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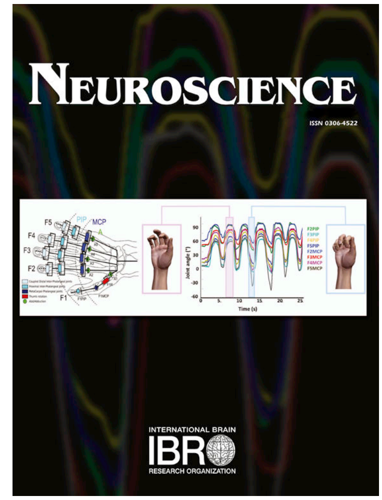

Research Article

Music style not only modulates the auditory cortex, but also motor related areas

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Title

Music style not only modulates the auditory cortex, but also motor related areas.

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Data availability statement

Data will only be made available via a request to the Authors and when the conditions of such a request should be clearly stated.

Ethics approval statement

The study was approved by the University of La Laguna Ethics Committee according to the Declaration of Helsinki.

Disclosure

All authors declare no conflict of interest.

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Abstract

The neuroscience of music has recently attracted significant attention, but the effect of music style on the activation of auditory-motor regions has not been explored. The aim of the present study is to analyze the differences in brain activity during passive listening to non-vocal excerpts of four different music genres (classical, reggaeton, electronic and folk). A functional magnetic resonance imaging (fMRI) experiment was performed. Twenty-eight participants with no musical training were included in the study. They had to passively listen to music excerpts of the above genres during fMRI acquisition. Imaging analysis was performed at the whole-brain-level and in auditory-motor regions of interest (ROIs). Furthermore, the musical competence of each participant was measured and its relationship with brain activity in the studied ROIs was analyzed. The whole brain analysis showed higher brain activity during reggaeton listening than the other music genres in auditory-related areas. The ROI-analysis showed that reggaeton led to higher activity not only in auditory related areas, but also in some motor related areas, mainly when it was compared with classical music. A positive relationship between the melodic-MET score and brain activity during reggaeton listening was identified in some auditory and motor related areas. The findings revealed that listening to different music styles in musically inexperienced subjects elicits different brain activity in auditory and motor related areas. Reggaeton was, among the studied music genres, the one that evoked the highest activity in the auditory-motor network. These findings are discussed in connection with acoustic analyses of the musical stimuli.

Keywords

Music; music genre; auditory-motor areas; fMRI.

Introduction

Listening to music is an aesthetic human experience where individuals pay attention to interpretation and evaluate the result of this interpretation (Reybrouck et al., 2018). Music processing involves several brain areas, leading to a complex pattern of brain activity when listening to it. This activation is necessary to process and to interpret each of the elements of sound (i.e., tone, timbre and intensity) and each of the elements of music (i.e., harmony, melody and rhythm) (Patterson et al., 2002; Grahn and Brett, 2007; Grahn and McAuley, 2009).

The brain areas activated during music listening do not only include the auditory regions, but also the motor regions (Grahn and Brett, 2007; Chen et al., 2008; Gordon et al., 2018). Interactions between the auditory and motor systems of the brain allow the detection and anticipation of temporally predictable moments in a song (Penhune and Zatorre, 2019). In this sense, the premotor cortex (PMC) and the supplementary motor area (SMA) are involved in rhythm detection (Kung et al., 2013; Merchant et al., 2015; Rajendran et al., 2018); and the inferior frontal gyrus (IFG) and the precentral gyrus (PreCG) presented a music-related activity that is linked to movements associated to the music, i.e., a match between music and movement related to that music (e.g., while dancing or playing an instrument) (Lahav et al., 2005; Furukawa et al., 2017). Auditory-motor interactions are important to understand the link between music perception, dancing or even speech (Gordon et al., 2018).

Music genre or style is an essential category for understanding human preferences of music, but it is largely unknown how abstract categories of music genre are represented in the brain (Nakai et al., 2018). In this sense, one can consider that everyone may have their own music categories and they do not have to coincide with others; and others may believe that everyone has different preferences, but she/he recognizes that a piece belongs to a category rather than to another with relative coherence. The different music styles are defined by their specific acoustic features and instrumental complexity (Wang et al., 2013; Percino et al., 2014). Surface musical features are robust attributes for effective music genre recognition typical of human subjects (in contrast with structural, top-down processing musical characteristics such as those learned by enculturation), as reported by previous work on automatic genre classification (Tzanetakis and Cook, 2002; Chen et al., 2019). Thus, listening to different music styles would lead to a different brain activity pattern. In this regard, the complexity of rhythm sequences has been shown to be an important factor in modulating the activity of the premotor areas (Bengtsson et al., 2009). However, no previous study has focused on the effect of music style on the activity of the auditory and motor areas. The putative modulatory effect that the music style may have in the auditory-motor regions might be useful in some neurological diseases (e.g., Parkinson disease), where music is often used to improve movement performance, particularly gait (de Bruin et al., 2010; Ashoori et al., 2015); and/or sports science, where specific motivational music seems to optimize running economy (Bood et al., 2013).

Therefore, the aim of the present work is to describe the brain activity, using functional magnetic resonance imaging (fMRI), during passive listening of four different instrumental (non-vocal) music styles (classical, reggaeton, electronic and folk). Furthermore, the study also aims to identify differences between the studied music styles in brain activity during passive listening, focusing on the auditory and motor related regions.

Experimental procedures

Subjects

Twenty-eight healthy, right-handed (Edinburgh Handedness Inventory (Oldfield, 1971)) < 25) subjects were selected (16 women), with a mean age of 26.7 (SD = 8.29). They had never played a musical instrument and they had received no musical training (including voice) other than normal school education. None of them had a history of neurological, psychiatric or auditory problems. A survey of musical habits was completed for each participant to determine the frequency of music listening and the rate of music download (the frequency of music download per week).

Written informed consent was explained and signed.

Data acquisition and processing

Data for the experiment were collected at the Magnetic Resonance for Biomedical Research Service of the University of La Laguna. Two task-based fMRI runs and a 3D anatomical T1 were obtained on a 3T General Electric (Milwaukee, WI, USA) scanner.

Task-based functional images were obtained using an echo-planar imaging gradient-echo sequence and an 8 channel head coil (TR = 2000ms, TE = 22.1ms, flip angle = 90◦, matrix size = 64 × 64 pixels, 36 slices/volume, interslice gap = 1 mm, slice thickness = 4 mm). The slices were aligned to the anterior commissure – posterior commissure line and covered the whole cranium. Functional scanning was preceded by 16 s of dummy scans to ensure tissue steady-state magnetization.

A whole-brain three-dimensional structural image was acquired for anatomical reference. A 3D fast spoiled gradient – recalled pulse sequence was obtained with the following acquisition parameters: TR = 10.4 ms, TE = 4.2 ms, flip angle = 20, matrix size = 512 × 512 pixels, .5 × .5 mm in plane resolution, slice thickness = 2 mm.

Auditory stimulus was presented using the software Presentation® and MRI-compatible headphones (VisuaStim Digital®).

After checking the images for artefacts, task-fMRI data were preprocessed and analyzed using Statistical Parametric Mapping software SPM12 (Wellcome Trust Centre Neuroimaging, 2014); released 13th January 2020, running in MATLAB R2013b [v. 8.2.0] (The MathWorks, 2013)). The images were spatially realigned, unwarped, and normalized to the Montreal Neurological Institute (MNI) space using standard SPM12 procedures. The normalized images of 2 × 2 × 2 mm were smoothed by a full width at half maximum (FWHM) 8 × 8 × 8 Gaussian kernel.

Study design

During the two task-fMRI runs, subjects were asked to listen different fragments of melodies corresponding to 4 different music styles: classical, reggaeton, electronic and folk. fMRI responses were measured during naturalistic music listening (participants have no specific task but attentively listen to continuous and real-world music of different genres). Each fMRI run presented only two different music-styles (classical & reggaeton and electronic & folk). Each music style was represented by three different 14-second-length melodies. The order of the melody's presentation was pseudorandom, and the order of the fMRI runs was counterbalanced between subjects. The control condition for both runs consisted of the background sound listening (MRI equipment during imaging acquisition). The melodies and the control condition were presented 2 times for 14 seconds each (6 repetitions/music style). During image acquisition, participants were instructed to keep their eyes closed and to concentrate on what they were listening to. In this sense, participants performed a passive listening, that is defined as an attentive listening while remaining still (Gordon et al., 2018). A questionnaire after the scan confirmed that none of the subjects fell asleep.

Acoustic analysis of the selected musical excerpts (or stimuli)

Twelve musical excerpts were selected which comprised the four musical genres of interest (three excerpts per genre): (1) classical, (2) reggaeton, (3) electronic and (4) folk. The excerpts were amplitude-normalized to ensure that the combined left and right channels of the recorded stimuli had identical root-mean-square (RMS) amplitude values without allowing signal clipping. As a result, volumes across excerpts were matched.

The audio file format for each musical excerpt was stereo, PCM S16 LE (s16l), with a sample rate of 44,1 kHz and bit depth of 16 bit. For each listener, the loudness of each musical excerpt was adjusted to a comfortable but audible level (around 75 dB). The beats per minute (BPM) of each excerpt are listed below:

Clas#1: 115 bpm

Clas#2: 128 bpm

Clas#3: 115 bpm

Reg#1: 88 bpm

Reg#2: 99 bpm

Reg#3: 95 bpm

Elec#1: 128 bpm

Elec#2: 130 bpm

Elec#3: 133 bpm

Folk#1: 80 bpm

Folk#2: 62 bpm

Folk#3: 115 bpm

Additionally, a total of 24 acoustic descriptors were extracted frame-by-frame from the excerpts using MIR Toolbox (Lartillot and Toiviainen, 2007) (see supplementary table 1) and then compared between genres (classical, electronic, folk, and reggaeton). The extracted descriptors represent frequently used acoustic features in psychoacoustic literature, which comprised both low-level and high-level features. A window length of 25 ms with a 50% overlap was used to extract the low-level features, and a window size of 3 s with a 33% overlap was used to extract the high-level features. The larger 3 s temporal window for high-level features was chosen as it corresponds to typical estimates of the length of the auditory sensory memory (Fraisse, 1982). Low-level features included timbral aspects of the acoustic signal, such as brightness, spectral centroid and roughness. High-level features included rhythmical and tonal aspects of the music (such as pulse and key clarity). Overall, low-level feature processing seems to predominantly rely on bottom-up mechanisms which represent detailed stimulus information. High-level feature processing, however, seems to be modulated by top-down cognitive processes because of enculturation, familiarity, and listening history (such is the case of rhythmical and tonal musical features (Burunat et al., 2017).

A multiple-sample test for equal variances (Levene's test) was performed per feature ($p < 0.05$) to compare the acoustic variability across genres of the excerpts. Levene's test revealed significantly unequal variances for each acoustic feature for at least one genre compared to the others, suggesting that acoustic variance was not homogeneous across genres. Additionally, a Welch's ANOVA (the best approximation to the classic ANOVA when the condition of equal variance is not met (Welch, 1951)) showed significant differences across genres ($p < 0.05$). This is not surprising, as musical genres are defined to a large extent by their own particular acoustic footprint (Wang et al., 2013).

To mention some of the differences found in relation to the low-level features, electronic music had significantly higher values for brightness (increased power at high frequencies) compared to the rest of the genres. Classical music, on the other hand, had the significantly lowest values for spectral flatness (measure of the noisiness of the power spectrum, i.e., timbral complexity), in other words, classical music tended to have a more tone-like quality (as opposed to noise-like quality) when compared to the other genres. Similarly, roughness (estimate of the perceived dissonance) scored highest in electronic and reggaeton music.

As for the high-level features, classical and folk music showed significantly less pulse clarity than electronic and reggaeton music (supplementary figure 2). In other words, electronic and reggaeton displayed a simpler, more salient beat compared to classical and folk music. The same pattern of genre pairs was also observed for fluctuation centroid (electronic & reggaeton > classical & folk) and fluctuation entropy (classical & folk > electronic & reggaeton). Both rhythmical features represent the mean average frequency of periodicities in the 0-10 Hz range and the noisiness of the fluctuation spectrum (indicative of a high level of rhythmic complexity), respectively (Alluri et al., 2012). As for mode, which measures the strength of the major/minor mode, differences were subtle amongst genres with classical music having the lowest values (leaning towards minor mode) amongst all genres. Finally, values for key clarity, which is an estimate of the music's tonal clarity, were significantly lower for reggaeton compared to the rest of the genres.

In sum, despite their heterogeneity as per acoustic content in the selected music sample, some similarities were observed, i.e., classical and folk seemed to be more similar in terms of their high-level acoustic content than both electronic and reggaeton.

Simple T contrasts

A block design in the context of a general linear model was used, for individual subject analyses (first level), to look for differences in brain activity during the periods of listening and the control condition. The considered contrasts in the analysis were as follows: classical > control; reggaeton > control; electronic > control and folk > control. The first-level contrast images were then used in a random-effects group analysis (second level). Group analysis was performed using the random effect approach, using an ANOVA design and including the age, gender and Edinburgh Handedness Inventory score (Oldfield, 1971) as covariates. The statistical significance was established using the Family Wise Error rate (FWE) = 0.05, with a minimum cluster size of ten voxels. In the results section the result of each contrast is described with its statistics value (i.e.) with de degree of freedom (df), which is the total number of valid values minus 1.

Region of Interest analysis

A region of interest (ROI) analysis was performed in auditory and motor related areas using the Marseille ROI toolbox (MarsBaR). Auditory and motor related regions were extracted from the Brainnetome atlas (http://atlas.brainnetome.org/index.html). On the one hand, auditory related areas of both hemispheres were divided into: primary auditory cortex (BA41), secondary auditory cortex (BA42), Wernicke's area (BA22 caudal and rostral) and associative auditory areas (BA21 caudal and rostral; BA37 dorsal-lateral; and the anterior part of the Superior Temporal Sulcus [aSTS]) (figure 1).

On the other hand, the ROI analysis of the motor related areas included the premotor cortex (PMC), the precentral gyrus (PreCG) and the inferior frontal gyrus (IFG) of both brain hemispheres. The PMC was divided into five parts: medial, dorsal-lateral, ventral and ventral-lateral. The IFG was also divided into five parts: BA44 dorsal, BA44 opercular, BA44 ventral, BA45 caudal and BA45 rostral. Finally, the PreCG was divided in five regions: hand and face region; upper limb region; trunk region; tongue and larynx region and lower limb region (figure 1). A repeated measures ANOVA test was performed, and statistical significance was considered when a corrected p-value was less than 0.05. Bonferroni's multiple comparison test was performed when a contrast showed statistical significance to identify the music styles that led to a significantly different brain activity.

[FIGURE 1]

Correlation analysis between brain activity and musical abilities

The Music Ear Test (MET) was used to measure the musical competence of each participant. MET has been designed for measuring musical abilities in both musicians and non-musicians. In short, it consists of 104 trials in which participants judge whether two musical phrases are identical or not (Wallentin et al., 2010). It is based on two subtests: the melodic subtest and the rhythm subtest. A correlation analysis was performed between the MET global score and the score in each subtest and brain activity in selected ROIs for each music style. The Pearson correlation coefficient was calculated for each pair (brain region – MET score) and statistical significance was considered when the p-value was below 0.05.

Results

Whole brain analysis

As expected, the four music styles led to a notable activation of the auditory related areas in the temporal lobe (figure 2; table 1). Additionally, during reggaeton listening, extensive significant activity in premotor areas and basal ganglia was identified. Electronic and folk music also led to significant activation of premotor areas but with a much lower extension than reggaeton (figure 2; table 1).

[FIGURE 2]

[TABLE 1]

The ANOVA test was used to identify differences among the music styles. This analysis showed significant differences in the following contrasts: reggaeton vs. classical music, reggaeton vs. electronic music and folk vs. electronic music (figure 3; table 2). In the first two contrasts, higher activity for reggaeton in the superior temporal gyrus was identified bilaterally (t_{27}=10.74, FWE<0.05 and t_{27}=9.39, FWE<0.05 for left and right superior temporal gyrus, respectively, in the contrast reggaeton vs. classic; and t_{108}=9.54, FWE<0.05 and t_{27}=9.89, FWE<0.05 for left and right superior temporal gyrus, respectively, in the contrast reggaeton vs. electronic). On the other hand, higher activity for folk than electronic music was also shown in both superior temporal gyri (t_{27}=11.15, FWE<0.05 and t_{27}=9.13, FWE<0.05 for right and left superior temporal gyrus, respectively).

[FIGURE 3]

[TABLE 2]

Brain activity in specific auditory and motor related areas during listening to different music styles

A ROI analysis in auditory and motor related areas was performed to locate the differences in the BOLD signal amongst the studied music styles (see Methods; figure 1). Regarding auditory related regions, differences between the different music styles were identified in two regions. Firstly, the caudal part of the left Wernicke's area (BA22 caudal) showed statistical significance in the repeated measure ANOVA test ($p=0.0061$). Comparisons between groups showed significantly higher activity during reggaeton than classical music listening ($t_{27}=3.210$; $p < 0.05$ [corrected for multiple comparisons]) (figure 4d). The homologous region in the right hemisphere also showed a higher activity during reggaeton listening than the other music styles, but these differences did not reach statistical significance ($p=0.0540$) (figure 4c). Secondly, differences in the right secondary auditory cortex (BA42) were also identified ($p=0.0181$). Multiple comparisons showed that reggaeton listening led to higher activity in the right secondary auditory cortex (BA42) compared to electronic music ($t_{27}=2.767$; $p < 0.05$ [corrected for multiple comparisons]) (figure 4a). The homologous contralateral region did not present statistically significant differences in brain activity between music styles ($p=0.1095$) (figure 4b). The rest of the studied auditory-related ROIs did not show differences in the BOLD signal between the studied music styles (supplementary figure 1).

[FIGURE 4]

On the other hand, regarding motor related areas, different brain activity between music styles was found in four of the selected ROIs. The left BA45, in its caudal and rostral portions, showed significant differences between music styles ($p=0.0086$ and $p=0.0409$, respectively) (figures 5b and 5d). However, the multiple comparison tests only identified specific differences between music styles for the caudal part. They were identified in the contrast classical vs. reggaeton and classical vs. electronic. Higher activity during reggaeton listening was identified in both previously indicated contrasts ($t_{27}=3.095$ and $t_{27}=2.929$; $p < 0.05$ [corrected for multiple comparisons]) (figure 5b). The homologous parts of the BA45 in the right hemisphere did not show significant differences (caudal: p=0.1934; ventral: p=0.1356) (figures 5a and 5c).

The left BA44 also showed differences between music styles in its opercular and ventral parts (p=0.0209 and p=0.0269, respectively) (figures 5f and 5g). The main difference was identified between classical and reggaeton music in both regions. In this regard, higher activity during reggaeton than classical music listening was identified (left BA44op: t_{27}=3.141; left BA44v: t_{27}=3.055; $p < 0.05$ [corrected for multiple comparisons]) (figures 5f and 5h). Finally, the right BA44 did not show differences between music styles (opercular: p=0.2165; ventral: p=0.6905) (figures 5e and 5g). The rest of the studied motor-related ROIs did not show differences in the BOLD signal between the studied music styles (supplementary figure 1).

[FIGURE 5]

Relationship between music competencies and brain activity in auditory-motor ROIs during passive listening to different music styles

The activity in several auditory ROIs showed a relationship with the music competence of each participant. In this regard, brain activity during reggaeton listening and melodic MET score were positively correlated in the left primary auditory cortex (CC=0.522; p=0.005), the right and left secondary auditory cortex ([CC=0.397; p=0.040] and [CC=0.433; p=0.024], respectively) and the caudal part of the right Wernicke's area (BA22c) (CC=0.388; p=0.045) (figure 6d). On the other hand, a negative relationship between the brain activity while listening to electronic music in the caudal part of the right associative auditory area (BA21c) and rhythm-MET score was identified (CC=-0.402; p=0.042) (figure 6e).

Bearing in mind the motor-related ROIs, brain activity in different parts of the precentral gyrus during reggaeton listening showed a positive correlation with the melodic-MET score. More specifically, activity in the right PreCG (corresponding to upper limb, tongue & larynx and head & face regions) showed a positive correlation with melodic-MET score (correlation coefficient [CC] = 0.563, 0.538 and 0.596, respectively; p=0.002, 0.003 and 0.001, respectively) (figure 6a); the activity of left PreCG (corresponding to upper limb, tongue & larynx, lower limbs and head & face regions) presented a positive correlation with melodic-MET score (CC = 0.461, 0.476, 0.458 and 0.434, respectively; p=0.015, 0.012, 0.015 and 0.024, respectively) (figure 6b); and the right PMC (ventral-lateral and dorsal-lateral) showed a positive correlation with melodic-MET score (CC = 0.447 and 0.423, respectively; p=0.019 and 0.027, respectively) (figure 6c). No other region showed significant correlations between brain activity during reggaeton listening and the melodic/rhythm MET scores. Furthermore, none of the studied regions showed any significant correlation between brain activity in motor related ROIs during the listening to other music styles and the melodic/rhythm MET scores.

[FIGURE 6]

Discussion

The present work has analyzed the differences in brain activity during passive listening to four different music styles/genres (classical, reggaeton, electronic and folk). In the whole brain analysis, the main result was the presence of higher brain activity during reggaeton listening than the other music genres in auditory related areas. The ROI analysis showed that reggaeton led to higher activity not only in auditory related areas, but also in some motor related areas, mainly when it was compared to the activity elicited by classical music. Finally, a positive relationship between the melodic MET score and brain activity during reggaeton listening was identified in some auditory and motor related areas. All these findings will be discussed below.

Differences in brain activity between different music genres listening

Auditory cortices activation was common to all genres, reflecting the key neural basis for auditory processing. However, some differences were identified between genres. Classical music elicited less activation compared to the other genres; and reggaeton elicited the highest degree of activation in terms of extent and diversity of brain areas.

The bilateral superior temporal gyrus (STG) is the site of the primary and association auditory cortex, responsible for sound perception. Its right hemispheric equivalent usually has greater ability to resolve spectral information compared to its left hemisphere counterpart (Zatorre et al., 2002; Tervaniemi and Hugdahl, 2003). Thus, the right STG is dominant in the processing of melody, pitch, harmony and timbre (Zatorre and Samson, 1991; Liégeois-Chauvel et al., 1998; Watson, 2006). Robust supporting evidence on how the two hemispheres integrate different aspects of auditory information to make sense of the auditory input comes from lesion studies (with unilaterally brain-damaged patients, reporting that right temporal lesions cause amusia, or deficits in the discrimination of melodies) (Liégeois-Chauvel et al., 1998; Nicholson et al., 2003; Murayama et al., 2004; Cutica et al., 2006), and neuroimaging studies (Plante et al., 2002; Zatorre et al., 2002; Hesling et al., 2005).

The differences in brain activity between different music genres identified here may be associated with the acoustical differences between the selected musical excerpts. In this sense, the highest pulse clarity was in reggaeton (i.e., high pulse clarity facilitates the listeners' ability to track the tempo of the music, to tap or dance to it). In line with the present results, music with high pulse clarity has been associated with an increased activation in the bilateral STG (BA 22), as well as the right primary auditory cortex (BA 41) (Alluri et al., 2012). Furthermore, the activation of bilateral auditory areas (Heschl's gyrus, planum temporale, and anterior and posterior STG) has been positively associated with pulse clarity (Burunat et al., 2017).

Moreover, the lowest fluctuation entropy was in reggaeton excerpts. This musical feature represents the amount of noise in the spectral fluctuations, i.e., it is a measure of the rhythmic complexity (having several co-existing rhythms of different periodicities). Thus, low fluctuation entropy indicates a clearer beat (Burger et al., 2013; Mathur et al., 2015).

Bearing in mind the activation of motor related areas, reggaeton was the music genre that led to the highest activity in those regions. As shown in figure 2 and table 1, reggaeton listening recruited basal ganglia structures (including the thalamus) and cerebellar regions, which are not recruited when the other genres were listened. These structures are crucial for rhythm perception, even in the absence of movement. Beat perception in auditory rhythms is sustained by interactions in the auditory and motor systems (Zatorre et al., 2007; Grahn and McAuley, 2009; Kung et al., 2013). These seem to particularly drive temporal predictions involved in rhythm perception (Zatorre et al., 2007; Patel, 2014). Recent fMRI evidence indicates that listening to salient rhythms in the absence of any overt movement recruits a cortico-subcortical functional network including the auditory cortex, the PMC, the putamen, and the supplementary motor area (Grahn and McAuley, 2009). The cerebellum is another key area that shows significant activity while listening to rhythms (Chen et al., 2008), in line with its prominent role in temporal processing and motor control (Kotz et al., 2014). Both, the basal ganglia and the cerebellum, have a crucial function in rhythm processing as it is strongly linked to internal generation of the beat (i.e. internally beat perception, that is, having the feeling to follow the beat) (Grahn and McAuley, 2009; Kung et al., 2013). This is substantiated by Parkinsonian literature documenting cases of patients with abnormal putamen activity who show deficits in discrimination of changes in rhythms that have a beat (Grahn and Brett, 2009).

Interestingly, the right IFG showed significant activity for all genres except for classical music. This specific area is the right hemispheric homologue of Broca's area and its role as a core area in music processing is well-supported by previous works. For instance, inferior fronto-lateral areas, with a right asymmetry, are core areas engaged in the processing of musical syntax using chord sequence and melody paradigms (Maess et al., 2001; Janata et al., 2002a; Koelsch et al., 2002, 2005, Tillmann et al., 2003, 2006). Additionally, this area has also been observed to increase its activation related to auditory working memory load during music listening (Janata et al., 2002b; Burunat et al., 2014). Furthermore, this area has been reported to be active when participants spontaneously generated melodic phrases vs. linguistic sentences (Brown et al., 2006). In short, activations within the IFG seem to underpin music-syntactic processes (Koelsch et al., 2006; Patel, 2014). Considering the results of the present work, it seems to be difficult to speculate on why the right BA44 (a part of the right IFG) responds to all genres except for classical music. One explanation may be that previous works have been focused on musicians, unlike the present study which only included musically inexperienced subjects.

In any case, the largest differences in brain activation during music genre listening comparison were identified when classical music and reggaeton were compared to each other. Apart from the abovementioned acoustic differences, another explanation for this finding may be the different degree of familiarity with each genre and/or the musical preference of participants. It should be noted that participants had never received musical training, thus their exposure to classical music (which is mainly heard in specific environments) might be more limited compared to reggaeton (which is currently widely heard, see IFPI music consumer report in 2019). The effect of familiarity on music processing has been previously reported. In this regard, the STG has been shown to be positively correlated with the degree of autobiographical salience of the music (i.e. personal experience) that is being listened to (Janata, 2009). Previous research also shows that non-musicians, as well as musicians, engage sensorimotor regions while listening to, producing and imagining music, particularly when that music is familiar (Halpern and Zatorre, 1999; Janata and Grafton, 2003; Leaver et al., 2009). Furthermore, differences in electroencephalographic activity during motor imagery task using and auditory stimuli with different levels of familiarity have been reported (Ivaldi et al., 2017). However, it is widely accepted that listening to music leads to different patterns of motor areas in musicians than non-musicians. We believe that musicians may show activation in regions involved in playing an instrument or humming; while non-musicians may show activation in other motor areas that are probably associated with dancing or doing movements following a rhythm. On the other hand, the effect of musical preference is supported by Pereira et al (2011) who reported that some brain regions, including the motor cortex and Broca's area, were more active in response to liked vs. disliked music (Pereira et al., 2011). In addition, because genres differ to each other in various acoustical and musical features, playing a specific genre of music may lead to different auditory sound encoding profiles while listening to this genre of music (Tervaniemi, 2012). This has been reported in jazz (Vuust et al., 2005) and in rock musicians (Tervaniemi et al., 2006). This could also lead to different brain circuitry activation across active listeners to different genres of music.

Correlation analysis between brain activity for each music genre and MET scores

Correlation analysis showed an association between musical competence and brain activation within specific brain structures for reggaeton and electronic music. In the case of reggaeton, listeners with higher melodic competence exhibited increased cortical activation compared to listeners with lower melodic competence in regions such as the bilateral auditory cortices, including the right Wenicke's area. Furthermore, a right-lateralized response of the primary auditory cortex for listeners with melodic acuity was observed. As mentioned above, a right hemispheric specialization for melody processing is supported by clinical and neuroimaging studies (see above).

Additionally, the activity of the PreCG (BA4) during reggaeton listening showed a similar positive correlation with melodic competence. The specific area of the PreCG where this correlation was identified corresponded to the upper/lower limbs and to the head (face, tongue, and larynx) motor control regions. This could suggest that listeners are engaged in action-simulation during listening (singing or dancing). In the same vein, the right PMC was similarly correlated with melodic abilities. The ventral PMC, as part of the human representation of the mirror neural network, represents internal patterns of trained movements (Binkofski et al., 2000). This is plausible, if we consider that music listening in musicians can induce motor imagery as a mental representation of the musician's motor repertoire for the intended sounds as a result of tightly coupled substrates of action and perception (Haslinger et al., 2005; Leaver et al., 2009; Herholz and Zatorre, 2012). Thus, music listening could induce similar mirror-like mechanisms in those musically competent non-musicians.

In the case of electronic music, a negative association between rhythmic competence and brain activation was found in the caudal part of the right associative auditory cortex (BA21). In other words, listeners with the lowest rhythmic acuity had larger brain responses in BA21. In a study on individual differences in rhythmic ability, this area has similarly been found to correlate negatively with a span task that measured auditory short-term memory (STM) capacity (Grahn and Schuit, 2012). This meant that participants with low STM capacity activated this area more than participants with high STM capacity (Grahn and Schuit, 2012). A tentative hypothesis to explain such results is that listeners who have difficulty in processing rhythmical aspects of the electronic music excerpts are using more auditory neural resources to process the music, hence the increased engagement of the auditory system.

In any case, the correlational analyses supported the idea that musical competence drives, to a certain degree, the regional activation pattern in certain areas.

In conclusion, listening to the four music genres studied here (i.e., classical, reggaeton, electronic and folk) led to an increased activation of the auditory related areas in the temporal lobe. Reggaeton, electronic and folk music also led to significant activity in motor related areas. When the studied music genres were compared to each other, mainly reggaeton, the genre with the highest pulse clarity, showed higher activity in auditory and motor related areas. Thus, the acoustic footprint of each musical genre seems to be associated with the differences in brain activity among genres. Furthermore, the effect of familiarity with each music style may also be associated with such differences. Finally, a positive relationship between melodic competence and brain activity during reggaeton listening in auditory-motor regions was observed.

Limitations

Some limitations of the present work should be considered. Firstly, one cannot completely rule out the possibility that the auditory-motor and motor differences found in the present study may be biased by the different processing of this scanner noise. As argued in Skouras et al. (2013), the effects of noise do indeed exist and are unavoidable, even when adopting a sparse sampling technique (Skouras et al., 2013).

On the other hand, using a higher magnetic field scanner might reveal more fine-grained differences amongst genres within the auditory cortical areas that are hidden to the performed analyses (see for instance (Sengupta et al., 2018), who used a 7T scanner).

Future studies should also include other variables, for example the familiarity ratings to the musical stimuli, preference for musical genre or the listening hours per week, which would give a better sizing of the modulation effect of the music style in the brain activity pattern.

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Figure legends

Figure 1. Anatomic representation of the regions included in the ROI analysis.

Figure 2. The axial slices show the BOLD signal during listening to each studied music style (indicated in at the left). FWE < 0.05; k=10 voxels.

Figure 3. *3D brain models showing statistically significant comparisons between different music styles.* FWE < 0.05; k=10 voxels.

Figure 4. Box-and-whiskers plots showing brain activity in two selected regions of interest (in both hemispheres each one) belonging to the auditory related areas. A Differences in the repeated measures ANOVA test were identified (p=0.0181) and comparisons between groups showed higher activity for reggaeton than electronic music (corrected p-value < 0.05) in the right secondary auditory cortex (BA42); **B** No significant differences in brain activity between music styles listening were identified in the left secondary auditory cortex (p=0.1095); **C** No differences were identified in the right Wernicke's area (caudal part [BA22c]) (p=0.0540); **D** Brain activity in the left Wernicke's area (BA22c) showed statistical difference between music styles (p=0.0061), with higher activity during reggaeton than classical music listening (corrected p-value < 0.05).
(n.s.: no significant)
Boxes depict the median and the 25^{th} and 75^{th} quartile.
Whiskers show the 5^{th} and 95^{th} percentile.

Figure 5. Box-and-whiskers plots showing brain activity in four selected regions of interest (in both hemispheres each one) belonging to the motor related areas. No significant differences in the repeated measures ANOVA were identified between music styles in the right BA45 caudal and rostral parts [**A** and **C**] and the right BA44 opercular and ventral parts [**E** and **G**]. The left BA45 shows significant differences between music styles in its caudal (p=0.0086) and rostral part (p=0.0409) [**B** and **D**], but only for the caudal part, multiple comparisons detected significant differences between classical & reggaeton music and electronic & reggaeton music [**B**]. The left BA44, in its opercular and ventral parts [**F** and **H**] also showed differences between music styles (p=0.0209 and p=0.0269, respectively) and the main difference was found between classical and reggaeton music.
(n.s.: no significant)
(*: corrected p-value < 0.05)
Boxes depict the median and the 25^{th} and 75^{th} quartile.
Whiskers show the 5^{th} and 95^{th} percentile.

Figure 6. Correlation analysis between MET scores and brain activity in auditory-motor regions of interest. A Relationship between brain activity in the right precentral gyrus (BA4) and melodic MET score during reggaeton listening; **B** Relationship between brain activity in the left precentral gyrus (BA4) and melodic MET score during reggaeton

listening; **C** Relationship between brain activity in the right premotor cortex (BA6; dorsal-lateral and ventro-lateral) and melodic MET score during reggaeton listening; ~~d)~~ **D** Relationship between brain activity in some auditory ROIs (primary and secondary auditory cortex; associative auditory area) and melodic MET score during reggaeton listening; **D** Relationship between brain activity in the caudal part of the associative auditory area (BA21) and rhythm MET score during electronic music listening.

BA4ul: Brodmann Area 4 (upper limbs)
BA4tl: Brodmann Area 4 (tongue and larynx)
BA4hf: Brodmann Area 4 (hand and face)
BA6vl: Brodmann Area 6 (ventral – lateral)
BA6dl: Brodmann Area 6 (dorsal – lateral)
PAC: Primary Auditory Cortex
SAC: Secondary Auditory Cortex
BA22c: Broddman Area 22 caudal (Wernicke's area)
BA21c: Broddman Area 21 caudal (associative auditory area)
R: right
L: left

Table 1. Activation peaks with their locations for each music style simple T contrasts (FWE=0.05 at peak level; k=10 voxels).

			CLASSICAL > Control		
	T	***Z***	***x***	***y***	***z***
Left Superior temporal gyrus	*17.30*	*> 8.00*	*-50*	*-10*	*-4*
	16.81	*> 8.00*	*-50*	*-24*	*0*
	15.51	*7.62*	*-58*	*-18*	*2*
Right Superior temporal gyrus	*15.44*	*7.61*	*54*	*-20*	*2*
	14.43	*7.41*	*62*	*-24*	*6*
	14.27	*7.38*	*52*	*-10*	*0*
Right Inferior Frontal Gyrus	*5.70*	*4.52*	*46*	*16*	*22*
			REGGAETON > Control		
	T	***Z***	***x***	***y***	***z***
Left Superior temporal Gyrus	*18.24*	*> 8.00*	*-46*	*-24*	*-2*
	18.13	*> 8.00*	*-48*	*-12*	*-4*
	14.95	*7.51*	*-56*	*-18*	*2*
Right Superior temporal Gyrus	*16.33*	*7.77*	*52*	*-20*	*2*
	15.49	*7.62*	*52*	*-10*	*0*
	14.57	*7.44*	*60*	*-16*	*8*
Right Medial frontal gyrus	*10.19*	*6.35*	*6*	*-2*	*64*
Right Basal Ganglia	*7.46*	*5.36*	*18*	*-2*	*12*
Left Putamen	*6.61*	*4.98*	*-20*	*-4*	*10*
Left Thalamus	*5.74*	*4.54*	*-6*	*-8*	*10*
Left Insula	*7.34*	*5.31*	*-36*	*24*	*2*
Left Inferior frontal gyrus	*7.00*	*5.16*	*-44*	*18*	*10*
Right cerebellum	*7.23*	*5.26*	*2*	*-38*	*-14*
Right brainstem	*5.88*	*4.61*	*10*	*-30*	*-16*
Right Middle frontal gyrus	*6.50*	*4.93*	*44*	*16*	*20*
	6.47	*4.92*	*48*	*2*	*46*
Right Inferior frontal gyrus	*6.45*	*4.90*	*40*	*32*	*6*
Left Inferior frontal gyrus	*6.27*	*4.81*	*-46*	*30*	*18*
			ELECTRONIC > Control		
	T	***Z***	***x***	***y***	***z***
Left Superior temporal gyrus	*18.09*	*> 8.00*	*-48*	*-12*	*-4*

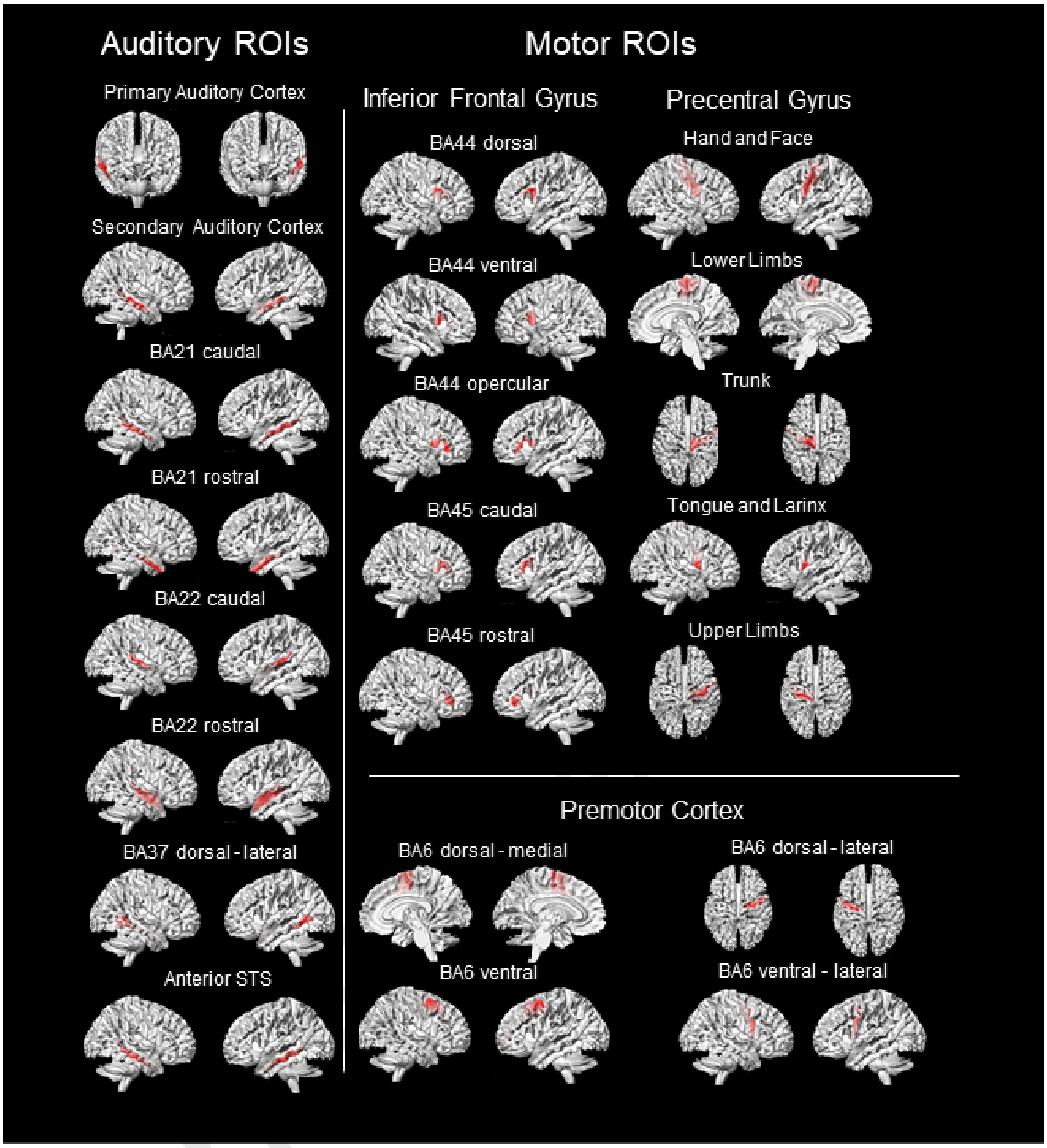
	15.34	*7.59*	*-46*	*-24*	*0*
	12.00	*6.85*	*-62*	*-24*	*4*
Right Superior temporal gyrus	*17.08*	*> 8.00*	*60*	*-20*	*4*
	14.75	*7.47*	*52*	*-10*	*-2*
Right Middle temporal gyrus	*14.42*	*7.41*	*60*	*-30*	*-2*
Superior Frontal Gyrus	*8.50*	*5.78*	*8*	*2*	*62*
Left Hippocampus	*7.69*	*5.46*	*-22*	*-10*	*-18*
Left Cerebellum	*7.18*	*5.24*	*-26*	*-60*	*-36*
Right Brainstem	*7.10*	*5.21*	*6*	*-34*	*-18*
Left Brainstem	*6.80*	*5.07*	*-6*	*-34*	*-14*
Right Inferior frontal gyrus	*6.50*	*4.93*	*48*	*20*	*22*
FOLK > Control					
	T	***Z***	***x***	***y***	***z***
Left Superior temporal gyrus	*20.43*	*> 8.00*	*-46*	*-14*	*-4*
	17.68	*> 8.00*	*-46*	*-22*	*0*
	11.67	*6.77*	*-60*	*-24*	*4*
Right Superior temporal gyrus	*18.28*	*> 8.00*	*58*	*-16*	*6*
	18.12	*> 8.00*	*54*	*-22*	*2*
	15.79	*7.67*	*60*	*-32*	*-2*
Left Inferior frontal gyrus	*8.40*	*5.74*	*-40*	*22*	*2*
Left Precentral gyrus	*6.76*	*5.05*	*-44*	*18*	*8*
Right Brainstem	*7.41*	*5.34*	*6*	*-34*	*-18*
Left Brainstem	*6.88*	*5.11*	*-4*	*-36*	*-18*

Table 2. Activation peaks with their locations for comparisons among music styles. Those contrasts that did not show any significant peak in any direction have not been included (FWE=0.05 at peak level; k=10 voxels).

Reggaeton > Classical						
	k	*T*	*Z*	*x*	*y*	*z*
Left Superior temporal gyrus	*844*	*10.74*	*6.51*	*-42*	*-28*	*2*
Right Superior temporal gyrus	*641*	*9.39*	*6.09*	*44*	*-20*	*-4*
		8.76	*5.87*	*40*	*-22*	*4*
		6.84	*5.09*	*58*	*-22*	*2*
Right Transverse temporal gyrus	*10*	*7.51*	*5.38*	*64*	*-12*	*10*
Reggaeton > Electronic						
	k	*T*	*Z*	*x*	*y*	*z*
Left Superior temporal gyrus	*276*	*9.54*	*6.14*	*-40*	*-28*	*2*
Right Superior temporal gyrus	*247*	*9.89*	*6.25*	*42*	*-20*	*2*
		8.12	*5.63*	*52*	*-18*	*4*
Folk > Electronic						
	k	*T*	*Z*	*x*	*y*	*z*
Right Superior temporal gyrus	*1139*	*11.15*	*6.63*	*42*	*-20*	*2*
		7.38	*5.33*	*44*	*-30*	*6*
		6.62	*4.99*	*42*	*-14*	*-6*
Left Superior temporal gyrus	*908*	*9.13*	*6.00*	*-36*	*-28*	*4*
		7.66	*5.45*	*-44*	*-22*	*-4*
Left Inferior parietal lobule	*10*	*4.08*	*3.54*	*-50*	*-38*	*22*

Highlights

- The effect of music style on the activation of auditory-motor regions has not been explored until now.
- Brain activity during listening of different music styles (classic, reggaeton, electronic and folk) have been analyzed.
- Higher brain activity during reggaeton listening than the other music genres in auditory-related areas was identified.
- Reggaeton led to higher activity in some motor related areas, mainly when it was compared with classical music.


Auditory ROIs
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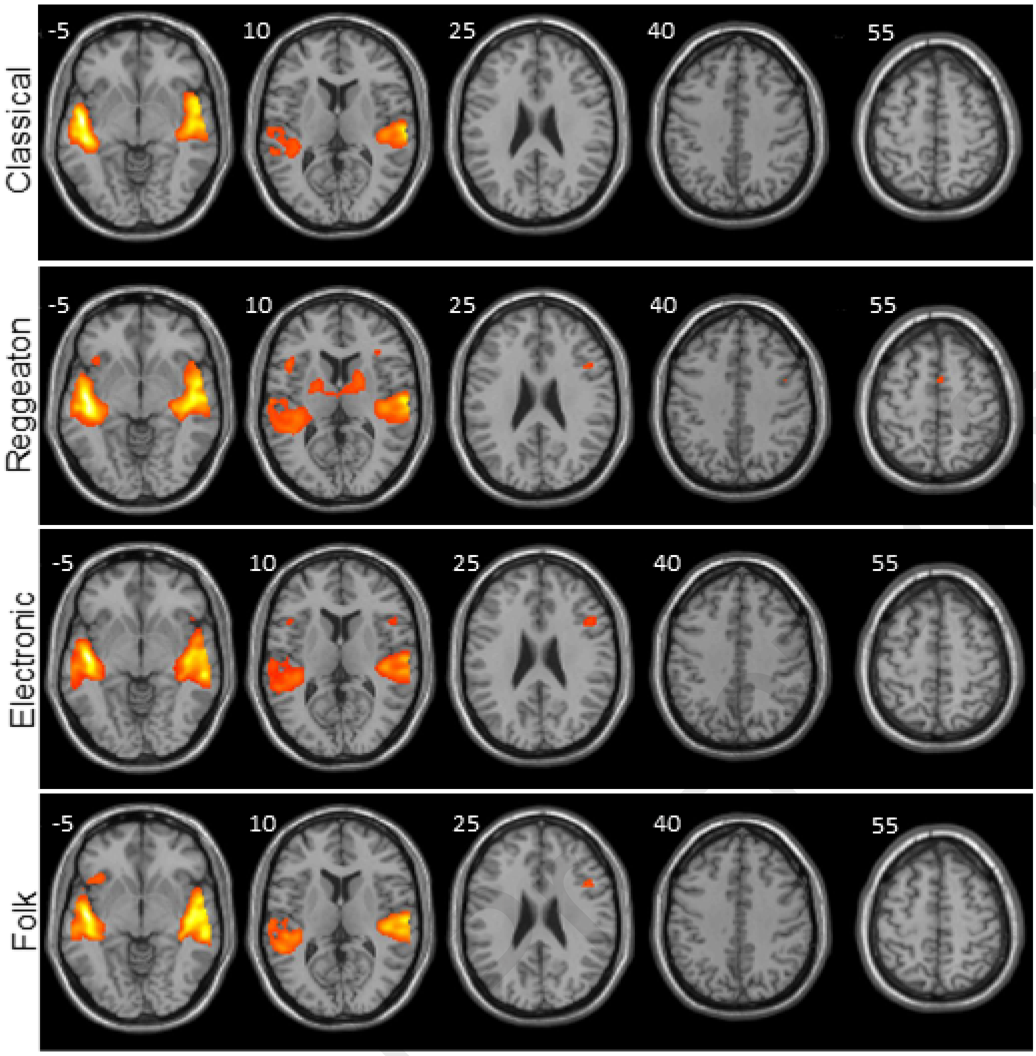
BA22 caudal
BA22 rostral
BA37 dorsal - lateral
Anterior STS
Inferior Frontal Gyrus
BA44 dorsal
BA44 ventral
BA44 opercular
BA45 caudal
BA45 rostral
Precentral Gyrus
Hand and Face
Lower Limbs
Trunk
Tongue and Larinx
Upper Limbs
Premotor Cortex
BA6 dorsal - medial
BA6 ventral
BA6 dorsal - lateral
BA6 ventral - lateral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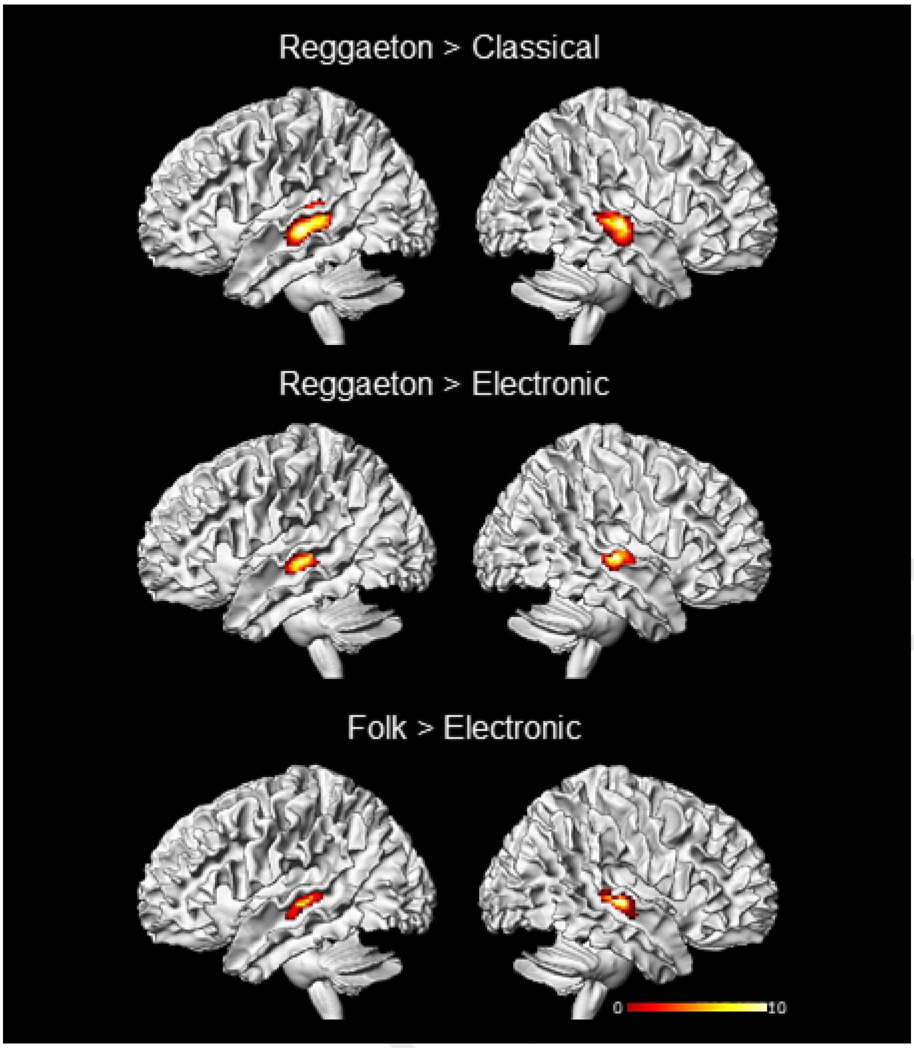
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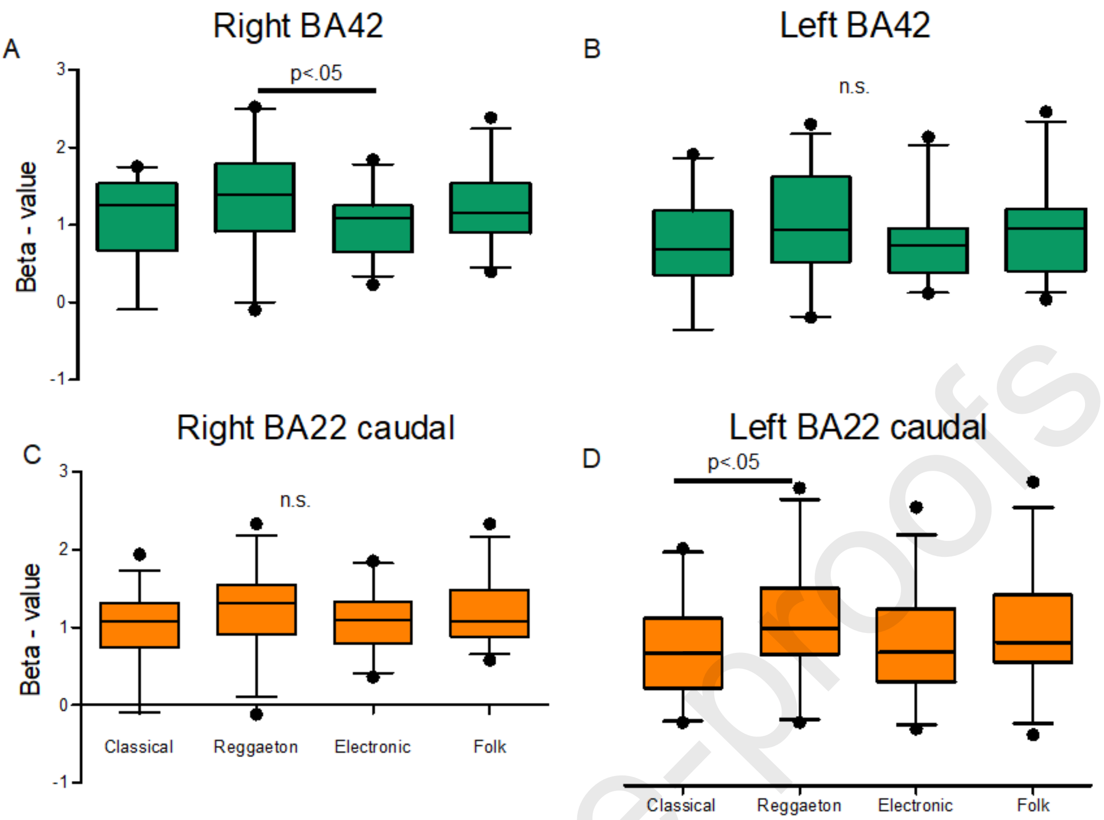
Right BA42
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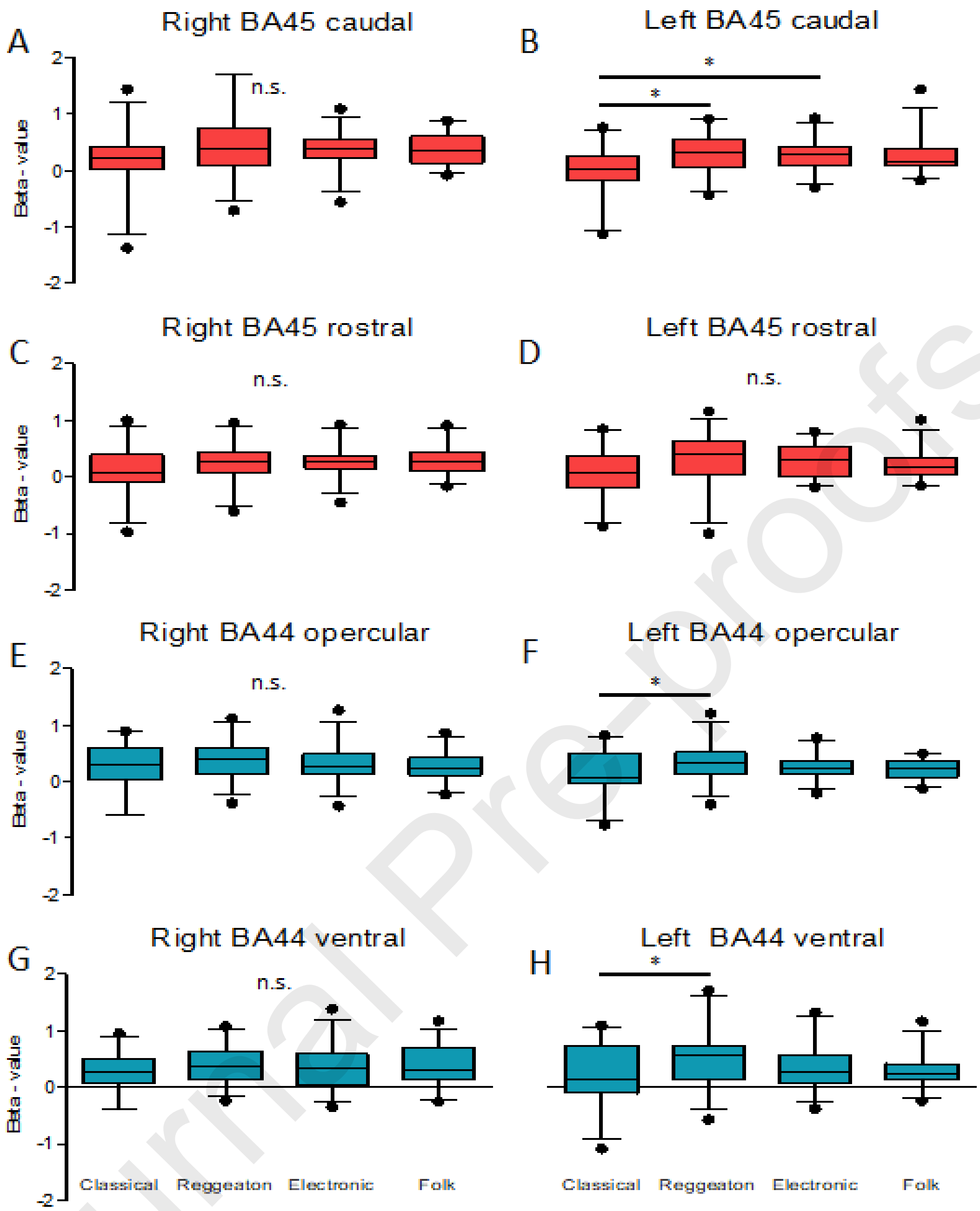
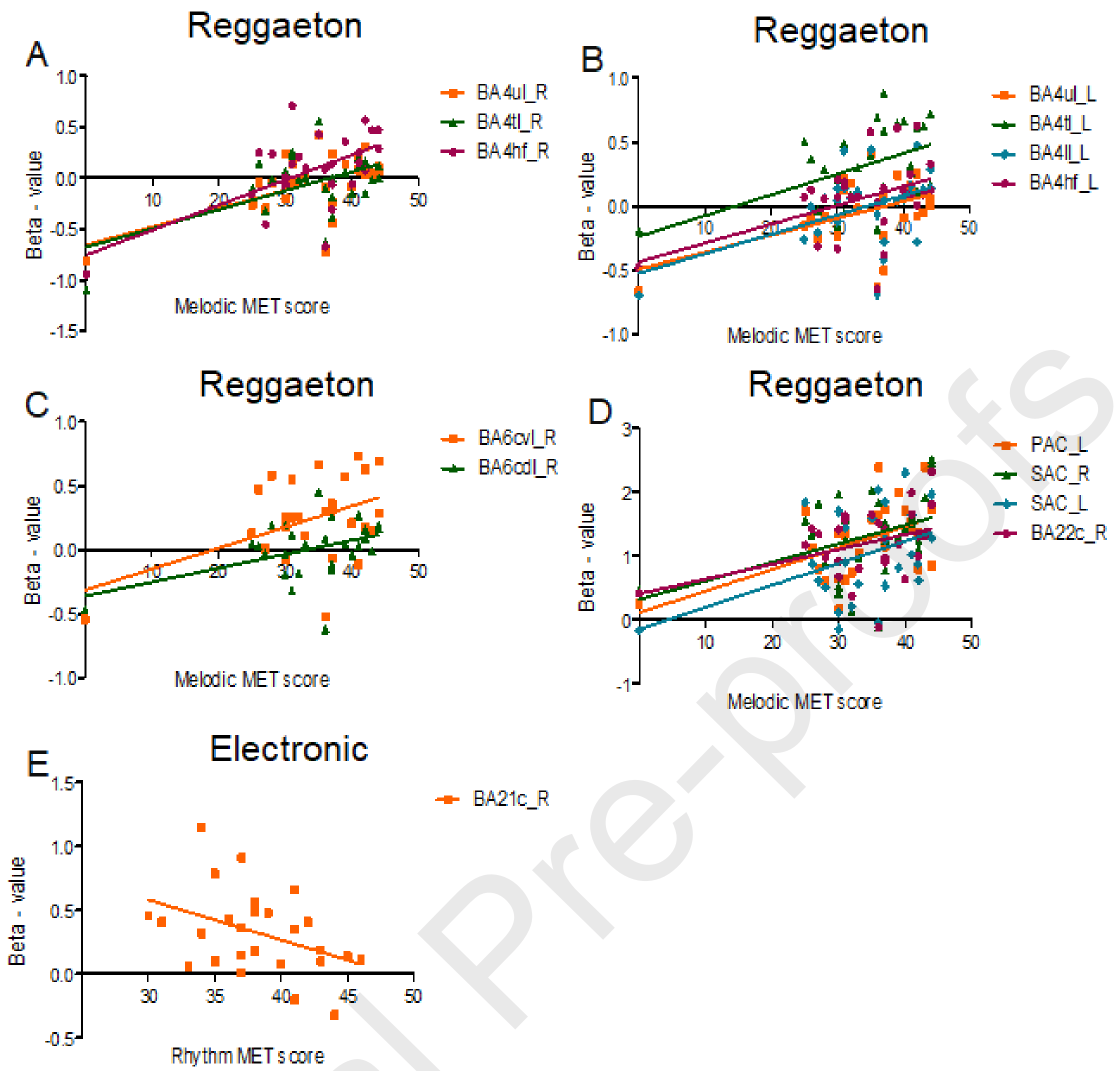
Left BA42
B
n.s.
Right BA22 caudal
C
n.s.
Beta - value
3
2
1
0
-1
Classical
Reggaeton
Electronic
Folk
Left BA22 caudal
D
p<.05
Classical
Reggaeton
Electronic
Folk


A
Right BA45 caudal
B
Left BA45 caudal
C
Right BA45 rostral
D
Left BA45 rostral
E
Right BA44 opercular
F
Left BA44 opercular
G
Right BA44 ventral
H
Left BA44 ventral
Beta - value
n.s.
*
Classical
Reggeaton
Electronic
Folk


A
Reggaeton
Beta - value
Melodic MET score
BA4ul_R
BA4tl_R
BA4hf_R
B
Reggaeton
Beta - value
Melodic MET score
BA4ul_L
BA4tl_L
BA4ll_L
BA4hf_L
C
Reggaeton
Beta - value
Melodic MET score
BA6cvl_R
BA6cdl_R
D
Reggaeton
Beta - value
Melodic MET score
PAC_L
SAC_R
SAC_L
BA22c_R
E
Electronic
Beta - value
Rhythm MET score
BA21c_R