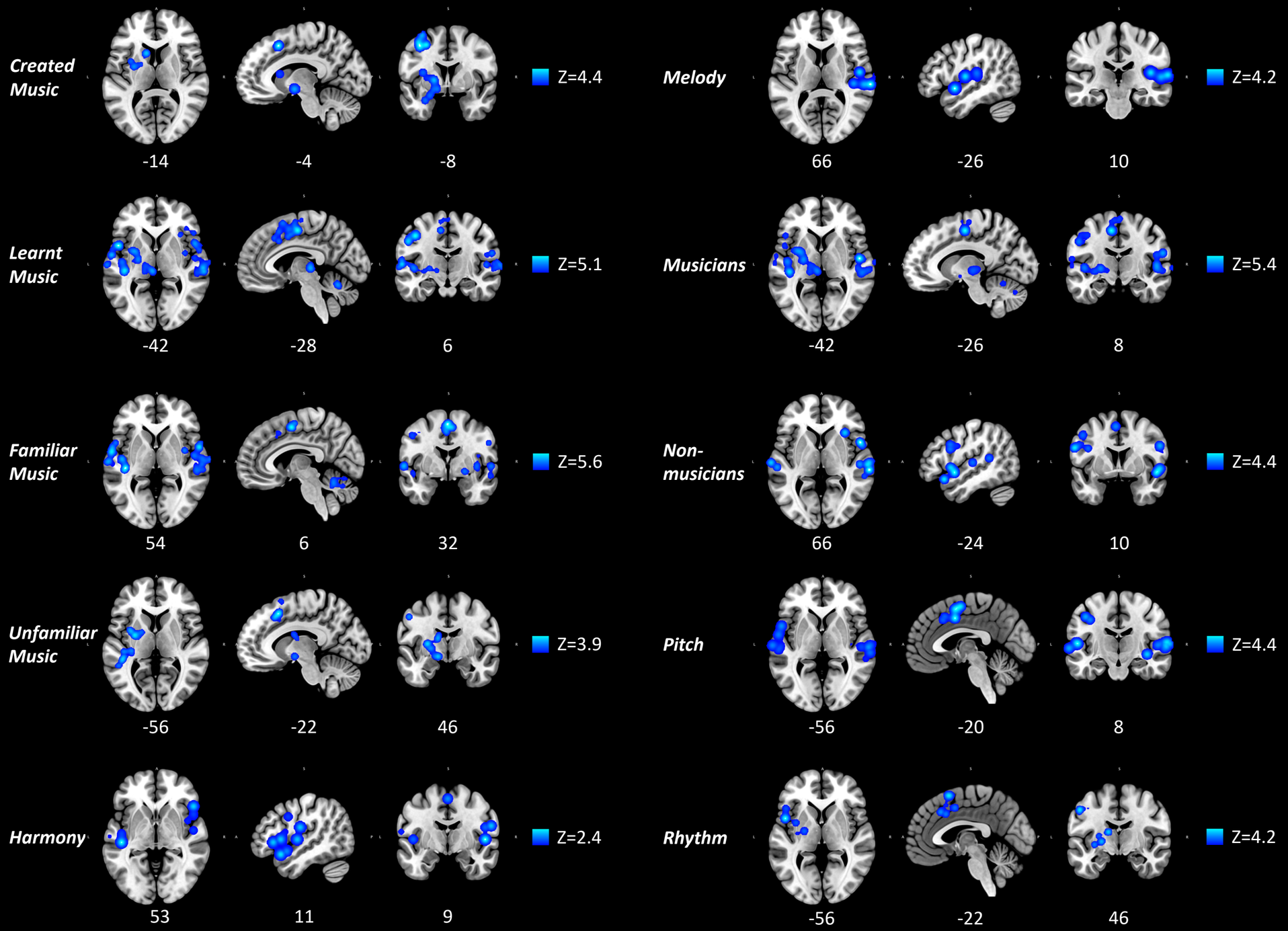


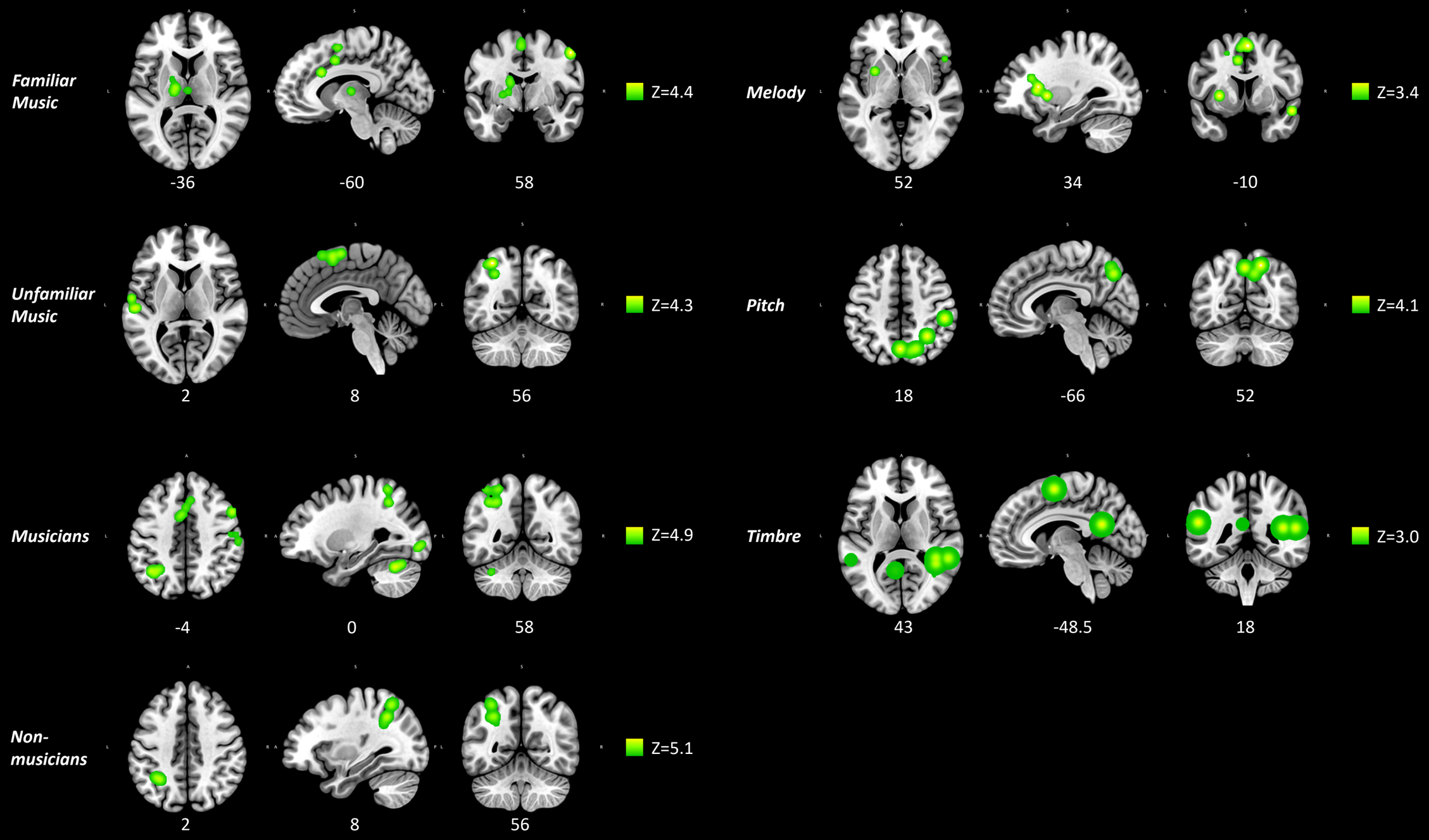
Imagery - Production



Perception - Imagery


Positive Emotion
-52
-14
0
Z=4.9
Negative Emotion
-36
-32
-12
Z=3.5
Familiar Music
-60
-16
4
Z=6.5
Unfamiliar Music
-52
-16
2
Z=8.7
Harmony
46
-16
4
Z=5.2
Melody
60
-20
4
Z=4.5
Memory
-48
26
6
Z=3.8
Musicians
54
-20
4
Z=6.5
Non-musicians
-56
-20
4
Z=9.4
Pitch
-28
-28
56
Z=3.8
Rhythm
60
-34
8
Z=5.1
Structure
48
14
-6
Z=4.4
Timbre
50
-20
6
Z=5.3
Tonality
48
12
20
Z=5.0


Created Music
-14
-4
-8
Z=4.4
Melody
66
-26
10
Z=4.2
Learnt Music
-42
-28
6
Z=5.1
Musicians
-42
-26
8
Z=5.4
Familiar Music
54
6
32
Z=5.6
Non-musicians
66
-24
10
Z=4.4
Unfamiliar Music
-56
-22
46
Z=3.9
Pitch
-56
-20
8
Z=4.4
Harmony
53
11
9
Z=2.4
Rhythm
-56
-22
46
Z=4.2


Familiar Music
-36
-60
58
Z=4.4
Unfamiliar Music
2
8
56
Z=4.3
Musicians
-4
0
58
Z=4.9
Non-musicians
2
8
56
Z=5.1
Melody
52
34
-10
Z=3.4
Pitch
18
-66
52
Z=4.1
Timbre
43
-48.5
18
Z=3.0