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The functional brain networks activated by music listening: A neuroimaging meta-analysis

and implications for treatment

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Abstract

Objective: Previous behavioral studies show that music listening enhances attention and working memory in both healthy and clinical populations. However, how music listening engages brain functional networks remains elusive due to inconsistent results from previous findings.

Method: A meta-analysis of functional magnetic resonance imaging data using Seedbased d Mapping with Permutation of Subject Images was performed. Studies that presented music listening paradigms to healthy individuals were included. Subgroup analyses were performed to investigate the effects of music genres on brain activation. To examine functional network correlates, voxels that were significantly activated by music listening were overlaid onto cortical, subcortical and striatal network parcellations.

Results: Whole-group analysis showed that ventral attention, somatomotor, default, dorsal attention, frontoparietal and limbic networks significantly coactivated during music listening (familywise error-corrected ps < .01). Specifically, music listening activated multiple frontal, temporal, subcortical and cerebellar regions. Subgroup analyses revealed that classical music, but not songs or simple tunes, activated the limbic network. Meta-regression analysis revealed nonsignificant correlations between years of music training and all brain regions activated during music listening.

Conclusions: Music listening bilaterally activated multiple cortical, subcortical and cerebellar regions encompassing multiple brain networks that were not modulated by music training experience. It is recommended that music listening can be applied to people with neurological disorders to modulate the disordered functional brain networks known to underlie the pathophysiology of these diseases, while future studies may help delineate the effects of music preferences on brain activation patterns among these patients to promote the development of evidence-based medicine.

Keywords: music, fMRI, meta-analysis, resting state network, SDM-PSI

Key Points

- How music listening engages brain networks supporting different cognitive functions remains unclear.
- Music listening leads to an increase of activation in ventral attention, somatomotor, default, dorsal attention, frontoparietal and limbic networks.
- Music listening may help regulate the disordered brain network organization in people with neurological disorders such as Autism Spectrum Disorder and Alzheimer's Disease.
- Future studies may help delineate the effects of music preferences on brain activation patterns among these patients to promote the development of personalized medicine.

Music has long been considered to be a therapeutic modality (Aldridge, 1993; Hillecke, Nickel, & Bolay, 2005; Thaut, 2015). Among various forms of therapeutic music activities (Schlaug, Altenmüüller, & Thaut, 2010), music listening has been applied to a broad spectrum of healthy and clinical populations given its ease of administration and high cost-effectiveness (Mok & Wong, 2003), as well as its ability to modulate a wide range of neuropsychological functions (Peretz & Zatorre, 2005). Specifically, behavioral studies have shown promising results that music listening can enhance attention and working memory. For healthy elderly, listening to classical music can improve episodic memory recall in elderly (Bottiroli, Rosi, Russo, Vecchi, & Cavallini, 2014). For 6-month-old normal-developing infants who regularly listen to lullabies, classical music listening could promote longer attention and eye contact with new people who sang a familiar melody (Boer & Abubakar, 2014). For people with neurological disorders, a study showed that working memory performance was improved in people with Alzheimer's disease who listened to classical music (AD(R. G. Thompson, Moulin, Hayre, & Jones, 2005), while both attentional control and working memory performance were improved in patients with stroke (Särkämö et al., 2008); for patients with chronic visual neglect secondary to stroke, music listening has been shown to enhance visual awareness indicated by improved performance in multiple visual perceptual tasks (Soto et al., 2009).

In view of the cognitive-enhancing effects of music listening and its potential application in neurological rehabilitation, researchers have been exploring how music listening modulates the neurobiology of the brain (Blood, Petrc, Worsley, Pike, & Zatorre, 2000; Karmonik et al., 2020). Specifically, it has been hypothesized that music listening can modulate the activation of multiple functional networks in the human brain, resulting in domain-general improvements in cognitive performance (Karmonik et al., 2016; Stefan Koelsch, 2009). Human brain functional networks, usually studied with functional magnetic resonance imaging (fMRI) techniques, involve interactions among different brain regions, with each identified functional network supporting different cognitive and perceptual functions (Yeo et al., 2011). For example, the limbic network has been suggested to be responsible for emotion and memory (Rolls, 2015), the salience network has been associated with attentional control (Vinod Menon & Uddin, 2010), and the default mode network may participate in the coordination of other functional networks to support efficient information processing (Raichle, 2015). Indeed, fMRI studies on music listening have generally indicated that music listening induces widespread coactivations across various functional networks, although the networks reported to be activated have been inconsistent across studies. For instance, some studies have shown that the limbic system, including the ventral striatum, amygdala and hippocampus, is activated (Ball et al., 2007; Blood et al., 2000; V. Menon & Levitin, 2005), while other studies have shown that the theory-of-mind network (Stefan Koelsch, 2009), which comprises frontotemporal regions including the medial and superior temporal gyri (Whitehead & Armony, 2018), and the frontal brain regions (i.e., inferior frontal gyrus, orbital frontolateral cortex and the anterior insula (Stefan Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005) are activated during music listening.

The aforementioned inconsistent results might be due to limited study power, different definitions of functional brain networks used, and varied significance thresholds used. Heterogeneous participants' characteristics and experimental designs might also induce result inconsistencies across studies. For participants' characteristics, previous studies have shown that music experiences are modulated by age (Morrison, Demorest, & Stambaugh, 2008) and gender (Schafer & Sedlmeier, 2010) differences. Participants' musical training background could also be highly varied across studies; for example, although both Tervaniemi et al. (2006) and Janata et al. (2002) investigated the fMRI activation pattern during music listening, Tervaniemi et al. (2006) recruited subjects without music training, but Janata et al. (2006) studied the effects in musicians. For experimental designs, neuroimaging studies investigating the effects of music listening on brain activation patterns would sometimes adopt heterogeneous baseline conditions. For example, although both Baumgartner et al. (2006) and Dyck et al. (2011) presented classical music with mood-congruent emotional faces to the participants, Baumgartner et al. (2006) used emotional face viewing as the baseline condition, while Dyck et al. (2011) requested the participants to keep their eyes closed during baseline fMRI recording. In addition, previous empirical studies have shown that listening to different music genres can induce different brain activation patterns. For instance, Liu et al (2020) showed that music with lyrics activated additional brain regions (i.e. supplementary motor area and middle temporal gyrus) when compared to classical music listening; Brattico et al. (2011) showed that sad music with lyrics.

Performing a meta-analysis with previously published neuroimaging data might be helpful in addressing these limitations. First, meta-analysis can increase the overall study power for the identification of consistently coactivated brain regions during music listening. Second, registering consistently coactivated brain regions identified across studies on a standardized brain atlas may be possible by means of performing meta-analysis (Kim, 2019; Zhang, Geng, & Lee, 2017), which could help identify which functional brain networks are consistently modulated by music listening. Last but not least, the between-study experimental design heterogeneity discussed above that might have contributed to inconsistencies in the results could be controlled by performing covariate and subgroup analyses enabled by Seed-based d Mapping with Permutation of Subject Images (SDM-PSI; Albajes-Eizagirre, Solanes, Vieta, & Radua, 2019). SDM-PSI is a coordinate-based neuroimaging meta-analysis software that imputes several effect sizes for each voxel for each individual study, such that different effect sizes that a voxel could have had in the unavailable raw study data could be estimated to avoid the biases associated with single imputation. Also, SDM-PSI is considered a more conservative approach when compared to other coordinate-based neuroimaging meta-analysis methods by adopting a less biased simulation of the population effect size, threshold-free cluster enhancement (TFCE) statistics (i.e., a familywise error correction method), which reduces the detection of false effects by controlling the familywise error rates below 5 % (Albajes-Eizagirre et al., 2019). Given age, gender and baseline conditions could contribute to the brain activation differences across studies, covariate analyses with these variables were conducted to minimize the impact of these factors on the meta-analytic results. To gain a more comprehensive understanding on the modulating effects of different music genres (i.e. classical music and music with/without lyrics), subgroup analyses were performed. Findings from this meta-analysis will extend previous knowledge of the neural mechanisms underlying the therapeutic effects of music listening, which will be invaluable for designing effective interventions for individuals with brain dysfunctions.

Method

Literature search

This study was conducted according to the Preferred Reported Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher, Liberati, Tetzlaff, Altman, & Group, 2009); PROSPERO registration number: CRD42020199912). A preliminary search was conducted in June 2020 to confirm the choice of keywords for the electronic database search. An extensive title/abstract/keyword search was then performed on 11 August 2020. To identify relevant studies, the electronic databases Scopus, Embase, ScienceDirect, PubMed and PsycINFO were used with the keywords ["music" AND ("fMRI" OR "functional magnetic resonance imaging")]. No limit was set on publication dates. A manual search of the reference lists in a previously published neuroimaging meta-analysis on music listening (Gordon, Cobb, & Balasubramaniam, 2018) was also conducted to identify additional studies for the current review.

Study inclusion

Studies that reported fMRI brain activation patterns from whole-brain analyses (Müller et al., 2018) in healthy subjects during passive music listening in contrast to a baseline condition without a music listening component were included in this meta-analysis. To identify studies that fulfilled our inclusion criteria, after the removal of duplicate records, title/abstract screening was conducted with the following exclusion criteria applied: 1) studies without peer-reviewed empirical data (e.g., book chapters, conference proceedings and editorials); 2) studies without an English version of the full text; 3) nonhuman studies; 4) studies without presenting musiclistening stimuli during experimental conditions; 5) studies not using fMRI to study brain activation; and 6) studies including participants with any neurological diagnosis, such as head trauma, epilepsy or neuropsychiatric disorders. The full texts of the remaining studies were then further examined for inclusion in the final dataset. Studies 1) without fMRI whole-brain analysis data available and/or 2) adopting a baseline comparison with music components (e.g., familiar music as the experimental condition and nonfamiliar music as the baseline condition) were excluded. The above screening processes were conducted by three research assistants (MHC, SC and AW) with their decisions recorded on an Excel spreadsheet. In cases of disagreement

regarding the inclusion/exclusion of a paper, the first author made the final decision based on the majority rule to ensure that the decision process was unbiased.

Data extraction and recoding

The demographic data, experimental details and fMRI statistical maps in a standard stereotactic space or peak coordinates information of the included papers were extracted. Citations were entered into a database by two research assistants (KYC and SCT) to minimize errors. Demographic data included the sample size, mean age (years), gender ratio (female: male), years of music training received by the participants and subject inclusion criteria. Experimental details included the task description in both the experimental and baseline conditions. The different characteristics of music-listening stimuli (e.g., music genre) were further recoded to facilitate our subgroup analyses. Experiments placed in the "classical music" subgroup involved the listening of classical music only, while the "song" subgroup involved the listening of music with concurrently sung lyrics; regarding the "simple tune" subgroup, participants were exposed to monophonic tone sequences.

Data analysis

Data were analyzed using SDM-PSI software (Albajes-Eizagirre, Solanes, Vieta, et al., 2019). First, extracted fMRI coordinates data were preprocessed with anisotropy = 1, isotropic full width at half maximum (FWHM) set at 20 mm, and a voxel size of 2 mm on a gray matter mask. Notably, the FWHM was set at 20mm given this value was within the optimal FWHM range of 15-30mm (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2008) and was found to optimize the balance between sensitivity and specificity in SDM analysis (Radua et al., 2011).

After the coordinate map for each study was formed, 50 imputations of subject images for each study were performed by the software. The imputed subject images for each study were analysed in group, followed by the meta-analysis of study images with participants' mean age, gender ratio (female: male), and baseline conditions as covariates. Finally, the meta-analysis images were combined using Rubin's rules variance estimator (Rubin, 1987), a standard approach for analyzing multiply imputed datasets (Marshall, Altman, Holder, & Royston, 2009), to investigate brain activation during music listening. To delineate the moderating effects of the nature of the different music stimuli on brain activation patterns, subgroup analyses were performed for different music genres (i.e., classical music, contemporary music and songs). To explore the effects of music training on brain activation during music listening, a meta-regression was performed between mean years of music training and brain activation. The significance level of all analyses, including the meta-regression, was kept at a familywise-error rate (FWER) of 0.01 except for analyses with fewer than 10 experiments in which we reported the results yielded at p=0.005 (uncorrected) in accordance with a previous study (Radua et al., 2012) for exploratory purposes. To further understand how music listening engages functional brain networks, each local peak within the significant clusters identified in the meta-analysis was categorized based on their location within the seven functional networks defined by a series of human cerebral (Schaefer et al., 2018; Yeo et al., 2011), cerebellar (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011) and striatal (Choi, Yeo, & Buckner, 2012) parcellation studies. As defined by these studies using the same parcellation method, there are seven functional networks in the human brain, including the default network (DN) that coordinates other task-positive networks, somatomotor network (SMN) that is responsible for motor control and execution, frontoparietal network (FPN) that coordinates goal-directed behavior, dorsal attention network (DAN) for top-down

attention control, ventral attention network (VAN) that detects salient stimuli, limbic network (LIM) that serves for emotional processing and visual network (VIS) that processes incoming visual information. The network parcellation was chosen because of the standardized terminologies used across the cerebral, cerebellar and striatal regions and the fact that it was with large-scale data (i.e., with over one thousand participants' data being analyzed). To assess the heterogeneity across studies, I-squared values were calculated for the significant peak coordinates yielded from the main analysis (Higgins & Thompson, 2002), with I² values of 25 %, 50 % and 75 % being considered indicative of low, medium and high heterogeneity respectively. To assess the risk of publication bias, a test for funnel plot asymmetry was conducted for the significant peaks in the main analysis. The peak coordinates of brain regions were also assessed by Harbord-Egger bias tests (Harbord, Egger, & Sterne, 2006) to show differences between individual l values based on listening or not listening to music stimuli. Significant Harbord-Egger bias tests indicate "small study effects".

Results

Study selection

After the initial search, a total of 2811 studies were retrieved from the electronic databases. In addition, 17 studies were retrieved from Gordon et al. (2018), and 6 studies were further identified during a supplementary search. After removing 1902 duplicate records, the titles and abstracts of 935 records were screened. After applying the exclusion criteria, 331 records were excluded, while 604 records remained for the full-text screening. In the full-text screening, 270 records were excluded, and 334 records remained for further screening. A total of 297 records were excluded at the last stage of screening. Thirty-seven studies (including 50

experiments) were included in the meta-analysis. The complete process of article selection is outlined in *Figure 1*.

Characteristics of the included studies

The included studies represented 703 healthy individuals with normal hearing ability, who did not have any neurological/neuropsychiatric disorders, participated in passive music listening tasks. Regarding the music genre, 16 studies (with 21 experiments) involved classical music listening (Agustus et al., 2018; Altenmüller, Siggel, Mohammadi, Samii, & Münte, 2014; Aubé, Angulo-Perkins, Peretz, Concha, & Armony, 2013; Baumgartner, Lutz, Schmidt, & Jäncke, 2006; Demorest et al., 2010; Dyck et al., 2011; Flores-Gutiérrez et al., 2007; Janata, Tillmann, & Bharucha, 2002; Jeong et al., 2011; Langheim, Callicott, Mattay, Duyn, & Weinberger, 2002; Li, Cheng, & Tsai, 2019; Steven J. Morrison, Demorest, Aylward, Cramer, & Maravilla, 2003; Mutschler et al., 2010; Ohnishi et al., 2001; Reason et al., 2016; Trost, Ethofer, Zentner, & Vuilleumier, 2012), 13 studies (with 17 experiments) involved instrumental and tone sequence listening (Brown & Martinez, 2007; Escoffier, Zhong, Schirmer, & Qiu, 2013; Green, Jääskeläinen, Sams, & Rauschecker, 2018; M. Groussard et al., 2010; Mathilde Groussard et al., 2010; Petr Janata et al., 2002; Steven J. Morrison et al., 2003; Petrini, Crabbe, Sheridan, & Pollick, 2011; Rogalsky, Rong, Saberi, & Hickok, 2011; Schön et al., 2010; Tervaniemi et al., 2006; Tillmann, Janata, & Bharucha, 2003; Wallmark, Deblieck, & Iacoboni, 2018), and six studies (with seven experiments) involved listening to songs with lyrics (Berns, Capra, Moore, & Noussair, 2010; Bishop, Wright, & Karageorghis, 2014; Herholz, Halpern, & Zatorre, 2012; Janata, 2009; Sammler et al., 2010; Schmithorst, 2005). The remaining three studies (with five experiments) investigated brain activation when participants listened to a single-pitched rhythmic pattern and were excluded from the subgroup analyses (J. A. Grahn & Brett, 2007; Jessica A. Grahn & McAuley, 2009; Tsai, Chen, Chou, & Chen, 2010). The demographic details of the participants and experimental details of each experiment are listed in *Table 1*.

Brain activation during music listening

The whole-group analysis with age, gender ratio, and baseline condition as covariates showed that six of the functional networks, the VAN, SMN, DN, DAN, FPN and LIM, significantly coactivated during music listening (FWER-corrected ps < .01; *Table 2*). Specifically, music listening activated cortical regions including the bilateral inferior frontal gyri (IFG) and insula in the frontal lobe, the pre/postcentral gyri and Rolandic operculum, temporal lobe structures including Heschl's gyrus, the superior temporal gyrus (STG) extending to the temporal pole and the middle temporal gyrus (MTG), and midline structures including the supplementary motor area and the cingulate cortex. Regarding subcortical brain regions, the bilateral hippocampus and amygdala, as well as the thalamus and dorsal striatum (i.e. putamen), were activated. Regarding the cerebellum, the bilateral crus I and hemispheric lobule VI were activated. In terms of cluster size, music listening appeared to activate a more extensive set of cortical and subcortical areas in the right hemisphere than in the left hemisphere, while more extensive activations were found in the left hemisphere than in the right cerebellum (*Figure 2*).

Effects of the nature of the music stimuli on activation patterns

Subgroup analyses of experiments that exposed participants to classical music (21 experiments; *Table 3*; *Figure 3*), simple tunes/tonal sequences (17 experiments; *Table 4*; *Figure 4*) or music with lyrics (8 experiments; *Table 5*; *Figure 5*) revealed largely similar brain

activation patterns with slight differences between different types of music stimuli. In terms of functional networks, classical music, but not songs or simple tunes, was shown to activate the LIM. In terms of brain regions, regarding the frontal regions, classical music and songs predominantly activated the right IFG, and simple tunes engaged the bilateral IFG; regarding cerebellar and subcortical regions, classical music, but not songs or simple tunes, was found to significantly activate (FWER-corrected ps < .01) the left cerebellum crus I and II, bilateral amygdala and left hippocampus.

Meta-regression of years of music training and brain activation during music listening

Meta-regression analysis revealed nonsignificant correlations between years of music training and all brain regions activated during music listening at FWER-corrected p = .01 and uncorrected p = .0005.

Between-study heterogeneity and risk of publication bias

I-squared values for the peak coordinates of each significant cluster in the main analysis revealed very low to moderate between-study heterogeneity [I² for the right IFG (56, 8, 10) = 15.78%; I² for the left MTG (-52, -16, -8) = 24.02\%; I² for the left cerebellum crus I (-16, -70, - 28) = 9.05%; I² for the right cerebellum hemispheric lobule VI (28, -54, -22) = 25.45%; I² for the right anterior thalamic projections (16, 14, 6) = 1.14%; I² for the left postcentral gyrus (-52, -10, 50) = 46.38%; I² for the left anterior thalamic projections (-12, 12, 6) = 0.39%]. Visual inspection of the funnel plots for these peaks (*Figure 6*) did not reveal obvious asymmetries, with the exception that the plot for the left anterior thalamic projections (-12, 12, 6) deviated from the midline to the extreme left, which might indicate possible selective publication bias in the

estimated between-study heterogeneity. Harbord-Egger bias tests of these peaks were nonsignificant (all ps > .987), indicating nonsignificant small study effects.

Discussion

This meta-analysis aimed to identify the functional brain networks activated during passive music listening in healthy individuals. After conducting a comprehensive search with multiple electronic databases, manually searching the reference lists of previously published articles and applying the inclusion and exclusion criteria, 37 studies (with 50 experiments) were included in this study. In summary, this meta-analysis indicated three points. First, attentive music listening bilaterally activated multiple cortical, subcortical and cerebellar regions encompassing six of the functional networks, the VAN, SMN, DN, DAN, FPN and LIM. Second, different types of music elicited slightly different activation patterns, with only classical music eliciting significant activations in the cerebellum and LIM, including the hippocampus and amygdala, while listening to songs selectively activated the right but not the bilateral IFG. Third, formal music training was not shown to modulate the extensive brain activation induced by music listening, as evidenced by the nonsignificant results in the meta-regression between brain activation and years of music training of the participants.

Extensive activation of multiple brain networks during music listening

Our main analysis with age, gender and baseline conditions as covariates revealed that all functional networks except the VIS are significantly activated during music listening. Previous studies have shown that the VAN and DAN collaborate together to control attentional processes (Vossel, Geng, & Fink, 2014), with the VAN showing stronger activation during the detection of

salient stimuli (Kim, 2014) and the DAN being more activated when maintaining a stable level of attention for prolonged task performance (Esterman, Noonan, Rosenberg, & DeGutis, 2013). The FPN contributes to a person's ability to coordinate behavior in a goal-directed manner (Marek & Dosenbach, 2018), which has been found to be specifically activated during the phase of maintaining information in working memory tasks (Kim, 2019). The DN coordinates taskpositive networks (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006) that aid brain network organization (Raichle, 2015); specifically, increased coactivation of the DN and working memory-specific brain regions (e.g., the left dorsolateral prefrontal cortex and left inferior parietal lobule) has been found during the preparation stage before the execution of a working memory task, with the subsiding of DN activation during execution of the task (Koshino, Minamoto, Yaoi, Osaka, & Osaka, 2014). For the LIM, which has long been believed to be involved in both emotion and cognitive processing (Catani, Dell'Acqua, & De Schotten, 2013), coordinated enhancement in activation of the hippocampus and amygdala has been found to be critical for successful emotional association memory formation (Madan, Fujiwara, Caplan, & Sommer, 2017). Finally, the SMN is primarily involved in motor control and execution (Lemon, 2008); some brain regions. The activation of the bilateral supplementary motor area to auditory stimuli has been discussed as being vital for the facilitation of the flexible engagement of sensorimotor processes to guide auditory perception (Lima, Krishnan, & Scott, 2016). With reference to this evidence regarding the neuropsychological correlates of each brain network, our results could imply that music listening can enhance the functional brain networks that support attentional control and working memory performance. Consistent with a previous hypothesis (P. Janata et al., 2002; Karmonik et al., 2016), our results could also serve as a neurobiological explanation for the behavioral observations that music listening can improve attention and

memory in both healthy (Boer & Abubakar, 2014; Bottiroli et al., 2014; W. F. Thompson, Hall, & Pressing, 2001) and clinical (Särkämö et al., 2008; Soto et al., 2009; R. G. Thompson et al., 2005) populations. Although our results provide important insights regarding the neural mechanisms underlying the clinical effects of music listening, how music listening modulates the interplay between these functional networks remains unknown. Future studies might investigate the modulatory effects of music listening on this interplay in terms of changes in functional connectivity (Zhu, Liu, Mathiak, Ristaniemi, & Cong, 2019).

Music listening and mirror neuron hypothesis

Auditory mirror neurons, which fire both when macaques perform hand/mouth actions and when they listen to sounds of similar actions (Keyser, Kohler, Umilta, Nanetti, Fogassi, Gallese, 2003), have also been found evident in humans (Gazzola, Aziz-Zadeh & Keysers, 2006). A previous meta-analysis showed that brain regions with mirror properties activated by auditory stimuli include bilateral precentral gyrus, left inferior and middle frontal gyrus, left supplementary motor area, left inferior parietal lobule and left superior temporal gyrus (Molenberghs, Cunnington & Mattingley, 2012). A recent study further suggested that these cortical mirror neuron regions form an integrated network with the cerebellum (i.e. hemispheric lobules V and VI; crus I, VIIIa and VIIIb) and basal ganglia (i.e. putamen, globus pallidus and subthalamic nucleus; Errante & Fogassi, 2020) in support of auditory-motor interaction (Zatorre, Chen & Penhune, 2006). It has been hypothesized that music activities engage the mirror neurons (Molnar-Szakacs & Overy, 2006), and our results indeed showed that music listening activated some of the brain regions containing mirror neurons as well as the supportive networks, namely the left inferior frontal gyrus, the bilateral supplementary motor area, parts of the cerebellum (i.e. crus I/II and hemispheric lobule V/VI) and dorsal striatum (i.e. putamen and caudate nucleus). This finding provided meta-analytic evidence to support the recruitment of parts of the mirror neuron system during music listening. Moreover, it implies that mirror neurons may be the possible neural correlate that enable the interaction of music information with the motor system. Indeed, a recent study showed that music listening can modify gait patterns in both healthy individuals and patients with Parkinson's disease (Bartolo et al., 2020). To increase our understanding in this area of study, future research might examine how the mirror neuron system in people with or without neurological dysfunctions changes when listening to different genres of music. Also, given auditory mirror neurons are defined as neurons that are activated during both action execution and listening to the sounds generated by the similar action performed, the neuroimaging investigations of the whole-brain activation (instead of regions-of-interest analysis) during music imitation (i.e. reproduce the music stimulus after hearing it), rather than music listening only, may be worthwhile to be conducted to verify our claim. This also helps to provide a more comprehensive map of the mirror neuron system during music perception.

Nature of the music stimuli and differential brain activation patterns

The results from the subgroup analyses confirmed our hypothesis that listening to music of various genres elicited different brain activation patterns. The following three observations are particularly worth noting -1) right-lateralized IFG activation was specific to classical music and song listening but not for simple tunes; 2) songs and simple tune listening activated both the caudal (i.e. BA44) and rostral (BA47/48) part of the IFG, while classical music only activates the rostral IFG; 3) classical music but not simple tone sequences or songs was shown to engage the

cerebellum as well as the limbic system comprising the amygdala and hippocampus. For the first observation, the right-lateralized activation of the IFG for classical music and songs in healthy individuals was consistent with previous studies (Lai, Pantazatos, Schneider, & Hirsch, 2012) and might be attributed to the specialization of the right IFG for music hierarchical structure processing (Cheung, Meyer, Friederici, & Koelsch, 2018). In comparison to simple tunes (i.e., monophonic tone sequences), classical music and songs, which are usually homophonic or polyphonic in texture, involve a more complex hierarchical structure, which might in turn more consistently activate the right IFG (especially the opercular part) and result in the lateralized pattern observed in our meta-analysis. For the second observation, given that rostral IFG, BA47 in particular, is known for language processing and comprehension (Dronkers et al., 2004; Alfredo et al., 2017), the consistent involvement of the rostral IFG across the three music genres might imply that the human brain interprets music as language and attempts to identify the meaning of music. In addition, the right rostral IFG is also known for its ability to track changing emotions (Goodkind et al., 2011), in the context of music listening, such function may enable us to continuously interpret the emotional changes in a piece of music. Regarding the activation of caudal IFG, it is not surprising that BA44 is activated during song but not classical music listening, as it is within the Broca's regions which has been long regarded as the hub for spoken language processing (Amunts et al., 2004; Heim et al., 2009). For the third observation, in contrast to previous studies (S. Koelsch, Fritz, Cramon, Müller, & Friederici, 2006), we did not yield significant activations in the limbic system when participants listened to songs. There are two possible reasons accounting for this discrepancy. First, the song subgroup analysis involved only a limited number of experiments (n=7), which might have had inadequate power to detect the expected significant activation. Additionally, given that the engagement of the LIM is highly

affected by the familiarity (Mueller et al., 2011; Pereira et al., 2011) and emotion elicited by the chosen music (Brattico et al., 2011; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007), it might be possible that the heterogeneity across studies in terms of song selection (with variable familiarity and emotion elicited) might have resulted in inconsistencies that led to a nonsignificant pooled effect. There is a need to further verify the effects of song listening on brain activation and the how familiarity and emotions modulate the activation of the hippocampus and amygdala; more empirical studies that report whole-brain data are encouraged such that a meta-analysis of song listening could be performed with adequate power in the future.

Treatment implications

Given that music listening can enhance the activation of functional networks supporting attention and memory performance, clinical populations with aberrant functional networks associated with impaired attention and memory performance might benefit from therapy using music listening as a treatment medium. Notably, such network modulatory effects were not, at least linearly, significantly correlated with years of music training received by the participants, implying that music listening could be applied to clinical populations regardless of their music training background. These clinical populations include individuals with autism spectrum disorder (ASD), who are characterized by altered mirror neuron system activation (Chan & Han, 2020), as well as atypical and dysregulated activations in multiple brain networks (Barendse et al., 2013; Keehn, Nair, Lincoln, Townsend, & Müller, 2016), that have been found to be associated with their global executive function deficits (Demetriou et al., 2018) and difficulties in social communication (Padmanabhan, Lynch, Schaer, & Menon, 2017). Other populations who may benefit from music listening include individuals with AD, in whom abnormal activations in

multiple resting-state networks, including the DN, LIM and salience network (Badhwar et al., 2017; Grieder, Wang, Dierks, Wahlund, & Jann, 2018), have been found to be associated with their autobiographical memory deficits (Greicius, Srivastava, Reiss, & Menon, 2004) . Indeed, a recent study performed by Rabeyron et al. (2020) showed that daily music listening for one consecutive month could improve social communication in children with ASD; for individuals with AD, listening to their favored music could enhance functional connectivity between multiple resting-state networks, including the DN (King et al., 2019) , while listening to a classical music piece familiar to all AD participants induced significant autobiographical memory improvement (El Haj, Postal, & Allain, 2012) . The clinical studies collectively provide preliminary evidence to support the therapeutic application of music listening in these clinical populations. To facilitate the development of music listening as a potential therapeutic modality, the dose-response and psychophysiological relationships, as well as how music preferences and genres impact the functional network interactions in these patients, should be more rigorously studied in the future.

Limitations

By employing an extensive literature search in multiple electronic databases as well as manually searching the reference lists of previously published papers relevant to our studies, we attempted to obtain a comprehensive set of original datasets for meta-analysis. Although we were able to include 37 studies with 50 experiments that fulfilled all of our inclusion criteria, some studies that did not provide whole-brain analysis data had to be excluded from our meta-analysis to avoid introducing potentially biased results. Future studies with whole-brain data are warranted to provide a more comprehensive picture regarding the neural basis of music listening.

Furthermore, our study included only data from healthy individuals, which limited the generalizability of the results given that brain activation in response to music listening might be affected by various neurological diseases (Hillman, 2014). More empirical studies are recommended that specifically investigate the neural mechanisms of music listening in patients with various neurological disorders to further promote the development of evidence-based medicine. In addition, although we presented the different brain activation patterns when participants listened to music of different genres, no statistical tests were conducted to compare the difference in activations between these three subgroups. Moreover, although we attempted to control for the between-study heterogeneity induced by different participants' characteristics and baseline conditions adopted in individual studies and to minimize the effects of the variations in significance thresholds across studies by using a more conservative statistical estimate (i.e. TFCE), we could not fully control for the varying thresholds, thus affecting the accuracy of our results. Notwithstanding this limitation, we offered preliminary evidence that music listening of different genres can induce different activation patterns, and the differences among these stimuli have to be further verified with empirical studies.

Conclusion

Multiple beneficial effects have been documented after music listening, but the underlying neural mechanisms remain elusive. By conducting a neuroimaging meta-analysis using SDM-PSI, we investigated the effects of music listening on brain activation in healthy individuals. The results showed that passive music listening bilaterally activated multiple cortical, subcortical and cerebellar regions encompassing multiple functional networks that were not modulated by music training experience. Additionally, different types of music elicited slightly different activation patterns. It is recommended that music listening could be applied to various groups of people with neurodevelopmental disorders to support their attention and working memory through modulation of disordered functional brain networks known to underlie the pathophysiology of these diseases, while future studies may help delineate the effects of music preference on the brain activation patterns among these patients to promote the development of evidence-based medicine.

Author Note

This research was supported by the research grant [ZE65] from the Hong Kong Polytechnic University. The authors declare that there is no commercial or financial conflict of interest. We thank Miss Shanjin Chan, Miss K.Y. Cheung, Miss M.H. Choi, Miss S.C. Tsang and Miss Anisha Wong for their efforts in supporting the article screening, study inclusion and data extraction processes. The authors declare that there is no commercial or financial conflict of interest.

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Expt	- -	D	emograph	ic Data	Experimental Design			
. No.	Study	N	Mean Age (years)	Ratio of gender (F:M)	Additional subject inclusion criteria	Music stimuli	fMRI task	Baseline
1	Agustus (2018)	20	66.6	10:10	Intact cognitive ability (i.e. score at least 27/30 in MMSE)	Classical music	Listening to classical music excerpts	Rest
2	Altenmuller (2014)	18	28.7	9:9	N/A	Classical music	 Listening to classical music excerpts Ratings for emotions, arousal and liking of the excerpts 	Rest
3	Aube (2013)	47	26.4	20:27	Right-handed	Classical music	 Listening to classical music excerpts Press button on target tone 	Listening to different vocalizati ons (laughter, cries, scream, coughs & yawn)
4	Baumgartner (2006)	9	24.78	9:0	Right-handed	Classical music	Viewing of fear-, sad-, and happy-inducing pictures and listening to emotional classical music excerpts	Viewing emotionall y inducing pictures
5	Berns (2010)	27	14.6	14:13	N/A	Songs	 Listening to song excerpts Rating for likability 	Rest
6	Bishop (2013)	12	21.2	6:6	N/A	Songs	Listening to song excerpts	Rest
7	Brown (2007)	6	23.5	3:3	Right-handed	Simple tunes	Listening to instrumental music with eyes closed	Rest
8	Demorest (2010)	16	28.6	8:8	< 1 year of private music lessons and < 3	Classical music	 Listening to familiar classical music Memory test 	Rest

Table 1: Summary of participants' demographic data and experimental designs of included studies

					years of ensemble			
9	Demorest (2010)	16	28.6	8:8	<1 year of private music lessons and <3 years of ensemble	Classical music	 Listening to unfamiliar classical music Memory test 	Rest
10	Dyck (2011)	30	25.5	16:14	N/A	Classical music	 Viewing of happy- inducing pictures Listening to happy classical music excerpts 	Fixation cross
11	Dyck (2011)	30	25.5	16:14	N/A	Classical music	 2) Viewing of sad- inducing pictures 2) Listening to sad classical music excerpts 	Fixation cross
12	Escoffier (2013)	16	21.7	7:9	N/A	Simple tunes	 Listen to instrumental tunes pitch discrimination and rating for emotions 	Rest
13	Flores- Gutiérrez (2007)	19	25	8:11	 No formal music training Right-handed 	Classical music	Listening to classical music excerpts	White noise
14	Grahn (2007)	27	24.5	8:19	Right-handed	Rhythm	Rhythm discrimination task	Rest
15	Grahn (2009)	35	29.9	12:23	Right-handed	Rhythm	Tempo change discrimination task	Rest

 Table 1 (cont'd)

Expt Demographic Data						Experimental Design		
. No.	Study	N	Mean Age	Ratio of gender (F:M)	Additional subject inclusion criteria	Music stimuli	fMRI task	Baseline
16	Green (2018)	22	Age range: 21-39	5:17	High English proficiency	Simple tunes	 Listening to tone sequences Count the number of harmonic chords in the tone sequence 	Visual stimuli (Gabor patches)
17	Groussard (2010)	20	22.85	10:10	N/A	Simple tunes	1) Listening to instrumental tunes	Rest

							2) Rating for familiarity	
18	Groussard (2010)	20	24.55	10:10	1) No formal music training 2) No absolute pitch	Simple tunes	 Listening to instrumental tunes Rating for familiarity 	Verbal expression
19	Herholz (2012)	10	27	5:5	Right-handed	Songs	 Listening to the song excerpts Silently read the lyrics presented in rhythm with the tune 	Neutral- mood video viewing
20	Janata (2009)	13	20	11:2	N/A	Songs	 Listening to the song excerpts Rating for familiarity 	Rest
21	Janata (2009)	13	20	11:2	N/A	Songs	 Listening to the song excerpts Ratings for emotions 	Rest
22	Janata (2002)	12	28.5	7:5	 With music training Right-handed 	Classical music	Listening to classical music excerpts	Rest
23	Janata (2002)	8	26	4:4	N/A	Simple tunes	 Detect timbre deviation Detect tonality violation 	Rest
24	Jeong (2011)	15	22.8	10:5	Right-handed individuals	Classical music	Listening to classical music excerpts	Fixation cross
25	Jeong (2011)	15	22.8	10:5	Right-handed individuals	Classical music	Listening to classical music excerpts	Fixation cross
26	Langheim (2002)	6	27	4:2	N/A	Classical music	Listening to self- chosen classical music excerpt	Rest
27	Li (2019)	23	22.44	11:12	N/A	Classical music	 Listening to happy and sad mood inducing music Reading positive/negative words 	Imagery g of neutral scenes without music

28	Morrison (2003)	6	38.3	4:2	 With music training No absolute pitch 	Classical music	Listening to classical (baroque period) music excerpts	Rest
29	Morrison (2003)	6	34.2	4:2	 With music training No absolute pitch 	Classical music	Listening to classical (baroque period) music excerpts	Rest
30	Morrison (2003)	6	38.3	4:2	 With music training No absolute pitch 	Simple tunes	Listening to simple Chinese music melodies	Rest
31	Morrison (2003)	6	34.2	4:2	 With music training No absolute pitch 	Simple tunes	Listening to simple Chinese music melodies	Rest

 Table 1 (cont'd)

Expt		D	emographic	Data		Experimental Design			
. No.	Study	Ν	Mean Age (SD)	Ratio of	Additional subject	Music stimuli	fMRI task	Baseline	
				gender	inclusion				
				(F:M)	criteria				
32	Mutschler (2010)	19	22.74	11:9	N/A	Classical music	Listening to classical music excerpts	Rest	
33	Ohnishi	14	Age range:	12:2	1) With music	Classical	Listening to classical	Rest	
	(2001)		20-27		training	music	music excerpts		
					2) Right-handed		_	_	
34	Ohnishi	14	Age range:	12:2	1) With music	Classical	Listening to classical	Rest	
	(2001)		20-27		training	music	music excerpts		
					2) Right-handed				
35	Petrini	16	21.75	8:8	N/A	Simple	Listening to	Fixation	
	(2011)					tunes	improvised	cross	
							instrumental tunes		
- 26				0.10	N T / A	<u>C1 ' 1</u>	1) T	XX7 / 1 *	
36	Reason	22	23.3	9:13	N/A	Classical	1) Listening to	Watching	
	(2016)					music	classical (baroque	dancing	
							period) music excerpts	performan	
							2) Watching dancing	ce	
							performance		
37	Rogalsky	20	22.6	11:9	Right-handed	Simple	Listening to simple	Rest	
	(2011)					tunes	instrumental tunes		

38	Sammler (2010)	12	29	6:6	Right-handed	Songs	Listening to the song excerpts	Rest
39	Schmithorrst (2005)	15	37.8	4:11	N/A	Songs	Listening to unharmonized and harmonized songs with lyrics	Random tones
40	Schon (2010)	13	24	8:5	Right-handed	Simple tunes	 Listening to three- note melodies Discrimination task 	Noise
41	Schon (2010)	13	24	8:5	Right-handed	Simple tunes	 Listening to trisyllabic sung words Discrimination task 	Noise
42	Schon (2010)	18	26	9:9	Right-handed	Simple tunes	 Listening to trisyllabic sung words Discrimination task 	Noise
43	Tervaniemi (2006)	17	25.1	8:9	1) No music training 2) Right-handed	Simple tunes	Listening to improvised instrumental tunes	Speech
44	Tillmann (2003)	15	19.4	9:6	 With music training Right-handed 	Simple tunes	Listening to instrumental tunes	Rest
45	Trost (2012)	15	28.8	7:8	N/A	Classical music	Listening to classical music with eyes closed	Atonal random melodies
46	Tsai (2010)	15	Age range: 20-26	13:2	Right-handed	Rhythm	Listening to unlearned percussion music	Pink noise
47	Tsai (2010)	15	Age range: 20-26	13:2	Right-handed	Rhythm	Listening to learned percussion music	Pink noise
48	Tsai (2010)	15	Age range: 20-26	13:2	Right-handed	Rhythm	Listening to learned melodic music	Pink noise
49	Wallmark (2018)	15	19.1	8:7	Right-handed	Simple tunes	Listening of 2 second novel instrumental tunes	Silence
50	Wallmark (2018)	20	19.1	13:7	Right-handed	Simple tunes	Listening 16-second novel instrumental tunes	Silence

Cluster	Cluster size	Max. SDM- Z	Brain region	Peak MNI	Anatomical position (Brodmann area)	Resting-state network
1	23781	9.138	Frontal	56,8,10 46,8,0 8,6,64 52,-4,52 -2,44,18	R inferior frontal gyrus, opercular part (BA44,47,48) R insula (BA48) R/L supplementary motor area (BA6,23) R middle frontal gyrus (BA6) L anterior cingulate gyri (BA11,32)	VAN SMN DN DAN FPN
			Central	64,-4,18 50,2,2 44,0,50 -2,26,36	R postcentral gyrus (BA43) R rolandic operculum (BA48) R precentral gyrus (BA4,6) L/R median cingulate gyri (BA23,24)	— LIM
			Parietal	4,-36,28	R posterior cingulate gyri (BA23)	
			Temporal	44,-6,-12 54,-10,6 62,4,-2 62,0,-16	R superior temporal gyrus (BA48) R heschl gyrus (BA48) R temporal pole, superior temporal gyrus (BA38) R middle temporal gyrus (BA21)	
			Subcortical	34,-4,4 20,-8,-12 20,-10,-18	R lenticular nucleus, putamen (BA48) R hippocampus R amygdala	
2	12333	8.366	Frontal	-42,0,6 -54,18,18	L insula (BA48) L inferior frontal gyrus, triangular part (BA45,48)	SMN DN
			Central	-60,-2,6	L rolandic operculum (BA48)	
			Parietal	-56,-26,18	L supramarginal gyrus (BA42)	
			Temporal	-52,-16,-8 -52,4,0 -54,-30,14 -32,-26,8	L middle temporal gyrus (BA22,48) L temporal pole, superior temporal gyrus (BA48) L superior temporal gyrus (BA22,42) L heschl gyrus (BA48)	

Table 2: Brain activation during music listening (overall analysis)

Ta	bl	e 2	(cont	'd)
			1	

Cluster	Cluster size	Max. SDM-Z	Brain region	Peak MNI	Anatomical position (Brodmann area)	Resting-state network
3	6046	6.983	Cerebellar	-16,-70,- 28 -16,-64,- 26 -14,-72,- 44 -24,-76,- 38 -28,-48,- 36 -26,-58,- 50	L cerebellum, crus I L cerebellum, hemispheric lobule VI L cerebellum, hemispheric lobule VIIB L cerebellum, crus II Middle cerebellar peduncles L cerebellum, hemispheric lobule VIII	FPN VAN DAN DN
4	3998	5.157	Cerebellar	28,-54,-22 38,-70,-32 10,-48,-14	R cerebellum, hemispheric lobule VI R cerebellum, crus I R cerebellum, hemispheric lobule IV/V	VAN DN DAN FPN SMN
5	935	4.659	Subcortical	16,14,6 12,0,12 0,-12,6	R anterior thalamic projections R caudate nucleus L/R thalamus	FPN
6	349	4.602	Central	-52,-10,50 -40,-10,52	L postcentral gyrus (BA6) L precentral gyrus (BA6)	SMN DAN
7	127	4.237	Subcortical	-12,12,6	L anterior thalamic projections	FPN

Cluster	Cluster size	Max. SDM- Z	Brain region	Peak MNI	Anatomical position (Brodmann area)	Resting-state network			
1	9719	6.999	Frontal	42,-2,-4 50,10,2 34,16,-22	R insula (BA47,48) R inferior frontal gyrus, opercular part (BA48) R inferior frontal gyrus, orbital part (BA38,47)	DN SM VAN			
			Central60,4,14R rolandic operculum (BA48)64,-4,18R postcentral gyrus (BA43)	- LIM					
			Temporal	60,-8,-16 48,-10,-12 62,6,-2 66,-2,6 18,-6,-18 50,18,-26	R middle temporal gyrus (BA21) R superior temporal gyrus (BA21,22,48) R temporal pole, superior temporal gyrus (BA20,38) R heschl gyrus R parahippocampal gyrus (BA28) R temporal pole, middle temporal gyrus (BA38)	-			
			Subcortical	22,-4,-18	R amygdala (BA34)	-			
2	7935	5.292	Frontal	-40,-2,6	L insula (BA38,48)	SM			
						Central	-58,-2,10 -62,-12,18	L rolandic operculum (BA48) L postcentral gyrus (BA48)	VAN LIM
			Parietal	-52,-24,20	L supramarginal gyrus (BA48)	_			
			Subcortical	-20,-6,-16 -16,-8,-18 -30,-8,8	L amygdala (BA34) L hippocampus (BA35) L lenticular nucleus, putamen (BA48)				
3	4008	5.272	Cerebellar	-14,-66,- 30 -16,-74,-	L cerebellum, hemispheric lobule VI (BA18,19,37) L cerebellum, crus I (BA37) L cerebellum, crus II	FPN VAN DN			

Table 3: Brain activation during classical music listening

				26 -14,-76,- 40		LIM
4	44	5.130	Frontal	6,4,66	R supplementary motor area (BA6)	VAN
5	6	4.559	Central	50,4,48	R precentral gyrus	VAN

Table 4: Brain activation during simple tunes listening

Cluster	Cluster size	Max. SDM-Z	Brain region	Peak MNI	Anatomical position (Brodmann area)	Resting-state network
1	7629	6.159	Frontal	56,8,8 46,8,0 50,18,-12	R inferior frontal gyrus, opercular part (BA6,44,48) R insula (BA47,48) R inferior frontal gyrus, orbital part (BA38)	DN SM VAN — FPN
			Central	44,-30,18 62,-12,22 60,2,18	R rolandic operculum (BA48) R postcentral gyrus (BA4,6,43) R precentral gyrus (BA6,44,48)	
			Temporal	58,-22,-4 54,-26,-4 50,-14,6 60,6,2	R superior temporal gyrus (BA21,22,41) R middle temporal gyrus (BA21) R heschl gyrus (BA48) R temporal pole, superior temporal gyrus (BA38,48)	
			Parietal	66,-20,18	R supramarginal gyrus (BA22)	
			Subcortical	32,-4,4	R lenticular nucleus, putamen (BA48)	
2	5421	5.867	Frontal	-48,18,2 -50,10,4 -38,4,2	L inferior frontal gyrus, triangular part (BA45,48) L inferior frontal gyrus, opercular part (BA48) L insula (BA48)	SM DN VAN
			Central	-54,-22,26	L postcentral gyrus (BA48)	

Temporal	-54,-36,12 -60,-38,-6 -56,6,-2	L superior temporal gyrus (BA41,42,48) L middle temporal gyrus (BA22) L temporal pole, superior temporal gyrus (BA48)
Subcortical	-30,4,-2 -30,-10,-4	L lenticular nucleus, putamen (BA48) L putamen

Cluster	Cluster size	Max. SDM- Z	Brain region	Peak MNI	Anatomical position (Brodmann area)	Resting-state network
1	6874	5.143	Frontal	52,20,32 44,0,-10 50,18,-12 54,18,16	R inferior frontal gyrus, opercular part (BA44) R insula (BA48) R inferior frontal gyrus, orbital part (BA48) R inferior frontal gyrus, triangular part (BA38,47)	VAN DN FPN SMN
			Central	50,4,0 46,20,-6	R rolandic operculum (BA48) R precentral gyrus (BA44)	
			Temporal	58,-16,16 50,-12,-14	R superior temporal gyrus (BA21,22,48) R middle temporal gyrus (BA21)	
			Parietal	52,-42,28	R supramarginal gyrus (BA48)	
2	3806	4.613	Frontal	-42,-6,-2	L insula (BA48)	VAN — SMN _ DN
			Central	-58,-18,18	L postcentral gyrus (BA48)	
			Temporal	-50,-2,-2 -56,-20,-8	L superior temporal gyrus (BA42,48) L middle temporal gyrus (BA21,22)	
			Parietal	-60,-26,18	L supramarginal gyrus (BA42)	

Table 5: Brain activation during song listening



Figure 1: Flowchart of the article screening process



Figure 2: Brain activation patterns during music listening (*Notes: P* = *posterior; A* =

anterior; L = left; R = right; X/Y/Z = coordinates on X/Y/Z axes)



Figure 3: Brain activation patterns during classical music listening (*Notes: P = posterior; A*

= anterior; L = left; R = right; X/Y/Z = coordinates on X/Y/Z axes)



Figure 4: Brain activation patterns during simple tune listening (*Notes: P* = *posterior; A* =

anterior; L = left; R = right; X/Y/Z = coordinates on X/Y/Z axes)



Figure 5: Brain activation patterns during song listening (*Notes: P* = *posterior; A* = *anterior;*

L = left; R = right; X/Y/Z = coordinates on X/Y/Z axes)



Figure 6: Funnel plots for the most significant peaks in each clusters from the main analysis. (Notes: IFG = inferior frontal gyrus; MTG = middle temporal gyrus; Each dot represent a study; for right IFG and left MFG, the activation effect sizes are very similar for most of the studies, resulted in the overlapping of dots among studies)