

Investigating brain responses to section endings in tonal, classical and rhythmic music: an fMRI study

Mona Brun



Main Thesis, Department of Psychology

UNIVERSITY of OSLO

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Thank you for letting me take part in this project.

Abstract

Author: Mona Brun

Supervisors: Nils Inge Landrø and Bjørn Christian Østberg

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Our overall aim was to examine brain responses to different experiences of time in music with a particular focus on the question of how we experience large-scale music form. The present experiment was aimed at investigating the neural correlates to experiencing section endings in teleological (goal-directed) music as well as in rhythmic (groove-based) music.

We used functional magnetic resonance imaging (fMRI) on 14 human participants. Comparing transition points to continuous sections of the music we found that there was more neural activity in both musical genres at the transition points. Additionally we saw stronger blood-oxygen-level dependent (BOLD) fMRI activations at transition points in the rhythmical piece than in the classical piece. We did four region-of-interest (ROI) analyses, based on a priori expectations about the likely involvement of different brain areas in our task; the ventrolateral prefrontal cortex (VLPFC), the posterior temporal cortex (PTC), the dorsolateral prefrontal cortex (DLPFC) and the posterior parietal cortex (PPC). PTC was the only region that showed activations strong enough to survive the correction for multiple comparisons.

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1. Introduction

The last 10 years we have seen an increased use of neuroimaging and neural case studies to inform theories about the brain basis for musical behaviors, as well as an exponential increase in studies of music cognition in general. In the present study, the aim is to gain insights into the underlying neural processes of musical form and the experience of musical time, through investigating brain responses to section endings in tonal classical music and rhythmic music by way of fMRI.

The goal-directed, developmental form of the canonical works of the German-Austrian art music tradition from the baroque up to the 20th century has been linked to aspects of tonality, in particular functional harmony and thematic development (see for example; Schenker, 2004; Meyer, 1989; Kramer, 1988; McClary, 2000). Moreover, large-scale musical form is assumed to rely on the presence of a temporal structuring of segments into hierarchies of subsections (Cooper & Meyer, 1960; Lerdahl & Jackendoff, 1983). In musicological analyses, music theory and in compositional practice it is assumed that humans have the ability to perceive an overarching large-scale musical architecture and mapping large-scale musical form has been a central task in traditional musical analysis up to this day. Large-scale musical form commonly imply a hierarchy of musical sections with a clear beginning and an end, the latter in the form of so-called musical closures (Meyer, 1989). Such musical closures are particularly salient musical events and they are considered an important factor in building the overarching large-scale musical forms that characterize a majority of the canonical works within the Western art music tradition.

In tonal music a musical closure is commonly a tonal cadence (i.e., a specific chord sequence), but also other aspects than harmony may aid the segmentation process, such as rhythm, melody, dynamics etc. Temporal segmentation is also considered important for musical form, if on a smaller scale, in popular music songs, which are also structured as a hierarchy of sequences but within an overall binary form of verse and chorus (Danielsen, 2006).

1.1 Research into event segmentation

A possible human capacity to synthesize a large-scale temporal process into an overall musical form is thus likely to involve event segmentation at different levels. Temporal segmentation at a medium scale level (that is sections ranging from 10-20 seconds to 1-2 minutes) is likely to form the foundation of the overarching musical form. In regards to this process, the effect of musical closure has been investigated by measuring responses to musically unnatural stimuli using magnetoencephalography (MEG) and electroencephalogram (EEG) (Knoesche, 2005). In this study musically trained participants listened to short melodic fragments. These fragments were each presented in two versions. One version was clearly divided into two phrases where the other version consisted of only one phrase (being otherwise identical). Further, the participants had to perform a task that was unrelated to the purpose of the study, which was harmonic decision. In EEG, a centro-parietally distributed positive event-related potential (ERP) component peaked at about 550 ms after the offset of the phrase boundary was found. They called this component the closure positive shift (CPS) as it was taken to reflect the process of closing the prior phrase.

In a recent study the activity in the brain was observed during a movement transition in symphonies using fMRI (Sridharan, Levitin, Chafe, Berger & Menon, 2007). The study investigated the neural dynamics of event segmentation in entire musical symphonies from the 18th century under natural listening conditions, analyzing a 10 s window of brain responses surrounding movement transitions. The highest hierarchical level within a musical work is the *movement*, which is defined as “the primary self-contained section of large composition. While each movement may last from a few to ten or more minutes, transitions between movements take place over the time scale of a few seconds. Coarse-grained transitions like this are easily perceived by musically untrained listeners. A transition is not a sudden point event; it is prepared by way of melodic, harmonic, rhythmic and dynamic features, and is followed by the onset of a new section (Sridharan et al, 2007).

Sridharan et al. (2007) found activations in a strikingly right-lateralized network consisting of a ventral fronto-temporal network associated with detecting salient events followed by a dorsal fronto-parietal network associated with maintaining attention and updating working memory. This network showed peak responses during coarse-grained movement transitions, i.e. when paradoxically there were no stimuli. In their study the neural activity peaked when there was a brief period of silence between movements.

1.2 Research into harmony

In addition to a hierarchical structuring of musical segments, functional harmony and thematic development are assumed to play a role in the building up of large-scale musical form.

In human listeners the absolute values of a tone's pitch and duration are processed, and when there is more than one tone present it is the processing of tonal relations that gives rise to the appreciation of melody. To some extent tonal relations are computed even when only a single tone is presented. This could be because the listener is aware that the presented tone is higher or lower, longer or shorter, than a conceptual average tone encountered across the course of a lifetime. Tonal relations have been shown to be predominantly served by networks in the right temporal region and in the left dorsolateral prefrontal and right inferior frontal cortex (Zatorre, 1988), with particular deficits noted following lesions of the right anterolateral part of Heschl's gyrus (Johnsrude et al., 2000; Tramo et al., 2002; Zatorre, 1988). Tonal relations are important for large-scale temporal form, since both harmony and melody are considered effectual means in building musical form and signaling the end of a musical section.

Neural responses to musical harmony in between points of closure have been investigated by comparing brain responses while participants listened to classical music and scrambled versions of that same music (Levitin & Menon, 2003). It was found that Brodmann's area (BA) 47 was involved in processing the temporal coherence of music. However, in classical music tonal cadences normally coincide with section endings. Several different musical aspects thus normally point towards the same points of closure. Vuust et al. (2006) commented that due to the design of Levitin and Menon's experiment (2003), it was not possible to decide which of the disturbances in the music caused by the scrambling actually resulted in the activity in BA47. In addition to lack of temporal coherence, it could also have been generated by an absence of meaning linked with the lack of feasible harmonic progressions or recognizable melodies, or a general lack of a logical development of curves of musical tension and resolution (Vuust, Roepstorff, Wallentin, Mouridsen, Istergaard, 2006: 833).

A study by Koelsch in 2006 shows that a cortical network, comprising inferior frontolateral cortex (corresponding to BA 44), ventrolateral premotor cortex and anterior superior temporal gyrus, was involved in the processing of harmonic structure. In this study it was found that there was an increased difficulty in computing the relation between irregular chords function. Further it was found that the preceding harmonic context possibly led to a stronger activation of BA 44 and ventrolateral premotor cortex (VLPMC). As a result, the irregular chords may be perceived consciously as unexpected (Koelsch, 2006).

1.3 Research into rhythm

In their study from 2006, Vuust et al. show that BA 47 is bilaterally activated when musicians keep the rhythm. They say further that keeping the rhythm while listening to music is fundamental to an experience of musical tension between different layers of the musical structure and crucial for music to appear as a coherent, meaningful expression. In this study they contrasted different levels of metric tension within a piece of music by manipulating the relation between the musical material and the structural organization provided by the mental representation of the meter. The conclusion from this study was that BA 47 plays a significant role in mediating the experience of metric tension, which is one of the central meaningful structures in music. This finding is an experimental specification of the claim made, but not proven, by Levitin and Menon (2003) as also mentioned earlier.

Many studies report left lateralization of rhythm and right lateralization of meter.

Meter and rhythm, however, are not easily divisible musical components as any rhythm induces a sense of meter (Vuust et al., 2005). Moreover, neuropsychological and neuroimaging studies have shown that the motor regions of the brain contribute to both perception and production of rhythms. In studies where subjects only listen to rhythms, the basal ganglia, cerebellum, dorsal premotor cortex (DPMC) and supplementary motor area (SMA) are often implicated. Generally, it emerges from the literature that the analysis of rhythm may depend to a large extent on interactions between the auditory and motor systems (Zatorre, Chen, Penhune, 2007). Studies have also implicated the cerebellum in rhythm synchronization, suggesting that it has a crucial role in temporal processing.

There are some recent papers that focus specifically on the role of hierarchical temporal organization in rhythm processing. One of these suggests that meter facilitates the storing of a rhythm as a coherent whole, rather than as a chain of duration (Vuust, Ostergaard, Pallesen, Bailey, Roepstorff, 2009). Studies of melody and rhythm perception have elucidated mechanisms of hemispheric specialization (Limb, 2006). The prevailing view is that pitch, rhythm, and loudness are processed separately and then come together later (usually after 25-50 ms) to give us the impression of a fully realized musical object or phrase. This too shows that it takes time for us as listeners to experience the music as a whole (Levitin & Tirovolas, 2009).

Listening to music may also entail activation of motor systems (e.g. tapping to the musical beat) associated with producing the music. This is enabled through ventral premotor cortex (VPMC) links. It also engages a neural system, where the DPMC plays a crucial node, which extracts higher-order metrical information.

This latter mechanism may therefore be crucial in setting up temporal, and also melodic, expectancies that are at the heart of musical understanding (Zatorre et al., 2007).

1.4 Research into language and music

There has been an increased interest in the origins of music and its connection with language. Some results suggest that while some networks overlap with ones used for language processing, music processing may involve its own domain-specific processing subsystems (Schmithorst, 2005). In concern to the auditory cortex, the left hemisphere appears to be specialized for the processing of fine-grained temporal stimuli necessary for language comprehension. The auditory cortex of the right hemisphere, on the other hand, has a higher spectral resolution, suitable for processing of musical elements such as pitch (accuracy) (Schmithorst, 2005). Vuust et al. (2005) looked at musicians and how they exchange non-verbal cues as messages when they play together. Their results show a left-lateralization of the pre-attentive responses suggesting functional adaption of the brain to a task of communication, which is much like that of language. Activation of Broca's area, a region traditionally considered to subserve language, also turns out to be important in interpreting whether a note is on or off key (Limb, 2006).

1.5 On musicians versus non-musicians

Brain responses are not only determined by physical properties of the stimuli and the nature of cognitive operations involved.

The listener's competence and familiarity with the stimuli may affect neuronal processing. The impact of expert training is demonstrated in several studies. Vuust et al. (2005) found that pre-attentive brain responses recorded with MEG to rhythmic incongruence are left-lateralized in expert jazz musicians and right-lateralized in non-musicians. In a recent study, increased responses to strong rhythmic incongruity and also a heightened sensibility for more subtle incongruities for musicians than for non-musicians were found (Vuust et al., 2009).

Musicians also show additional activation in motor areas compared to non-musicians during rhythm perception (Grahn & Brett, 2007), and rhythm production in musicians produces greater activation in the DLPFC as well as right inferior frontal gyrus, regions shown to sub-serve working memory for music (Chen, Zatorre, Penhune, 2008). This difference is thought to represent a more advantageous cognitive strategy for reproducing rhythm, which relies on top-down as opposed to bottom-up processing.

In the auditory domain, structural magnetic resonance imaging has shown a greater volume of auditory cortex in professional musicians as compared with non-musicians. These findings are correlated with pitch perception ability. Musicians also show greater grey-matter concentration in motor cortices (Zatorre et al., 2007). A larger anterior corpus callosum has also been reported in musicians compared to non-musicians. These two latter findings are linked to how early the musical training started. Volume differences between musicians and non-musicians have also been reported in the cerebellar hemispheres, but only for men (Zatorre et al., 2007).

Even non-musicians are actively engaged, at least subconsciously, in tracking the ongoing development of a musical piece and forming predictions about what will come next (Levitin & Tirovolas, 2009). There is an important link between such predictive processes and the formation of event- boundaries. Findings from research seem to show that the differences between musicians and non-musicians, lie in what networks are being activated (Levitin & Tirovolas, 2009).

1.6 Music and emotions

Listening to music has also been shown to always bring forward an emotion in the listener. This connection has been investigated by many researchers (see e.g. Mitterschiffthaler et al., 2007; Koelsch et al., 2005). Music-induced emotion has been shown to recruit the reward-motivational circuit, including the basal forebrain, midbrain and orbitofrontal regions, as well as the amygdala (Zatorre et al., 2007). When we listen to music, the ventral tegmental area (VTA) mediates activity in the nucleus accumbens (NAc), hypothalamus, insula, and orbitofrontal cortex. This network represents the neural and neurochemical (via dopaminergic pathways) underpinnings of the anecdotal reports of pleasurable music (Menon & Levitin, 2005). In addition, the hippocampus has been found in positron emission tomography (PET) studies to activate during pleasant music, and the parahippocampal gyrus, which is also implicated in emotion processing, has been found to activate during dissonant music (Koelsch, 2006). This network of structures, which includes the amygdala and the temporal poles, is thought to be the neurological basis for the emotional processing of music (Koelsch, 2006).

In the study by Mitterschiffthaler et al. in 2007, the neural correlates of happy and sad affective states induced by music using fMRI was investigated. It was found that happy musical stimuli were associated with increased activation in the bilateral ventral and left dorsal striatum, left anterior cingulate cortex (ACC) and left parahippocampal gyrus. Sad musical stimuli led to increased activation in right medial temporal structures. Neural stimuli were, somewhat surprisingly, associated with increased BOLD responses in the left auditory association area and left posterior insula.

1.7 Hypothesis

In this study we want to investigate the differences in the activation of neural networks when musically untrained participants listen to continuous, unchanged (flow) parts of music compared to musical transition points (section endings) in teleological music, this be in both a classical piece and a rhythmic piece. Secondly we want to investigate similarities and differences across these two genres, especially at the transition points.

Regarding this we hypothesize activity in the VLPFC (BA 47 and BA 44/45), the PTC (BA 21/22), the DLPFC (BA 9) and the PPC (BA 40) during the transition in both genres. Sridharan et al. (2007) refer to, as mentioned earlier, a ventral network (VLPFC and PTC) and a dorsal network (DLPFC and PPC), and they found that these two distinct functional networks were active at transition points. In addition they found that the pattern of activation during the transition was predominantly right-lateralized.

We are especially interested to see if we will find the same kind of activity at transition points as Sridharan et al. In addition we want to investigate if there are any other areas active during transition points in both our genres.

The VLPFC and PTC have been consistently implicated in the detection of violations in musical expectancies or predictions (such as violations in chord and harmonic expectancies), even in musically untrained listeners (Levitin & Tirovolas, 2009). Neuroimaging and neurophysiological studies have demonstrated co activation of the DLPFC and PPC in the dorsal network during top-down signaling for feature or object attention and during manipulation/monitoring of information in working memory. The results of Sridharan et al. (2007) suggest that these regions form a tightly coupled network that plays an important role in directing and maintaining attention during the movement transitions and in the perceptual updating that ensues.

Further we also expect activity in visual cortex during the transition as a response to the process of constructing a visual representation of the musical form on the basis of event segmentation taking place in the transitions.

2. Materials and Methods

2.1 Participants

We recruited a group of 14 healthy participants with no formal musical training, 7 male with mean age: 33 years, range 30-39, 7 female with mean age: 30.3 years, range 22-36.

All participants underwent a MRI-security check list procedure, and gave informed consent in line with the ethics regulations. The participants were also scanned for possible amusia. The term amusia is generally applied to individuals with a supposed deficit in one or more aspects of music processing (Levitin & Tirovolas, 2009). The test used scanning for amusia was the MBEA, the Montreal Battery of Evaluation of Amusia, and was taken by each subject on the internet previous to the scanning. Each subject was also pre-screened for any history of neurological or psychiatric abnormalities, head trauma, or any other conditions that would prevent an MRI scan from being performed. Our instructions to each participant were kept as simple as possible; just listen to the music. Participants were not aware of the hypothesis being tested.

2.2 Stimuli and stimulus presentation

The stimuli used were classical, tonal and groove-based instrumental music. The classical piece was from the baroque period played by a small ensemble, Brandenburg concerto no 3 in G major, by Johann Sebastian Bach. The tempo was stable throughout the piece (approx. 93 bpm) and the duration of the music was 5 minutes and 57 seconds. The whole scan sequence was 6 minutes and 39 seconds, included 12 seconds with dummies (4 volumes) and 15 seconds silence (5 volumes) before the music started, as well as 15 seconds of silence after the music had ended. The piece was repeated twice for each subject (see timeline below), which gave a total of 2x10 transitions.

Brandenburg Concerto No 3. in G, BWV 1048 (Allegro) - Timeline (min:sec)

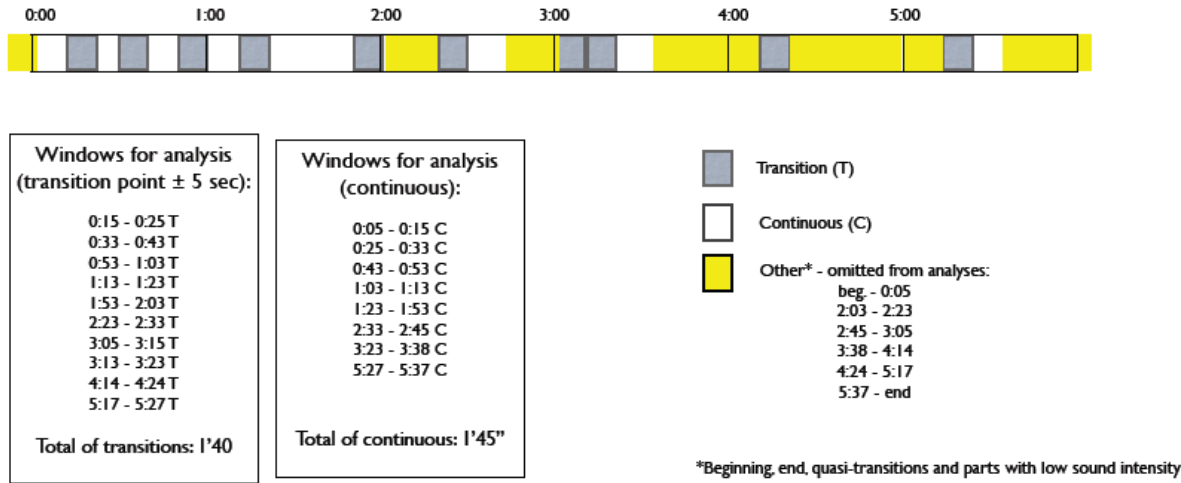


Figure 1. Timeline (min:sec) of J.S. Bach's Brandenburg Concerto No. 3. In G, BWV 1048 (Allegro)



Figure 2. Waveform representation of sound pressure level illustrating the dynamical variations in Brandenburg Concerto No. 3. The x- axis represents time and the y- axis represents sound pressure level (amplitude).



Figure 3. Visual representation of sound pressure level surrounding a transition point in Brandenburg Concerto No. 3. (marked in yellow). The x- axis represents time and the y- axis represents sound pressure level (amplitude). The transition point is marked by a red line. The “transition” itself is an extended time window (approximately 10 seconds wide, yellow highlighted area) surrounding the “point of transition”. A transition in classical music is not a sudden point event; it is prepared by way of melodic, harmonic, rhythmic and dynamic features, and is followed by the onset of a new section.

The rhythmical music example was a funk groove played on drums by drummer Clyde Stubblefield. The tempo was stable throughout (approx. 103 bpm) and the duration was 3 minutes and 12 seconds, with a total scantime of 3 minutes and 54 seconds including 12 seconds with dummies (4 volumes) and 15 seconds silence (5 volumes) before the music started, as well as 15 seconds of silence after the music had ended. The excerpt was repeated twice, which gave a total of 2x10 transitions (see timeline below).

Clyde Stubblefield: funk groove - Timeline (min:sec)

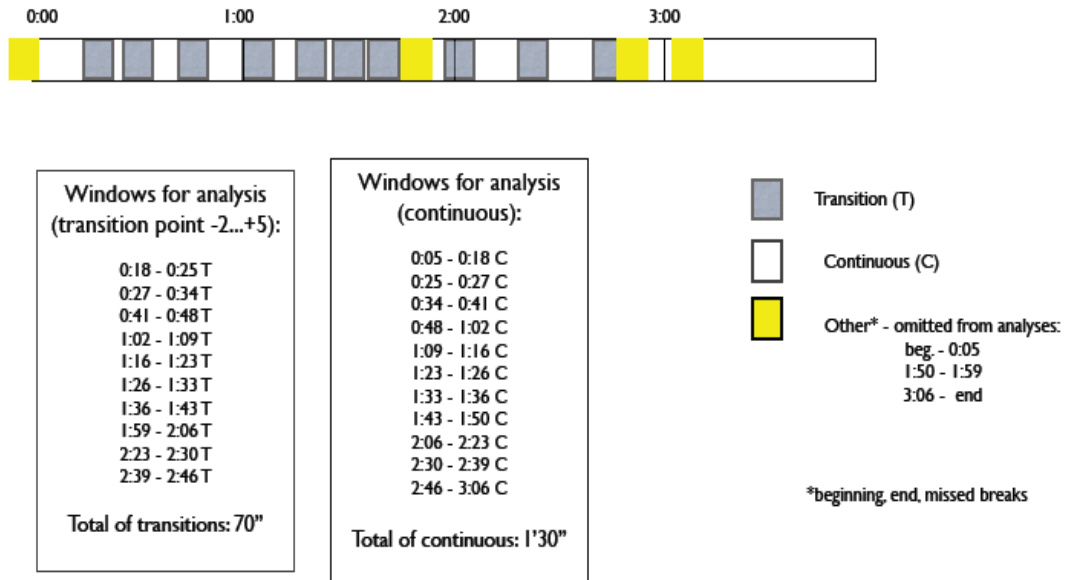


Figure 4. Timeline (min:sec) of Clyde Stubblefield: funk groove.

The start of the time window coincides with the appearance of musical indications on coming transitions, while the end of the time window is calculated so as to catch a possible processing where the coding of a longer musical section takes place.

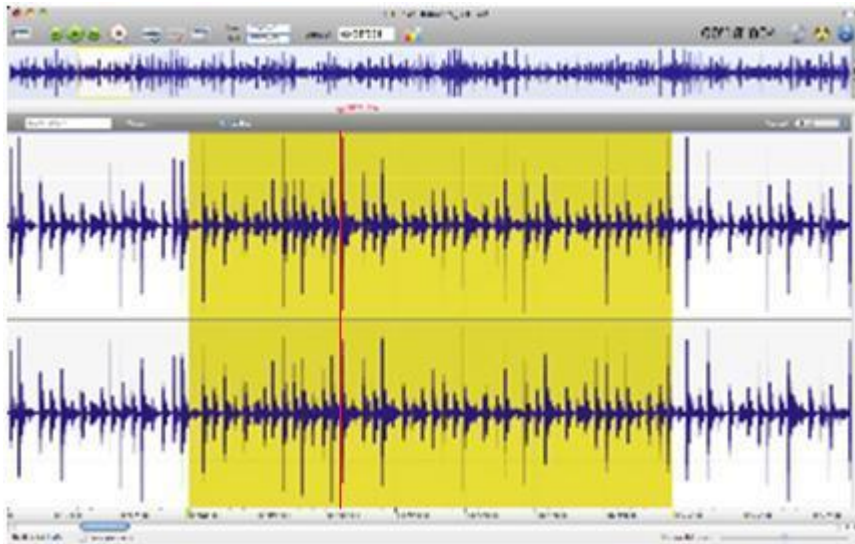


Figure 5. Visual representation of sound pressure level surrounding a transition point in funk groove (marked in yellow). The x- axis represents time and the y- axis represents sound pressure level (amplitude). The transition point is marked by a red line. The “transition” itself is an extended time window (approximately 7 seconds wide - 2 seconds (1 bar) before and 5 seconds after) yellow highlighted area) surrounding the “point of transition”.

The auditory stimuli were presented to the participants via noise-reducing headphones (Confon headphones).

2.3 Experimental design

We used long stretches of real music as our stimulus (as in the experiment of Sridharan et al. 2007), but isolated time windows surrounding the point of musical closure. The time window was of 10 sec duration in the classical piece (time window = closure point \pm 5 seconds), and of 7 sec duration in the groove-based music (time window = from 2 sec (one bar) prior to closure point to 5 sec after).

Data for flow parts were compared to transition parts for the whole group, in both musical categories, and the transition parts in the two musical pieces were compared to each other.

2.3.1 Rating Session

All 14 participants went through a procedure where they answered some questions after their scanning. These questions concerned whether they played an instrument, how interested they were in music, if they paid attention to the music under the scanning session, how well they noticed transitions in the music, if they were distracted by the noise from the MRI machine and if they had heard the musical pieces before, and if they knew them well. It was important for us to know if they knew the musical piece because we wanted to avoid the music to trigger specific memories linked to their personal histories. If a subject had a special emotional connection to one of the pieces, if they connected the music with a happening in their lives for example, this could trigger pictures in their brains and be a methodological problem.

Participants rated their answers from 1-5 on a Likert scale, except from their answer on whether or not they played an instrument, here they just answered yes or no, if yes, what kind of instrument, for how many years they had played, and what genre they played in. Some of our subjects did play an instrument, but they qualified as non-experts if they lacked analytical musical training.

2.4 Image Acquisition

BOLD imaging data were acquired with a GE Signa Excite 1,5 Tesla whole body MR unit at Curato AS, Tullinløkka in Oslo. An 8-channel high resolution brain array GE head coil was used to detect the data. Functional images were acquired using a Gradient Echo EPI pulse sequence, a single-shot echo planar imaging (EPI) in parallel (ASSET = 2) mode with a repetition time (TR) of 3000 ms and echo time (TE) of 40 ms and a flip angle of 80°. Our scanning range parameters had a field of view (FOV) of 24.0, slice thickness 3.0 and spacing on 0.3. The NEX (number of excitations) value was 1.00. The EPI sequence was optimised for minimal acoustic interference (by modifying the gradient rise times in the software). A scanning session started with two localizers (15 slices per localizer) and one calibration scan (82 slices), in order to correctly place the functional images in all participants.

The localizers had a FOV on 24.0 and a slice thickness of 10.0mm, calibration scan had a FOV on 30.0 and a slice thickness of 6.0 mm. We did 40 slices each for both fMRI sequences, the Bach piece and the rhythmic piece. This resulted in 5160 functional volumes for the Bach piece and 2960 functional volumes for the rhythmic piece. Each piece was repeated twice (given a total 10320 volumes for the Bach piece and a total of 5920 volumes for the rhythmic piece), for each participant we changed the order of the starting and ending piece.

Each scanning session consisted also of a structural scan which we ran after we had presented the musical pieces once, example; Bach-rhythmic-structural- rhythmic-Bach. We did a structural scan so that we could use SPM in the analysis and to check our subjects for possible pathology.

The structural scan had a length of 8.29 min and consisted of 90 slices. This sequence, an axial 3D FSPGR (fast spoiled Gradient echo) had an oblique scan plane, with a FOV of 28, slice thickness 2.0mm, TR value of 21.0, flip angle of 35 (this gives a T2- weighted sequence) and a NEX on 1. The total time for a complete session in the scanner was 39 minutes.

2.5 Data Analysis

2.5.1 Preprocessing

All images were converted from DICOM to NIfTI image format using nordicICE; NordicNeuroLab AS; Bergen, Norway). Images were then pre-processed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/spm8/>; Wellcome Trust Centre for Neuroimaging, London, UK). The functional images were realigned to the first volume and the mean image was co-registered to the anatomical image. Each subject's anatomical image was spatially normalized to the Montreal Neurological Institute (MNI) T1-weighted template image. The functional images were spatially normalized using the parameters obtained in the structural normalization, resampled to a voxel size of 2x2x2mm, and smoothed with a Gaussian smoothing kernel of 8 mm at full width at half maximum (FWHM). A high-pass-filter using a cut-off value of 128s and SPM8 AR1 function was applied to reduce low- and high frequency noise.

2.5.2 fMRI data- Whole Brain Analysis

To investigate possible differences in BOLD activity we performed a whole brain analysis. Based on the contrast images from the single subject fixed effects model, a random effects group model was produced in SPM8. One-sample *t*-tests were run. Our significance threshold was set to $p < 0.001$ (uncorrected; cluster defining threshold: 10 voxels).

2.5.3 fMRI data- ROI Analysis

Our four regions of interest were drawn on a pre-processed average of all the 14 participants to anatomically define ROIs, and were used to account for anatomical variability between the subjects. Region of interest analyses of these four areas were performed using WFU pickatlas v 2.4 (Maldjian et al., 2003; Maldjian et al., 2004). Masks were created using the pickatlas tool and the ROI analyses were then performed on the contrasts of interest in SPM by using these masks. The statistical analysis for estimation of signal change within our four regions of interest was conducted in the following steps. First we ran a fixed effects SPM analysis on the experiment model for each participant and used it to model random effects group designs. One-sample *t*-tests were run on all contrasts. Significance threshold was set to $p < 0.001$ uncorrected with a cluster defining threshold of 10 voxels.

3. Neuroimaging Results

The whole brain random-effects group analyses revealed some increased activations in the transition points in both the classical and rhythmic pieces compared to the continuous sections of the music. Whole brain analysis where transitions > continuous in the classical piece, found one cluster in the right superior temporal gyrus ($p < 0.01$, uncorrected; cluster defining threshold, $K_e > 35$ voxels) (table 1 & figure 6 a.). Where transitions > continuous in the rhythmical piece, the whole brain analysis found clusters in the brain areas; left cerebellum, left insula lobe, right superior temporal gyrus, left inferior frontal gyrus and right amygdala (table 2 & figure 6 b., figure 7 & 8).

We also did four region-of-interest (ROI) analyses, based on a priori expectations about the likely involvement of different brain areas in our task. These anatomical brain regions were as mentioned earlier; DLPFC, PPC, PTC and VLPFC. We did not find any clusters in the ROIs when threshold was set to $p < 0.001$ uncorrected with a cluster defining threshold of 10 voxels, but for both types of music there was a cluster in the right PTC that was significantly more activated during transitions compared to continuous music. Both types of music showed more activity in the posterior temporal cortex (table 3 & 4).

Table 1. Whole brain analysis: Brandenburg, Transition > Continuous

Brain region	Laterality	x	y	z	Peak z-score	Ke	p(uncorrected)
Superior temporal gyrus	right	44	-32	0	3.39	35	<0.001

Table 2. Whole brain analysis: Funk, Transition > Continuous

Brain region	Laterality	x	y	z	peak z-score	Ke	p(uncorrected)
Cerebellum	left	-10	-78	-35	4.04	27	< 0.001
Insula lobe	left	-36	22	-2	3.93	30	<0.001
Superior temporal gyrus	right	44	-24	6	3.83	13	<0.001
Inferior frontal gyrus	left	-60	20	20	3.63	10	<0.001
Amygdala	right	24	-8	-12	3.50	10	<0.001

Data are thresholded at $p < 0.001$ (uncorrected) and only clusters with > 10 voxels are reported. Anatomical brain region, hemisphere and coordinates are based on the Montreal Neurological Institute (MNI) system.

In addition we found a cluster of 23 voxles with peak coordinates 40 -48 0 and z-score 3.44. The peak of this cluster was not in any grey matter area and it is therefore not reported in the table. The grey matter area closest to this cluster is the right parahippocampal gyrus.

Table 3. fMRI ROI results.

Brandenburg, Transition > Continuous

ROI	Laterality	x	y	z	Peak z-score	p(uncorrected)
Posterior temporal cortex	Right	48	-32	0	3.18	< 0.001

Table 4. fMRI ROI results.

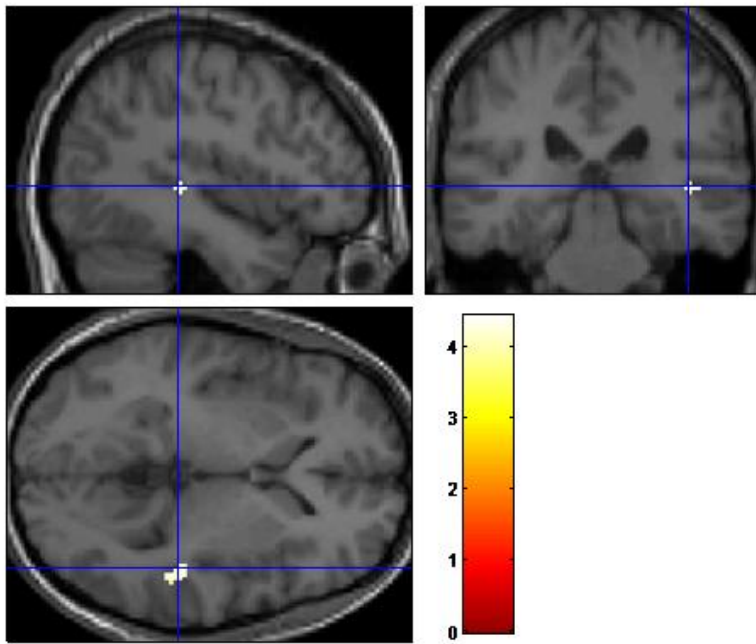
Funky, Transition > Continuous

ROI	Laterality	x	y	z	Peak z-score	p(uncorrected)
Posterior temporal Cortex	Right	48	-18	6	3.14	< 0.001

Data are thresholded at $p < 0.001$ (uncorrected) and anatomical brain region, hemisphere and coordinates are based on the Montreal Neurological Institute (MNI) system.

Figure 6. Differences in BOLD fMRI activations between musical transition points and continuous, unchanged (flow) parts of music, in a) transition>continuous in classical piece, showing the right superior temporal gyrus. b) Transition>continuous in rhythmic piece, showing left cerebellum. Colours refer to t-values.

a.



b.

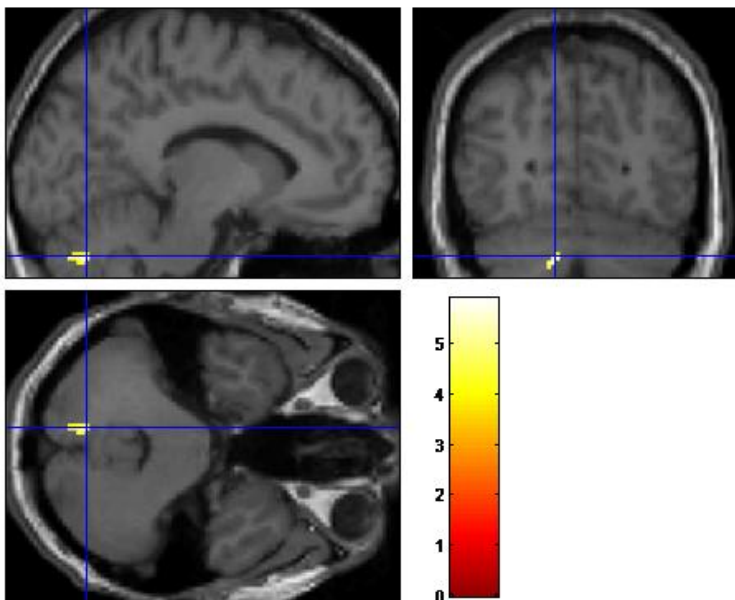
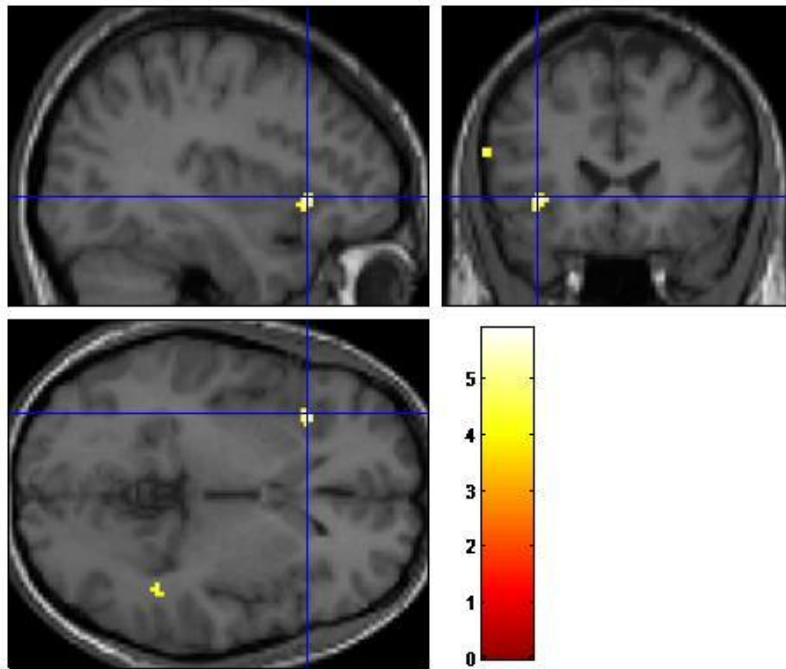


Figure 7. Differences in BOLD fMRI activations between musical transition points and continuous, unchanged (flow) parts of music in transition>continuous in rhythmic piece showing; a) the insula lobe and b) the amygdala. Colours refer to t-values.

a.



b.

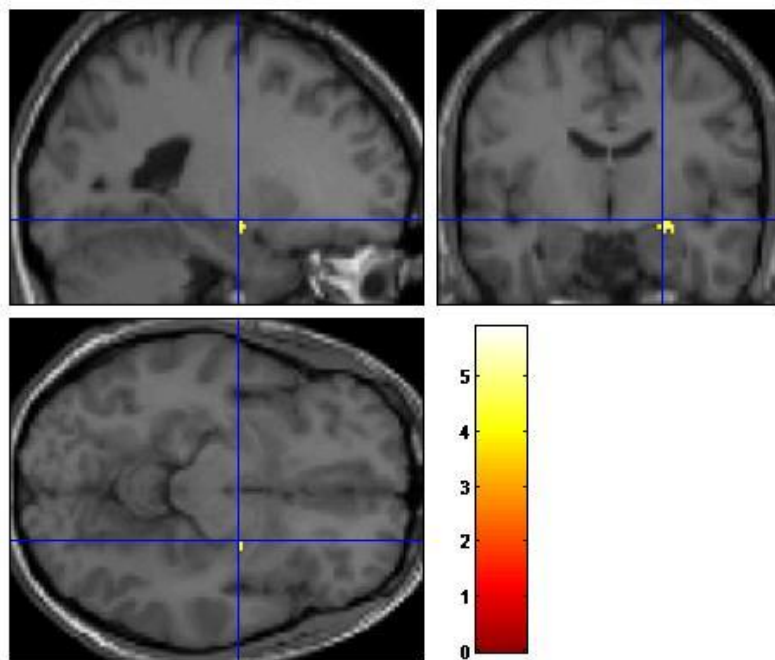
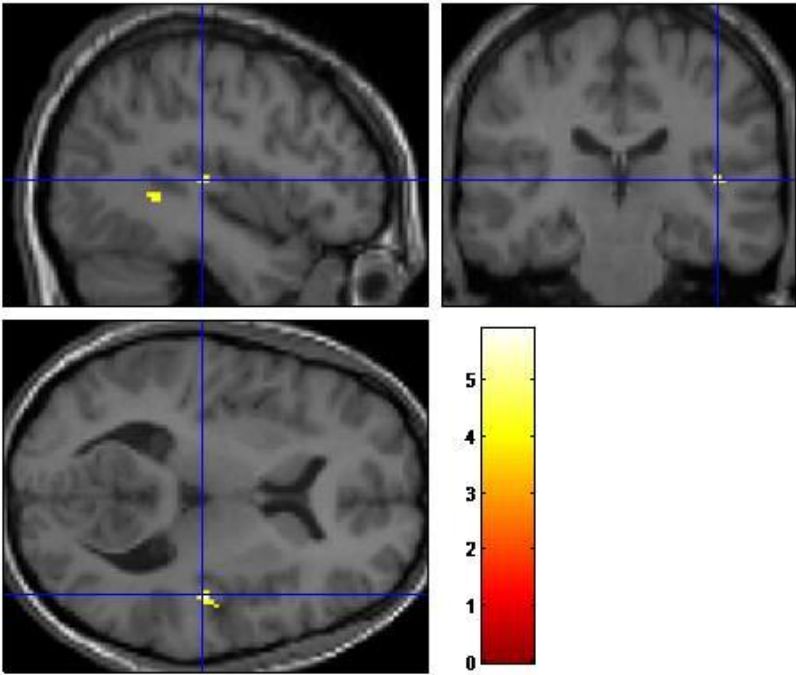
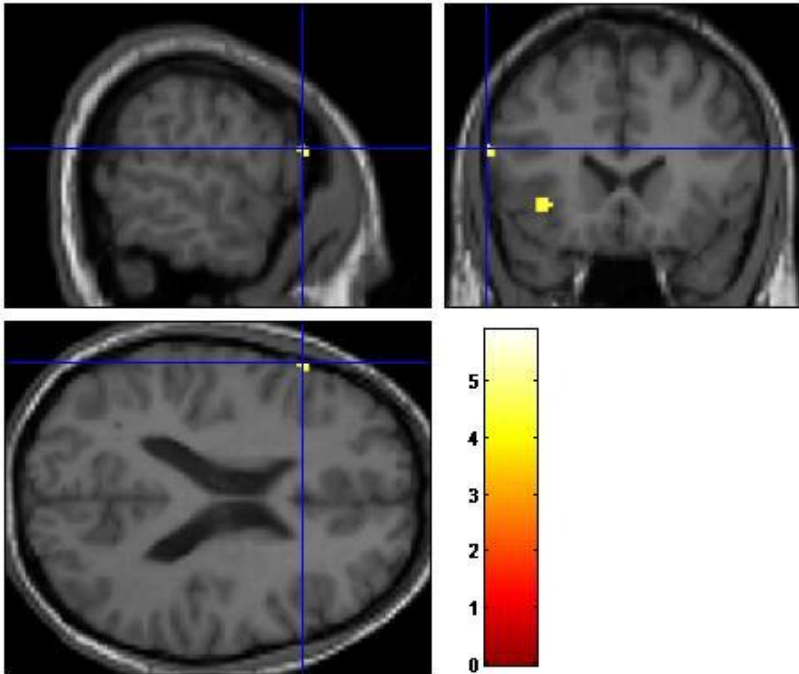


Figure 8. Differences in BOLD fMRI activations between musical transition points and continuous, unchanged (flow) parts of music in transition>continuous in rhythmic piece showing; a) the right superior temporal gyrus and b) the left inferior frontal gyrus. Colours refer to t-values.

a.



b.



4. Discussion

Following in the footsteps of Sridharan et al. (2007), we wanted to investigate possible differences in the activation of neural networks when listening to continuous, unchanged parts of music compared to musical transition points in teleological music. What we did in addition was to add a second genre for comparison, a rhythmic piece of music to compare to the classical piece, and to our knowledge this has not been done before. In Sridharan et al.'s study the transition points consisted of movement transitions where the tempo slows down before the transition point and where the transition is followed by a complete silence and then a new start. In our study we investigated the effect of section endings marked by harmonic and melodic features, but without tempo changes or stretches of silence. Contrary to Sridharan et al. (2007), both the classical piece and the rhythmic piece in our experiment have a steady tempo. This means that there are no tempo fluctuations in connection with the transitions, which is crucial in order to isolate the effect of syntactical closure (either in the form of harmony as in the classical piece or rhythm as in the rhythmic piece) and exclude the effect of a decrease in tempo. This was done to separate the effect of the melodic and harmonic features from the effect of changes in tempo or complete silence, but it also made the transitions less salient than the ones investigated in Sridharan et al.'s study. We did find some differences in neural activity comparing transitions and continuous parts of the music, but as we have seen, the findings were modest. This could of course partly be due to the fact that our transitions were not very salient compared to the transitions in the study of Sridharan et al. Our transitions were not very easy to notice, especially for an untrained listener.

We chose the same regions of interest as Sridharan et al. (2007). They found activity in two distinct networks of brain regions at the transition points, as mentioned earlier in the paper. This was a ventral fronto-temporal network, including the VLPFC (BA 47, 44/45) and the PTC (BA 21/22), which was active during the early part of each transition. Secondly they found a dorsal fronto-parietal network, including the DLPFC (BA 9) and the PPC (BA 40), which was active during the later part of the transition. A ROI analysis on these four regions, (VLPFC, PTC, DLPFC and PPC), confirmed that the pattern of activation during the transition was predominantly right-lateralized. All four ROIs demonstrated a significantly higher percentage of active voxels in the right compared to the left hemisphere.

We also found a right lateralization, but only in our ROI analysis (table 3 & 4) and our data are not substantial or strong enough to allow us to refer to this lateralization as a network. In comparison, we did not distinguish between an early- and a late part of the transition, we looked at the transition as a whole. Because of this there is a possibility that we have missed more detailed results. Still, the question about a possible lateralization in musical experience is fascinating and several studies suggest that musical stimuli such as, e.g tonal pitch perception and melody are processed by the right hemisphere, but that musical training emphasizes a leftward asymmetry (Limb, 2006; Zatorre et al., 2007 & Levitin & Tirovolas, 2009). The notion of right hemispheric specialization for non-verbal auditory functions stemmed from the idea that the cerebral hemispheres are specialized for dealing with entire functions such as music. The possibility that components of these functions might be lateralized differently as well is today largely accepted (Liégeois-Chauvel, Peretz, Babai, Laguitton, Chauvel, 1998).

Further, PTC was the only region of interest in our experiment that showed neural activations. For both types of music there were significant differences between transitions and continuous music in this area. The clusters found in these analyses were relatively large, extending into the right middle temporal gyrus and right Heschl's gyrus. The PTC, together with VLPFC, plays an important role in the detection of violations in musical expectancies and predictions, which could explain the neural activity in PTC at transitions in both genres.

Both in the classical piece and the rhythmic piece, our whole brain analysis showed clusters in the right superior temporal gyrus, suggesting more neural activity in this region at the transition points compared to the continuous parts (table 1 & figure 6 a, table 2 & figure 8 a). The temporal lobe is involved in auditory perception and in this lobe we find the primary auditory cortex. The superior temporal gyrus includes an area, within the sylvian fissure, where auditory signals from the cochlea (relayed via several subcortical nuclei) first reach the cerebral cortex. Liégeois-Chauvel et al. (1998) showed in their study that a right temporal cortectomy impaired the use of both contour and interval information in the discrimination of melodies. The excision of a part of the auditory areas (posterior part of the superior temporal gyrus) was found to be the most detrimental for pitch and temporal variation processing (Liégeois-Chauvel et al., 1998). This study underlined the importance of the superior temporal gyrus in melody processing. These findings support that the right temporal gyrus plays a crucial role in pitch and temporal variation processing and comprehension of melody, which again is important for recognizing transition points in music. Harmony and tonal relations have been shown to be predominantly served by networks in the right temporal region also by Zatorre in his study from 1988. Tonal relations are important for large-scale temporal form, since both harmony and melody are considered effectual means in building musical form and signaling the end of a musical section.

Therefore, this could again be one reason why we see neural activity in this particular region of the brain at transition in both musical pieces.

The whole brain analysis of the rhythmic piece also shows more activation at the transition points compared to the continuous sections. Significant activations were found in the superior temporal gyrus here as well. The superior temporal gyrus has been associated with the switching between familiar/unfamiliar auditory stimuli, so activation here could mean that the participants tried to recognize the music (Schmithorst, 2005). Whole brain analysis shows further significant activation in the left cerebellum (table 2 & figure 6 b). The cerebellum plays an important role in motor control but it is also involved in some cognitive functions such as attention and language and in addition probably also in some emotional functions such as regulating fear and pleasure responses. It contributes to coordination, precision and accurate timing. Earlier fMRI studies have linked the cerebellum, together with the basal ganglia, pre-SMA/SMA, and the anterior superior temporal gyri to rhythms in which accents arise at regular intervals (Levitin & Tirovolas, 2009), which again gives the feeling of a simple beat. Studies have also implicated the cerebellum in rhythm synchronization and suggested that it has a crucial role in temporal processing, which could be one possible reason why we got activity in the cerebellum at transitions in our rhythmical piece. Many studies also report a left lateralization of the experience of rhythm (Zatorre et al., 2007), correlating well with the activity in left cerebellum in our study, when listening to the rhythmic piece. According to this the cerebellum has a more crucial role in listening to rhythmical music compared to e.g classical music.

The left insula lobe and the right amygdala (table 2 & figure 7), also show more neural activity at transition points compared to the continuous parts of the music in the rhythmical piece.

The insula is a structure deep within the lateral fissure between the temporal lobe and the frontal lobe and plays a role in diverse functions usually linked to emotion or the regulation of the body's homeostasis. The amygdala is a part of the limbic system and is located deep within the medial temporal lobes of the brain. It performs a primary role in the processing and memory of emotional reactions. Insula and amygdala have been shown to be a part of a network representing the neural and neurochemical (via dopaminergic pathways) underpinnings of the anecdotal reports of pleasurable music (Menon & Levitin, 2005). Insula, amygdala, and partly cerebellum, are all brain areas implicated in emotions. Activation here, where rhythmic transitions > classical transitions, could reflect that a transition, more so in rhythmic music compared to classical, triggers emotions in the listener. This is only speculations on a plausible explanation. The left insula has also been connected to listening to neutral music relative to sad and happy music (Mitterschiffthaler et al., 2007). This is interesting knowing that we tried to avoid very expressive musical gestures that are supposed to trigger emotions in the listener.

The left inferior frontal gyrus shows activation at the transitions in the rhythmic piece (table 2 & figure 8 b). This is a region of the brain that has been associated with musical syntax and musical structure (Schmithorst, 2005). Tonal relations, or musical intervals (as opposed to large-scale musical structure), have been shown to be predominantly served by among others the inferior frontal gyrus (Levitin & Tirovolas, 2009). This could relate well to activity in this area while listening to rhythmic music. Grahn and Brett found in their study in 2007, that musicians show additional activation in motor areas compared to non-musicians during rhythm perception.

Another study showed that rhythm production in musicians produces greater activation in among others, the right inferior frontal gyrus (as opposed to our findings; activation in the left inferior frontal gyrus) (Chen et al., 2008). This difference is thought to represent a more advantageous cognitive strategy for reproducing rhythm, which relies on top-down as opposed to bottom-up processing.

Our results show more neural activity at transition points compared to continuous parts in both genres. A plausible explanation to this can be that there are dynamic brain changes underlying musical transitions and thus be an important component of the natural music listening experience, maybe more so in rhythmic music compared to classical.

We also thought initially before carrying out the experiment, that some of the things that might happen at the transition points would be some kind of a visual representation of what happened in the music. We did not get any activation in the visual cortex at a group level of analysis in neither of the two musical pieces. Thus no support has been found for this hypothesis in our data.

In order to try to isolate the effect of syntactical closure in the transition points, we wanted the music to be devoid of specific extra-musical associations (absolute-music) and to avoid very expressive musical gestures that are supposed to trigger big emotions in the listener. The first classical piece we thought of using in our experiment was “Eroica” by Beethoven. Our conclusion regarding this piece was that it was too grand and seemed to evoke emotional responses in those who listened to it. Further, regarding familiarity in the music, it was important for us to find out if our participants knew the two musical pieces used in the experiment.

One of the questions our participants had to answer after taking part in the experiment was whether they knew the music beforehand. One of our participants noted 5 on the Likert scale regarding this. We checked if the participant had any personal feelings, memories, personal happenings in life that could be triggered by this particularly music. The participant answered “no” on this question. Had the answer been “yes” this participant would have had to be excluded from the study, since we wanted the music to be devoid of specific extra-musical associations, if the music was well known, this could for example produce memories triggering mental pictures and big emotions in the participant.

Technical limitations like the background scanner noise during fMRI machine paradigms, is a challenge. Going through scientific articles concerning music and fMRI there seems to be little emphasis on this problem. In order to try to solve problems related to this, we first excluded parts of the music from the analyses because of unsatisfactory signal/noise ratio, the music was too transparent given the background scanner noise. Secondly, we tried to find the best set of headphones, both for quality of the sound and for keeping the signal/noise ratio as small as possible for the participants. We tested a few headsets before finding a set we thought were satisfactory. The third factor was to adjust the fMRI paradigms themselves, making sure that the scanner produced as little noise as possible, again trying to keep the signal/noise ratio in perfect balance, meaning producing good enough MRI pictures to read as well as keeping the noise at a minimum level.

To strengthen our results we could in addition have examined changes in autonomic nervous system reactivity using cardiovascular signals acquired simultaneously with the brain imaging data.

A very direct measure of the activity of nerve cells is delivered by EEG. EEG yields an excellent time resolution (fractions of a millisecond), but very poor spatial resolution. fMRI on the other hand, offers excellent spatial resolution (1 mm and less) and because of this, has become very popular in brain research.

5. Future Directions (final remarks)

In the future it could be interesting to do the same experimental design using musically trained individuals for comparison to this study. Regarding the problem with background noise from the MRI scanner, it could in addition be interesting to use the same experimental design, the same participants together with musically trained individuals for comparison, but then also use fMRI baby-protocols. These protocols give less noise from the MRI machine, which again affects the signal (fMRI; changes in intensity associated with the BOLD response). The question then would be; how would this influence the results (the BOLD responses). Investigating possible differences between transitions in these two genres is also a possible and interesting direction for further research.

While music perception utilizes neural substrates common to all types of auditory processing, it is clear that the brain processes music in a strikingly broad fashion, with neural activation patterns that reflect the use of language mechanisms, long term neural plasticity, emotion and reward systems.

The wide spectrum of musical ability, ranging from the musically gifted to the amusic individual, provides a quasiparametric variable with which to interpret such patterns of brain activity. As such, music promises to remain a singularly useful tool for the study of the brain.

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