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The chronnectome of musical beat

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ABSTRACT

Keeping time is fundamental for our everyday existence. Various isochronous activities, such as locomotion, require us to use internal timekeeping. This phenomenon comes into play also in other human pursuits such as dance and music. When listening to music, we spontaneously perceive and predict its beat. The process of beat perception comprises both beat inference and beat maintenance, their relative importance depending on the salience of beat in the music. To study functional connectivity associated with these processes in a naturalistic situation, we used functional magnetic resonance imaging to measure brain responses of participants while they were listening to a piece of music containing strong contrasts in beat salience. Subsequently, we utilized dynamic graph analysis and psychophysiological interactions (PPI) analysis in connection with computational modelling of beat salience to investigate how functional connectivity manifests these processes. As the main effect, correlation analyses between the obtained dynamic graph measures and the beat salience measure revealed increased centrality in auditory-motor cortices, cerebellum, and extrastriate visual areas during low beat salience, whereas regions of the default mode- and central executive networks displayed high centrality during high beat salience. PPI analyses revealed partial dissociation of functional networks belonging to this pathway indicating complementary neural mechanisms crucial in beat inference and maintenance, processes pivotal for extracting and predicting temporal regularities in our environment.

1. Introduction

Humans have a propensity to engage in isochronous actions, which may be rooted in evolutionary adaptation (Merker et al., 2009). In addition to producing sound patterns that are periodic over time, we are able to extract temporal regularities from the auditory environment, be it language or music (Kotz et al., 2009; Grube et al., 2013). We are thus capable of extracting a regular pulse from the auditory environment, which allows us to predict future rhythmical events to which we can then synchronize our movements (Drake et al., 2000; Honing, 2012; Maes et al., 2014).

When listening to music, we are spontaneously driven to find a beat, which makes beat perception fundamental to our experience of music and therefore key to explaining musical behavior (Large and Snyder, 2009; Vuust et al., 2018). To date our remarkable and possibly uniquely human ability to effortlessly perceive the beat in music keeps challenging cognitive scientists, who pursue to understand its underlying brain processes (Large and Palmer, 2002). A deeper understanding thereof would be key for explaining a range of musical behaviors, such as why moving to music is pleasurable (Large and Palmer, 2002; Large and Snyder, 2009; Zatorre and Salimpoor, 2013), or why listening to rhythms has a favorable effect on patients with neurodegenerative gait disorders (e.g., Parkinson's disease; Nombela et al., 2013; Ashoori et al., 2015; Thaut et al., 2018), stroke patients (Bradt et al., 2010), and autistic individuals (Wan et al., 2011). Such therapeutic potential is the reason why the neuroscience of rhythm has developed into a specific field of research among clinicians and scholars from many disciplines (Anvari et al., 2002; François et al., 2015).

Music with regular periodic pulse exists in every culture, affording coordination between performers and often at the same time inducing a synchronized motor response from listeners (Nettl, 2000). An obvious indicator of pulse sensitivity is our instinctive, almost subconscious, skill for motor synchronization to music which manifests at a young age (Trehub, 2001; Trainor, 2005). Undeniably, our proclivity for rhythmic movement is evidenced in infancy and to a greater extent to music and other metrically regular sounds than to speech (Zentner and Eerola, 2010). Such a predisposition to move with music is speculated to be rooted in the evolution of entrainment and social behavior, as

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synchronization with a beat is the simplest form of entrainment (Janata et al., 2012; Madison, 2006; Madison et al., 2011). It is therefore not surprising that music and dance have in some cultures evolved together (Cross, 2008; Wallin et al., 2000).

Beat perception comprises two different types of subprocesses (Cameron and Grahn, 2016). First, beat induction (beat finding) can be defined as generation of putative beats so as to entrain or synchronize to the isochronous deviations caused due to expressive timing in music or, in other words, active inference of perceived beat. Second, beat maintenance (beat continuation) can be described as mechanical, autonomous time keeping, which involves continual, sustained measurement of predictable intervals without significant need for attention.

The salience of musical beat varies between and within musical pieces, depending on the degree to which the music contains repetitive rhythmic patterns with a suitable rate. High beat salience is evoked by musical events that occur at regular intervals at a suitable tempo and have sharp attacks. The optimal tempo for beat salience has been found to lie in the vicinity of 100–120 events per minute, corresponding to a beat period of 500–600 ms (Parncutt, 1994; Toiviainen and Snyder, 2003; van Noorden and Moelants, 1999), which closely corresponds to the spontaneous tempo of walking (McDougall and Moore, 2005) and tapping (Fraisse, 1982). Beat salience has been found to be associated with the urge to move to music (Madison et al., 2011). Computational models of beat salience proposed so far can be divided into two categories based on the kind of music representation they use: symbolic models (e.g., Parncutt, 1994; Toiviainen and Snyder, 2003), which operate on notation-like music representations, such as MIDI, and audio models (e.g., Lartillot et al., 2008; Madison et al., 2011), which take music recordings as input.

It can be assumed that, during continuous listening to music, beat inference and beat maintenance exist concurrently, with beat inference being more prominent during moments of low beat salience, and beat maintenance during moments of high beat salience. Namely, within the framework of active perception, beat inference and maintenance can be regarded as predictive coding (Koelsch et al., 2019) with low and high certainty, respectively. Within this framework, the two processes could be considered to exist on a continuum instead of being dichotomous. This warrants the use of a continuous variable that measures the degree of beat salience throughout the musical pieces at each time point. The model by Lartillot et al. (2008), applied in the present study, allows the extraction dynamic variation of beat salience. The strength of this model is that it has been perceptually validated and therefore affords interpretability of the found neural correlates.

Cameron and Grahn (2016) provide a comprehensive review highlighting the roles of cortical, subcortical, and cerebellar regions in beat perception, including inference and maintenance. They highlight the need for dynamically investigating the time course of rhythm and beat perception. While neural correlates of musical beat have been investigated using naturalistic stimulation on both voxel-level (Alluri et al., 2012, 2013; Toiviainen et al., 2014) and network-level (Burunat et al., 2017), effects of musical beat salience on the temporal dynamics of overall functional connectivity in the brain have not been studied so far.

1.1. Beat and neural activation

When studying the brain processes which sustain timing, several motor-related brain regions have been found to be involved (Grahn, 2009). This has been considered a groundbreaking finding in music neuroscience, as merely listening to music in the absence of any overt movement engages motor resources of the brain. These include premotor cortex (PMC), supplementary motor area (SMA), and basal ganglia (Grahn and Brett, 2007; Chen et al., 2008; Bengtsson et al., 2009; Grahn and Rowe, 2009; Geiser et al., 2012; Teki et al., 2012; Kung et al., 2013). Rhythm thus activates the neural circuits involved in motor processing, which provides a possible account for the intimate connection between music and movement (Zatorre and Salimpoor, 2013).

Both the basal ganglia (especially the putamen) and the SMA seem to be particularly crucial to beat perception (Cameron and Grahn, 2016; Grahn and Brett, 2007). Motor areas, particularly the SMA, perform time prediction via top-down connections to the auditory cortex (Cadena-Valencia et al., 2018; Merchant and Honing, 2014; Merchant et al., 2015a,b; Merchant and Yarrow, 2016). The basal ganglia have been implicated in both beat finding (Grahn and Rowe, 2009) and beat continuation (Kung et al., 2013). More specifically, increased activation in the basal ganglia during rhythm perception has been reported to reflect the internal generation of upcoming beats once the temporal structure of the music has been established and it remains regular. In line with this, activation in the basal ganglia decreases in response to irregular rhythms, as these lead to modifications in beat prediction (Grahn and Rowe, 2013), while cerebellar activity increases, which is consistent with a distinct role for the cerebellum in absolute timing (Grube et al., 2010; Teki et al., 2012; Cameron and Grahn, 2016). In line with this, Spencer and Ivry (2013) review literature on cerebellum and timing and conclude that its role is key in "providing a precise, metrical representation of defined temporal intervals" rather than give rise to abstract temporal representations of underlying rhythms.

1.2. Beat and functional connectivity

Keeping time is likely to be an emergent network property, and hence merely localizing it to particular regions provides an incomplete picture of its neural underpinnings. Consequently, functional connectivity studies in rhythm perception have provided new insights by identifying associated auditory- and motor-related networks, which may facilitate the temporal predictions involved in rhythm perception (Zatorre et al., 2007; Patel and Iversen, 2014). However, functional connectivity studies are rare and have not sufficiently investigated this phenomenon beyond the General Linear Model (GLM) approach. In particular, a functional network of cortical and subcortical structures, consisting of auditory cortex, PMC, putamen, and SMA, seems to play a role during beat perception, especially when internal generation of the beat is required (Grahn and Rowe, 2009). This corroborates the hypothesis that the PMC and dorsal auditory regions mainly evolved to sustain the mechanisms of temporal sequencing (Leaver et al., 2009; Rauschecker and Scott, 2009). However, as indicated in Merchant et al. (2015), while one study reported increased auditory-premotor coupling as a function of beat salience in isochronous sequences (Chen et al., 2006; see also Assaneo and Poeppel, 2018) another study found this coupling to decrease as metric complexity increased (Kung et al., 2013). Because real music is a metrical stimulus, which comprises differentially accented groupings and subdivisions of beat and hence differentially salient beats, we should expect a pattern of connectivity in relation to beat salience that is different from what previously has been observed in studies using isochronous and equally-salient beats. On a more general note, the lack of consensus does not currently regard which brain areas are involved in the study of timing and rhythm, but more specifically, what connections exist amongst the relevant areas that give rise to particular timing behaviors (Grahn, 2009). Moreover, since beat perception unfolds over time when one listens to music (Cameron and Grahn, 2016), it is crucial to study how brain networks dynamically organize themselves in continuous naturalistic music listening situations.

Recent research on beat processing beyond the GLM approach investigated beat saliency using blind source separation techniques by means of Independent Component Analysis (ICA) in combination with Music Information Retrieval (MIR) methods (Burunat et al., 2017). Findings revealed a robust action-perception functional network of auditory and motor regions associated with variations in beat salience, which was concealed from a comparative GLM analysis. In particular, the motor areas of the network were found to correlate negatively with beat salience. Further elucidation of temporal dynamics of the brain mechanisms pertaining to beat processing will be necessary to fully characterize its nature.

1.3. Beat and chronnectome

Graph-based methods provide a useful tool for spatially characterizing network structures (Bullmore and Sporns, 2009), by representing regions or voxels in the brain as nodes in a graph. In the domain of music, graph theory has been used to investigate functional networks during music listening and their dependence on musical preference (Wilkins et al., 2014) and training (Alluri et al., 2017). A graph-theoretical measure commonly used in these studies is node centrality, which indicates the degree to which a region comprises an important hub in the brain's network. Various methods have been proposed to quantify node centrality. Closeness and betweenness centrality are often used in analyses considering at most a few hundred selected regions in the brain (Lohmann et al., 2010), but due to their computational complexity they are not feasible for voxel-based whole-brain analysis, an approach necessary for disentangling functional network structures with sufficient spatial accuracy and to avoid dependence on a particular choice of brain parcellation. For this purpose, Eigenvector Centrality (EC; Bonacich, 2007) is more appropriate. To estimate EC, a non-negative functional voxel-by-voxel connectivity matrix is first calculated. A common choice for the connectivity measure is Pearson's correlation added by one. Subsequently, Singular Value Decomposition is applied to the obtained connectivity matrix to obtain the first eigenvector. This vector contains the voxelwise centrality values. EC attributes high centrality values to voxels that are strongly connected to a large number of voxels that themselves are central, thereby providing a global indirect measure of functional connectivity. It therefore indicates for a given condition or task the important computational hubs in the brain's functional network. An appealing feature of EC is that, unlike closeness and betweenness centrality, it does not rely on thresholding and thus is a parameter-free method.

In previous studies, EC has been found to change as a function of stimulus (Koelsch and Skouras, 2014), task (García-García et al., 2015), and condition (Binnewijzend et al., 2013; Lou et al., 2015). While functional connectivity studies traditionally have assumed connectivity patterns that are static over time, dynamic functional connectivity studies have become increasingly common (for a review, see Preti et al., 2017). Calhoun et al. (2014) have coined the term "chronnectome" to refer to time-varying whole-brain connectivity patterns. Dynamic functional connectivity studies are most commonly based on sliding window approaches (Preti et al., 2017) or phase synchronization estimates (e.g. Glerean et al., 2012).

The present study investigates the effect of beat salience on the dynamics of whole-brain functional networks during continuous listening to music to investigate processes underlying beat inference (prevalent during low beat salience) and beat maintenance (prevalent during high beat salience). To this end, it employs dynamic graph analysis (Eigenvector Centrality) in tandem with computational estimation of beat salience from the musical stimulus, to obtain an overall view of how functional network centrality changes dynamically as a function of musical beat salience. Subsequently, targeted functional connectivity analyses (Psychophysical Interaction) are carried out to investigate how functional connectivity varies and is modulated by beat salience within and between brain regions that have previously been found to be involved in beat perception.

Due to scarcity and lack of consensus in previous research, specific hypotheses about the manifestations of the processes of beat inference and maintenance in whole-brain functional network connectivity are difficult to draw. However, we assume that network centrality in areas previously found to be activated by beat perception, such as cortical, cerebellar, and striatal motor areas, would be modulated by the process of inferring a salient beat. For specific hypotheses regarding the dependence of functional connectivity on beat salience, we assume, based on results obtained by Kung et al. (2013), that because music is a metrical stimulus, auditory-motor connectivity increases with low beat salience.

Doya (2000) posits that the cerebello-thalamo-striato-cortical motor pathway can be divided into smaller networks that play complementary roles in learning and motor control. The review paper highlights the role of the cerebellum as one that performs supervised learning wherein an internal representation of the data is already available. The cortex's role is described as one that performs unsupervised learning, which can be defined as data-driven approach of learning/and responding to the existence or lack of patterns in it/guided by on the context/the statistical properties of the stimulus (Bostan et al. 2013). In this approach, the pattern or structure has to be learnt based on the available data and context.

In this framework, one could surmise that the cerebello-thalamo-cortical motor pathway in conjunction with the auditory cortex is responsible for developing an internal representation of beat. However, once this template is formed, the cerebellum continues to process the beat and match the result with the formed template. One could then hypothesize that decreases in beat salience engender deviations from the template, which would then recruit higher-order cortical motor pathways to take over and learn how best to fill in the gaps based on the auditory information and short-term temporal context available. In other words, in the case of low beat salience, higher level cortical networks would be recruited to update the prediction minimizing prediction error fed forward from lover level areas. Once the beat is inferred, the maintenance may not rely on forward prediction error from the lower levels.

2. Methods

2.1. fMRI data acquisition

Participants: Seventy-seven healthy participants (age 29.6 ± 8.9, 43 females, 71 right-handed, 1 ambidextrous) with no history of neurological or psychological disorders participated in the fMRI experiment. The participants were screened for inclusion criteria before admission to the experiment (no ferromagnetic material in their body; no tattoo or recent permanent coloring; no pregnancy or breastfeeding; no chronic pharmacological medication; no claustrophobia). The participants had variable levels of music education, with a median of 3.5 years and an interquartile range of 11.25 years of formal music education.

Stimulus & task: Participants' brain responses were acquired with fMRI while they listened to an 8-min long piece of Argentinean tango, *Adiós Nonino* by Astor Piazzolla. This stimulus was chosen because it contains wide variations in the salience of musical beat. Participants' only task was to attentively listen to the music delivered via high-quality MR-compatible insert earphones (Avotec, Stuart, FL, USA) while keeping their eyes open. Foam was used to attenuate the gradient noise. The sound level of the stimuli was individually adjusted so that they were audible above the scanner noise but the volume stayed within safety limits (below 80 dB). The study protocol proceeded on acceptance by the ethics committee of the Coordinating Board of the Helsinki and Uusimaa Hospital District. The data collection was part of a broader project (Tunteet) involving additional tests and neuroimaging and neurophysiological measures (Alluri et al., 2015; Bogert et al., 2016; Burunat et al., 2014, 2015; Carlson et al., 2015; Haumann et al., 2016; Kliuchko et al., 2015, 2016).

Scanning: Scanning was performed using a 3T MAGNETOM Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) and a standard 32-channel head-neck coil, at the Advanced Magnetic Imaging (AMI) Centre (Aalto University, Espoo, Finland). Using a single-shot gradient echo planar imaging (EPI) sequence thirty-three oblique slices (field of view: 192×192 mm; 64×64 matrix; slice thickness: 4 mm, interslice skip: 0 mm; echo time: 32 ms; flip angle: 75°; voxel size: $2 \times 2 \times 2$ mm^3) were acquired every 2 s, providing whole-brain coverage per participant. T1-weighted structural images (176 slices; field of view: 256×256 mm; matrix: 256×256; slice thickness: 1 mm; interslice skip: 0 mm; pulse sequence: MPRAGE) were also collected for individual coregistration.

Preprocessing: Functional MRI scans were preprocessed on a Matlab

platform using SPM8 (Statistical Parametric Mapping), VBM5 for SPM (Voxel Based Morphometry; Wellcome Department of Imaging Neuroscience, London, UK), and customized scripts developed by the present authors. For each participant, low-resolution images were realigned on six dimensions using rigid body transformations (translation and rotation corrections did not exceed 2 mm and 2°, respectively), segmented into grey matter, white matter, and cerebrospinal fluid, and registered to the corresponding segmented high-resolution T1-weighted structural images. These were in turn normalized to the MNI (Montreal Neurological Institute) segmented standard a priori tissue templates using a 12-parameter affine transformation. Functional images were then blurred to best accommodate anatomical and functional variations across participants as well as to enhance the signal-to-noise by means of spatial smoothing using an 8 mm full-width-at-half-maximum Gaussian filter. Movement-related variance components in fMRI time series resulting from residual motion artifacts, assessed by the six parameters of the rigid body transformation in the realignment stage were regressed out from each voxel time series. Following this, spline interpolation was used to detrend the fMRI data. Next, temporal filtering was performed by Gaussian smoothing (kernel width: 4 s), as it provides a good compromise between efficiency and bias (Friston et al., 2000).

2.2. Musical feature extraction

Beat salience of the used stimulus was computationally estimated using the model proposed and perceptually validated by Lartillot et al. (Lartillot et al., 2008). The model is based on the use of a moving analysis window to obtain a dynamic estimate of beat salience. For each analysis window, the signal is first passed through a gammatone filterbank, after which the onsets are detected for each frequency channel using full-wave rectification, low-pass filtering, time differentiation and half-wave rectification. Following this, the autocorrelation function of the envelope is calculated for each frequency channel and these obtained functions are summed across channels to estimate periodicities present in its. Subsequently, the summary autocorrelation function is multiplied by a resonance curve (Toiviainen and Snyder, 2003), with the maximum at the lag of 500 ms, corresponding to the preferred tempo at the vicinity of 120 bpm. Finally, instantaneous beat salience is estimated as the height of the highest peak in the autocorrelation function. The method is schematically presented in Fig. 1. Beat salience depends on several musical parameters, including rhythmic complexity, timbre, and tempo. High beat salience is evoked by music that contains tones with sharp attacks occurring regularly at rates close to 120 bpm, while music that contains slow attacks or syncopation, or is played at low or high tempo, yields a lower beat salience. The present beat salience model has been validated using a rating study with 100 musical excepts representing a range of different musical styles (Lartillot et al., 2008). The perceptual data showed high inter-subject consistency and the model could predict them with high accuracy. This suggests that perceived beat salience of the present stimulus can be predicted by the present model.

In the present study we estimated the stimulus' beat salience using a 3-s window and a 1-s hop. These obtained time series had the mean value of 0.25 and std of 0.11. Subsequently, the obtained time series was convolved with canonical double-gamma hemodynamic response function and downsampled to conform with the sampling rate of the fMRI data. The original and convolved time series are presented in Fig. 2.

In addition to beat salience, 24 other musical features were extracted, representing a range of musical dimensions. For a full description of these variables, see Supplementary material. None of these features correlated significantly with beat salience, suggesting the absence of confounding factors in other musical dimensions.

2.3. Centrality analysis

Parcellation: To reduce the computational burden, the data of each participant was spatially downsampled by a linear factor of two, yielding 28,542 cubical voxels with 4-mm edges. The connectivity analysis used in this study is schematically presented in Fig. 3.

Windowing: For dynamic analysis of connectivity, we employed a sliding window approach, which is the most commonly used approach to estimate dynamic functional connectivity (Preti et al., 2017). To this end, each participant's data was windowed using a moving Gaussian window with a standard deviation of 10 scan intervals (20 s) and a hop size of one scan interval. This window has the effective width of approx. 31 secs

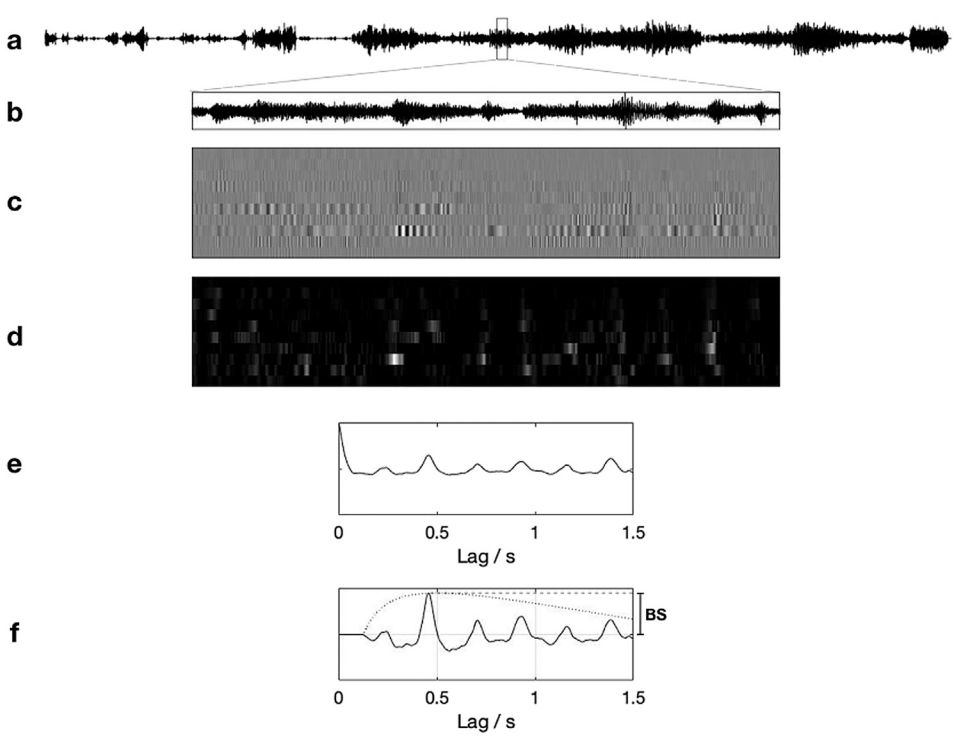

Fig. 1. Beat salience estimation method used in the present study: (a) audio signal; (b) windowed excerpt; (c) output of gammatone filterbank; (d) onset detection curves per frequency channel; (e) summary autocorrelation function of onset detection functions; (f) autocorrelation function multiplied by a resonance curve (Toiviainen and Snyder, 2003). The latter is displayed as a dotted line. Instantaneous beat salience (BS) is estimated as the height of the maximum of the autocorrelation function.

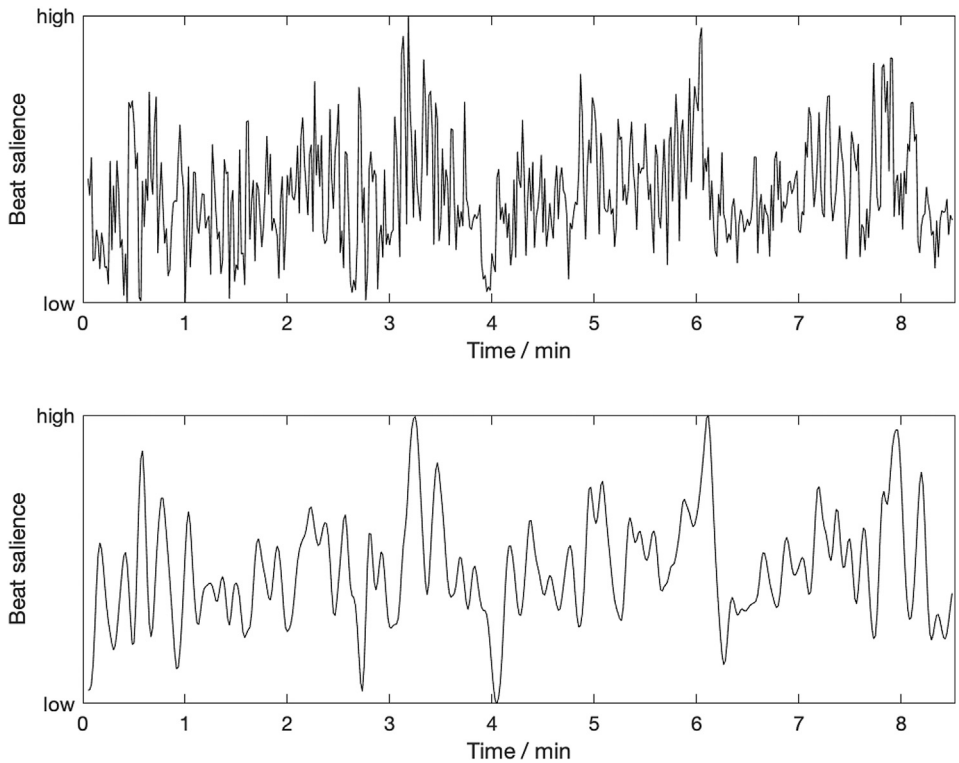

Fig. 2. Top: beat salience estimated from the stimulus used in the study. Bottom: beat salience convolved with hemodynamic response function. Units for the y axis are arbitrary and hence are marked as low and high.

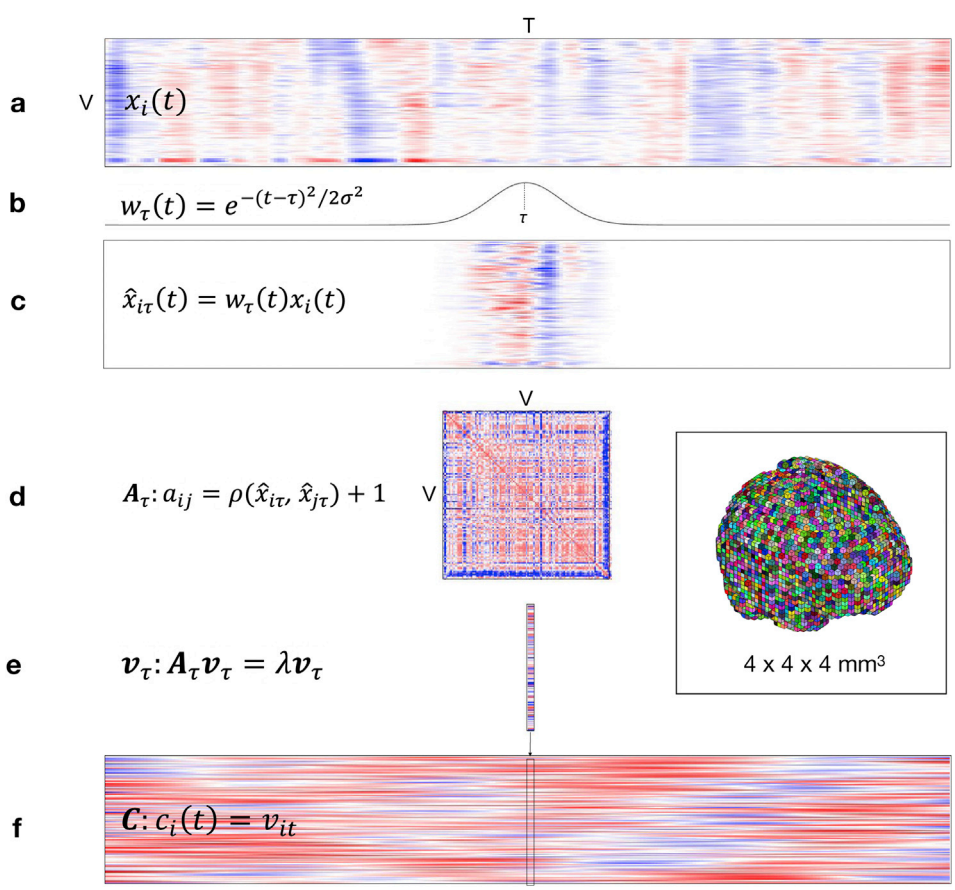

Fig. 3. Schematic representation of the dynamic centrality analysis: (a) BOLD time series data for voxels i = 1, …,V, T time points, voxel size $4 \times 4 \times 4\,mm^3$; (b) Gaussian window centered at time point τ; (c) windowed BOLD time series data; (d) instantaneous non-negative functional connectivity matrix at time point τ, obtained using Spearman correlation ρ; (e) first eigenvector of the connectivity matrix, obtained by solving the eigenequation, representing centrality map at time point τ; (f) eigenvector centrality time series obtained by carrying out steps b-e for all time points.

(Leonardi & Van De Ville, 2015), which lies within the range of 30–60 s recommended by Preti et al. (2017). A Gaussian window was used because of its superior spectral selectivity over a rectangular one (Leonardi & Van De Ville, 2015). The lower end of the recommended range was used, because the recommendation is based on resting-state data, and it can be assumed that connectivity dynamics with the present stimulation are faster than with resting state. For each window location, a functional connectivity matrix was estimated by calculating the Spearman correlation between each pair of windowed time series and adding unity to each element to make the matrix nonnegative.

Eigenvector centrality mapping: For each of the thus obtained matrices, the first eigenvector was obtained by power iteration method (von Mises, 1929). For each participant, this yielded a series of EC maps corresponding to each of the timepoints in the data.

Correlation with regressor: To assess the extent to which the dynamic EC of each voxel was modulated by the beat salience of the musical stimulus, the EC time series were correlated with the beat salience time series using Spearman correlation. For each participant, this yielded a spatial map indicating the strength and direction of modulation at each voxel. For significance estimation of the thus obtained correlation maps, a Monte Carlo simulation was carried out in which the centrality and correlation analysis was applied to BOLD time series phase-scrambled with FFT. This was repeated 10,000 times to obtain an empirical distribution of correlation values, which was then used to convert the correlation to z statistics. Subsequently, these maps will be referred to as the Centrality Modulation Maps (CMM).

Second-level analysis: For group-level inference, the participant-level CMMs were pooled using Stouffer's Z-score method (Stouffer, S., DeVinney, L. & Suchmen, 1949). This yielded a group-level CMM of z statistics. Subsequently, two types of analysis were performed. For network-level analysis, the group-level CMM was correlated with resting-state networks. For regional analysis, the map was thresholded, and correction for multiple comparisons was performed with cluster-size thresholding, where the respective thresholds were obtained using a null distribution obtained with a permutation test. Specifically, we performed 10.000 iterations, in which we correlated the group-level CMM with a phase-scrambled version of the beat salience regressor, pooled and thresholded the thus obtained map and kept the maximal cluster size.

2.4. Psychophysiological interactions analysis

Since centrality analysis as such does not provide any direct measure of interconnectivity between areas in the brain and how this might be modulated by beat salience, subsequent Psychophysiological Interactions (PPI) analyses were carried out. PPI evaluates how connectivity between two brain areas depends on an external variable, that is, how the presence or absence of an external variable modulates the connectivity. To this end, it employs a multiple regression model that predicts the time-course of a target region by the time-course of a seed region, an external variable, and the product thereof. The beta weights for the product variable are assumed to indicate the strength of connectivity modulation by the external variable (for more details, see (Friston et al., 1997)). As auditory-motor connectivity was of key interest in the present study, we restricted this analysis to regions associated with the processing of musical beat belonging to the cerebello-thalamic-striato-cortical motor pathway, specifically the motor and auditory cortices, basal ganglia, thalamus, and cerebellum. The seeds employed in the PPI analyses were selected in a data-driven fashion based on the group CMM obtained from the EC analysis. Subsequently, for each seed regressor, PPI analysis was performed with all voxels within the motor cortex (MC), auditory cortex (AC), basal ganglia (BG), thalamus (TH), and cerebellum (CE). Five separate PPI analyses were thus carried out, in each of which the target region comprised the union of the five aforementioned regions. Significance of participant-level PPI maps was estimated with an empirical distribution obtained from a Monte Carlo simulation based on FFT phase-scrambling of the beat salience time series. Pooling of the maps and cluster-size thresholding were carried out following the procedure described in chapter 2.4.2.

3. Results

3.1. EC analysis

The CMM was thresholded at a significance level of $p < .01$ (two-tailed, cluster corrected at FWE<0.01; cluster size threshold 100 voxels). Results are presented in Fig. 4 and Table 1a–b. As can be seen, high beat salience was associated with significantly increased centrality in several areas of the DMN, including right frontal areas, right angular gyrus, and bilateral precuneus. Low beat salience, in turn, was associated with significantly increased centrality in motor areas, including primary motor cortex, premotor cortex, and supplementary motor area, in right auditory areas, middle occipital gyrus, as well as in motor areas of the cerebellum.

To assess the degree to which the significantly correlated regions overlap with resting-state networks, the brain was parcellated according to the resting-state networks reported in Damoiseaux et al. (2006) by assigning each voxel to the network with highest loading and calculating, for positively and negatively correlating clusters separately, the proportion of their overlap with each of the networks. As can be seen in Fig. 5, highest overlap for positively correlating clusters was found with DMN (48%) and right central executive network (33%), and that for negatively correlating clusters for sensorimotor network (38%) and auditory network (15%).

3.2. Psychophysiological interactions analysis

To investigate in detail the modulatory effect of beat salience on functional connectivity between and within brain areas previously found to be associated with musical beat processing, we carried out Psychophysiological Interactions (PPI) analyses in the motor cortex (MC), auditory cortex (AC), basal ganglia (BG), thalamus (TH), and cerebellum (CE), with the beat salience time series as the psychological regressor. For seeds we selected voxels that displayed highest increase in EC during low beat salience in each of the aforementioned areas. This resulted in five seed residing in the left SMA ([-14 -10 64]), right STG ([58 -14 8]), left caudate ([-10 0 12]), thalamus ([-10 -4 12]) and right lobule VI ([34–70 -20]). For the purpose of the PPI analyses, each seed regressor was obtained as the mean time series of across voxels within a 6-mm radius from the respective seed. For each seed regressor, PPI analysis was performed with all voxels within MC, AC, BG, TH, and CE.

The group-level PPI maps for each seed region were thresholded at a significance level of $p < .01$ (two-tailed, cluster corrected at FWE<0.01; cluster size threshold 264 mm^3). To provide an overview of how beat salience modulated overall functional connectivity within and between the five regions of interest, Fig. 6 displays the strength of interaction for each pair of seed and target region, for both negative (high connectivity during low beat salience) and positive (high connectivity during high beat salience) interaction. As can be seen, during low beat salience connectivity from the AC seed increased to a great proportion of the MC, and to a somewhat lesser degree to AC, TH, and CE. For high beat salience, we observed a different pattern. Most notably, connectivity within AC and CE increased, and there was significant connectivity increase from the TH seed to MC, AC, and CE, and from the BG seed to AC and CE.

High beat salience: Clusters whose functional connectivity with the selected seeds manifested increased functional connectivity during high beat salience are shown in Table 2a (at the end of the manuscript). As can be seen, most significant increase in functional connectivity was observed within the AC and CE regions ($z = 5.7$, $z = 5.0$, respectively) as well as from the TH and BG seeds to right SMA ($z = 4.4$, $z = 3.9$, respectively). Overall, these results suggest that functional connectivity between auditory areas and sensorimotor cortex tends to increase when

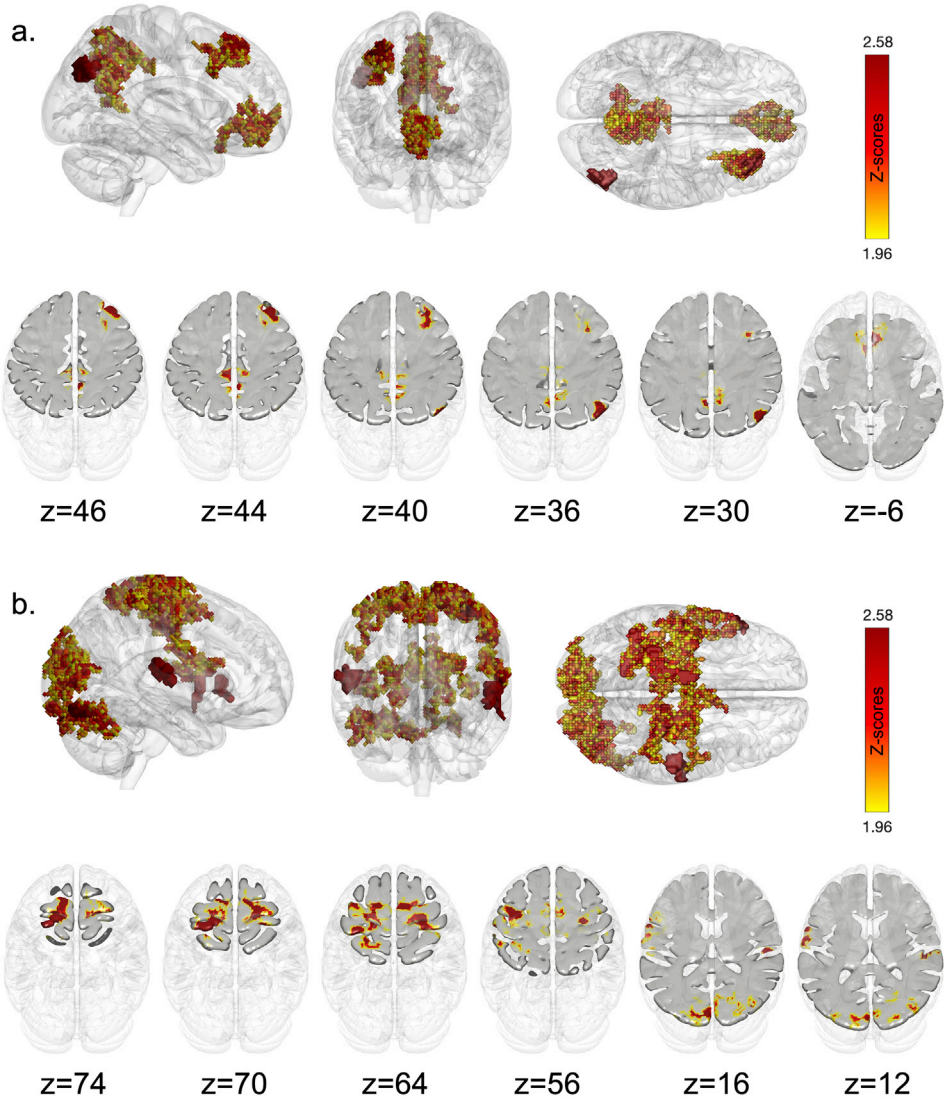

Fig. 4. Regions with significantly increased centrality during (a) high and (b) low beat salience ($p < .01$, two-tailed; cluster-size corrected at FWE 0.01; cluster-size threshold 800 mm^3).

Table 1a
Regions with increased centrality during high beat salience ($p < .01$, two-tailed, FWE<0.01 CS = 100).

Cluster#	L/R	region	N	MNI (mm)	max(Z)	BA	additional regions
1	R	MFG	211	34,34,44	4.05	9	IFG, SFG
2	R	AG	188	34,14,34	4.01	39	
3	R	IFG	185	6,42,-8	4.14	11	L ACG, R GR, ACG
4	R	Prec	131	2,-54,48	3.93	7	L Prec, MCG
5	R	Prec	125	6,-58,24	3.71	23	L Prec, Cun

music has high beat salience.

Low beat salience: Clusters whose functional connectivity with the selected seeds manifested increased functional connectivity during low beat salience are shown in Table 2b (at the end of the manuscript). As can be seen, for low beat salience most significant increase in functional connectivity was found from the AC seed (R STG) to left PoG ($z = -5.8$) and left STG ($z = -5.7$), as well as from the MC seed (L SMA) to left PoG ($z = -3.5$). Moreover, greater connectivity was observed between the right AC seed and the left STG ($z = -5.7$; $n = 138$) during low beat salience whereas high beat salience was associated within the right STG ($z = 5.7$; $n = 252$) with a reduced effect in the left STG ($z = 4.2$; $n = 71$).

4. Discussion

Using dynamic Eigenvector centrality analysis, we here showed that musical beat affects the brain networks' centrality pattern during music listening, with high beat salience increasing centrality in the Default Mode Network, and low beat salience increasing centrality in the motor and auditory cortices. Subsequent Psychophysiological Interactions Analyses with seeds selected from the Eigenvector centrality analysis results showed that functional connectivity between the motor and auditory cortices tends to increase during moments of low beat salience. This is the first study to employ dynamic whole-brain functional connectivity analysis with naturalistic musical stimulation. The analysis showed that functional connectivity from the basal ganglia and thalamus to sensorimotor and auditory cortices as well as cerebellum tends to increase during high beat salience. Finally, the results showed increased connectivity within cerebellum during moments of high beat salience.

4.1. Dynamic graph analysis

As can be observed in the results, low beat salience in the stimulus

Table 1b
Regions with increased centrality during low beat salience ($p < .01$, two-tailed, FWE<0.01 CS = 100).

Cluster#	L/R	region	N	MNI (mm)	max(Z)	BA	additional regions
1	L	PoG	605	−18,-34,72	−4.61	9	PCL,SPG,PrG,SMA,SFG,IPG
2	L	PoG	194	−50,-18,48	−4.86	4	IPG
3	L	PrG	156	−38,-10,60	−4.66	6	
4	L	IFG	141	−62,10,12	−4.52	6	RO,STG
5	L	SOG	118	−10,-94,20	−3.42	18	Cun, MOG
6	L	IFG	113	−50,22,4	−3.70	45	
7	R	PrG	356	30,.22,60	−4.21	6	SMA,PoG,SFG
8	R	IOG	306	46,-78,-16	−4.95	19	Lob VI, Cr I-II,FusG
9	R	STG	180	58,-14,8	−4.05		RO,SMG

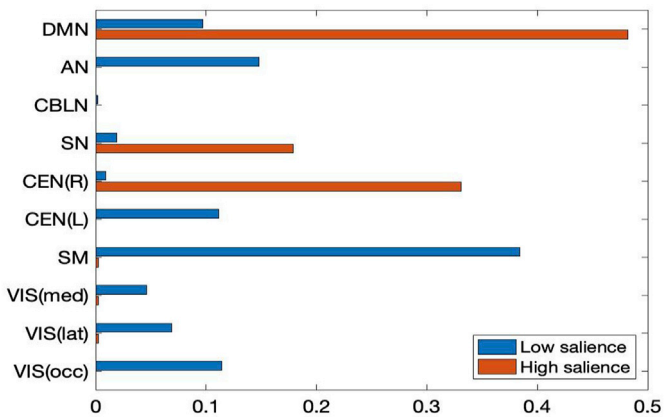

Fig. 5. Proportion of overlap between significant clusters correlating positively and negatively with beat salience, and resting state networks. DMN – default mode network, AN – auditory network, CBLN – cerebellar network, SN – salience network, CEN VR – right central executive network, CEN (L) – left central executive network, SM – sensorimotor network, VIS (med) – medial visual network, VIS (lat) – lateral visual network, VIS (occ) – occipital visual.

was associated with increased centrality in cerebellum and cortical auditory-motor regions while the key hubs of the DMN exhibited high centrality during high beat salience. Specifically, maintaining perceived beat during musical moments characterized by high beat salience was found to manifest as increased centrality in regions belonging to the DMN specifically in the bilateral precuneus, regions surrounding the right angular gyrus, MPFC, and bilateral posterior cingulate gyrus. Increase in activity in these regions has been previously implicated in decreased auditory-cognitive load (Alluri et al., 2012). Indeed, moments of high beat salience can be assumed not to require attentive beat finding and hence be considered as low load conditions, implying increased mind-wandering. García-García et al. (2015) observed increase in centrality of the precuneus and angular gyrus of the DMN in rest conditions versus task-based conditions (visual) which were associated with increased centrality in visual regions. This result is in accordance with the present findings, assuming that beat inference is considered to be a task which requires attentive listening, and beat maintenance, in contrast to beat inference, to be a rest condition.

On the other hand, increased centrality during low beat salience was found in premotor cortex, SMA, cerebellum in conjunction with auditory association areas, suggesting that beat inference might be associated with increased global connectivity in these areas. These results are in line with several studies that indicate the role of cortical motor regions in active beat finding (Chen et al., 2008; Grahn and Rowe, 2009; Kung et al., 2013). Specifically, the SMA has been implicated to be critical in internal/covert movement generation, which requires entraining to a rhythm (Jenkins et al., 2000; Wu and Hallett, 2013). Penhune et al. (1998) demonstrated the importance of the right STG as a locus in self-cued rhythm reproduction from auditory sequence/sequential temporal memory (Penhune et al., 1999). Furthermore, the posterior cerebellum has been implicated in timing perception and adjustment to sensory events via internal prediction models (Doya, 2000). However, the role of the cerebellum and basal ganglia in timing perception has been debated upon.

There was no evidence of significant correlation between centrality in the basal ganglia and beat salience, which probably indicates its role both in beat maintenance and beat finding. In line with this, Kung et al. (2013) posit that BG is active in both beat finding and beat maintenance/tapping to the beat. Several studies have indicated the BG's role in beat processing when the beat is highly salient and/or in the "preparation or production of well-learned motor responses" (Kung et al., 2013). Teki et al. (2011) demonstrate the existence of two dissociative networks underlying absolute and relative time keeping: one with the cerebellum as a focal point/precision clock that mediates absolute timing; the other a striato-thalamo-cortical network involved in beat-based time keeping or

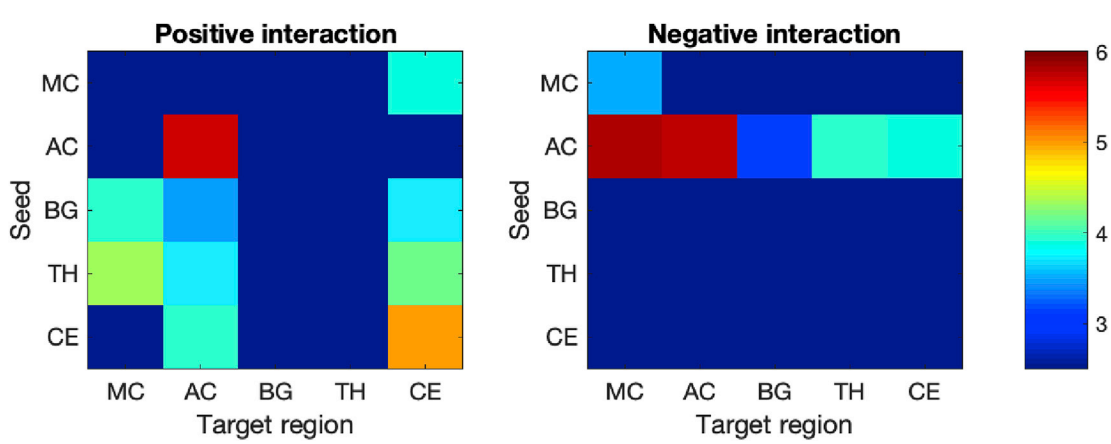

Fig. 6. Strength of interaction (maximal z statistic) for each pair of seed and target region, for both negative (high connectivity during low beat salience) and positive (high connectivity during high beat salience) interaction. MC – motor cortex, AC – auditory cortex, BG – basal ganglia, TH – thalamus, CE – cerebellum.

Table 2a
Clusters showing positive interaction with beat salience (increased connectivity during high beat salience). $p < .01$, two-tailed, FWE<0.01 CS = 33.

Seed 1: L SMA [-14 -10 64]							
Cluster#	L/R	region	N	MNI (mm)	max(Z)	BA	additional regions
1	L	Lob X	52	−18,-38,-46	3.89		Lob VIII-IX
Seed 2: R STG [58 -14 8]							
Cluster#	*L/R*	*region*	*N*	*MNI (mm)*	*max(Z)*	*BA*	*additional regions*
1	L	STG	71	−54,12,0	4.17	22	
2	R	STG	252	56,-14,4	5.70	22	
Seed 3: R Lob VI [34–70 -20]							
Cluster#	*L/R*	*region*	*N*	*MNI (mm)*	*max(Z)*	*BA*	*additional regions*
1	L	Lob IX	160	−10,-50,-32	3.67		Lob VIII, Verm IX-X
2	L	Lob VIII	89	−24,-56,-44	3.43		Lob VI, CR I
3	L	Lob IV-V	44	−14,-44,-20	3.81		Lob III
4	L	STG	40	−66,-44,14	3.46	22	
5	R	Lob VIII	1640	24,-54,-46	4.98		Cr I-II, Lob IV-IX, Verm VII-IX
6	R	Lob IV-V	180	8,-58,-16	3.91		Lob III-VI, Verm I-V
7	R	Lob IV-V	49	24,-34,-30	3.57		Lob III, VI
8	R	STG	45	70,-24,4	3.96	22	
Seed 4: L Caud [-10 0 12]							
Cluster#	*L/R*	*region*	*N*	*MNI (mm)*	*max(Z)*	*BA*	*additional regions*
1	L	Cr II	72	−20,-88,-40	3.71		Lob VIIB
2	L	STG	43	−66,-48,18	3.44	22	
3	R	STG	121	70,-24,4	3.41	22	
4	R	SMA	34	10,14,72	3.93		
5	R	Lob IV-V	33	12,-54,-12	3.11	19	Verm IV-V
Seed 5: L Thal [-10–4 12]							
Cluster#	*L/R*	*region*	*N*	*MNI (mm)*	*max(Z)*	*BA*	*additional regions*
1	L	Cr II	149	−20,-88,-40	4.11		Lob VIIB, VIII, Cr I-II
2	L	Cr I	102	−22,-76,-32	3.72		Cr II
3	L	STG	76	−66,-48,16	3.48	22	
4	L	SMA	56	−14,10,62	3.47	6	
5	L	STG	50	−56,-14,2	3.28	22	
6	L	PrG	45	−40,-4,38	3.01	6	
7	L	Lob VI	44	−36,-56,-28	4.02	37	
8	L	Cr II	34	−40,-64,-40	3.17		Cr I
9	R	STG	266	68,-22,4	3.72	22	
10	R	Lob IV-V	176	8,-52,-12	3.97	18	Lob III, VI, Verm I-V
11	R	Lob VIII	89	20,-62,-40	3.95		
12	R	SMA	80	10,14,72	4.35		
13	R	Cr II	66	14,-86,-46	3.80		
14	R	STG	49	60,-34,12	3.56	22	
15	R	Cr I	47	40,-68,-34	3.03		

maintenance.

In addition, the increased centrality observed in the secondary visual cortex extending to the intersection with the inferior temporal gyrus corroborates the results found by Levitin (2005). These extra-striate visual regions were found to be active during processing scrambled versions of 23-s classical music excerpts in comparison to their unscrambled counterparts. The scrambled versions were created by randomizing segments of a variable length (250–350 ms) which displayed a clear lack of continuing perceivable melody or harmonic structure leaving the listener to make sense of a potential existence of a rhythm thereby evoking the beat finding process.

The correlation analyses between beat salience and network centrality served as a first step in identifying the dynamically varying main effect. The PPI analyses revealed potential functional reorganization of the sub-networks of the cerebello-striato-cortical motor pathways.

4.2. PPI analyses

Fig. 7 displays schematically how functional connectivity within and between the regions of interest was found to be modulated by the different sub-processes (i.e. beat finding and beat maintenance) of beat perception. Our findings indicate that neural mechanisms allowing dynamic inference of beat comprise ongoing neural communication between SMA and auditory cortex. In turn, our findings suggest that dynamic maintenance of the beat relies on neural communication between basal ganglia, auditory cortex and cerebellum.

4.2.1. Motor cortex seed: SMA

Surmounting evidence exists supporting the increased coupling between auditory and motor regions during rhythm and beat perception (see Cameron and Grahn, 2016, for an overview). Importantly, this study clearly evidences increased coupling between the auditory and the sensorimotor regions with decreased beat salience. The SMA has been implicated to play an important role in internally cued sequences and internally generated movements vs externally cued sequences (Wu and Hallett, 2013; Jenkins et al., 2000). To add to this, the increased coupling between the SMA and the PMC during low beat salience reflect the action-based or action-oriented predictive processing approach/model that aims at minimizing prediction error by actively engaging the motor system internally to generate the motor commands needed to fulfill the predictions (Gebauer et al., 2015; Hawkins and Blakeslee, 2004). The increased connectivity between the SMA and cerebellum during high beat salience further reflects the potential presence of the aforementioned continuum of active perception with connectivity switching from cortical motor regions to cerebellar regions during moments of high beat predictability. These results are very much in line with Doya's (2000) division of roles of the cerebello-striatal-cortico motor pathway in learning. His approach highlights the role of greater within- and between-cortical region connectivity in extracting vital information from sensory input during unsupervised learning (beat finding reflected as AC-MC interaction) based on Hebbian plasticity. Subsequently, this learned information is then hypothesized to provide important input to those regions involved in supervised or reinforcement learning (beat maintenance) which is evidenced in our case as high positive interaction between MC and CE.

Based on the PPI analysis on this seed, one could hypothesize that the SMA is indeed recruited for the process of time-keeping, especially beat processing in musical stimuli. Our results further indicate (see Fig. 6) that it potentially draws information from the absolute time-keeper (that is, the cerebellum) for the purpose of beat maintenance and from cortical auditory-motor areas during beat inference. Therefore, we can assume that its role in beat inference, which requires higher cognitive functioning, is greater than that in beat maintenance which is an autonomic process predominantly modulated by cerebellar activity.

4.2.2. Auditory cortex seed: STG

The connectivity between the auditory cortex and the cerebello-thalamo-cortical motor pathway is significantly increased during low beat salience. The increased connectivity within the auditory regions during high beat salience is reflective of the results obtained in a previous study with the same stimulus (Alluri et al., 2012) wherein they found the right STG activations to correlate significantly with high beat salience albeit using univariate correlational analysis. Similarly, Burunat et al.

Table 2b
Clusters showing negative interaction with beat salience (increased connectivity during low beat salience). $p < .01$, two-tailed, FWE<0.01 CS = 33.

Seed 1: L SMA [-14 -10 64]							
Cluster#	L/R	region	N	MNI (mm)	max(Z)	BA	additional regions
1	L	PoG	75	−28,-32,70	−3.51	4	
2	L	PCL	71	−4,-20,74	−3.19	4	
Seed 2: R STG [58 -14 8]							
Cluster#	*L/R*	*region*	*N*	*MNI (mm)*	*max(Z)*	*BA*	*additional regions*
1	L	PoG	9335	−34,-34,68	−5.79	4	L PrG,PCL,SMA,STG; R PoG,PrG,PCL,SMA,STG
2	L	Lob VI	195	−24,-52,-22	−3.91	37	Lob IV-V
3	L	Thal	117	−16,-26,6	−3.53		
4	L	Lob VI	93	−10,-74,-12	−3.54	18	Cr I, Verm VI
5	L	STG	104	−40,0,-12	−4.95	48	
6	L	Lob IV-V	92	−8,-56,-8	−3.87		
7	L	Put	44	−28,-2,8	−3.10	48	GlP
8	L	STG	34	−62,-4,6	−5.72	48	
9	R	Lob VI	151	38,-54,-26	−3.78	37	
10	R	Thal	105	10,-20,0	−3.97		

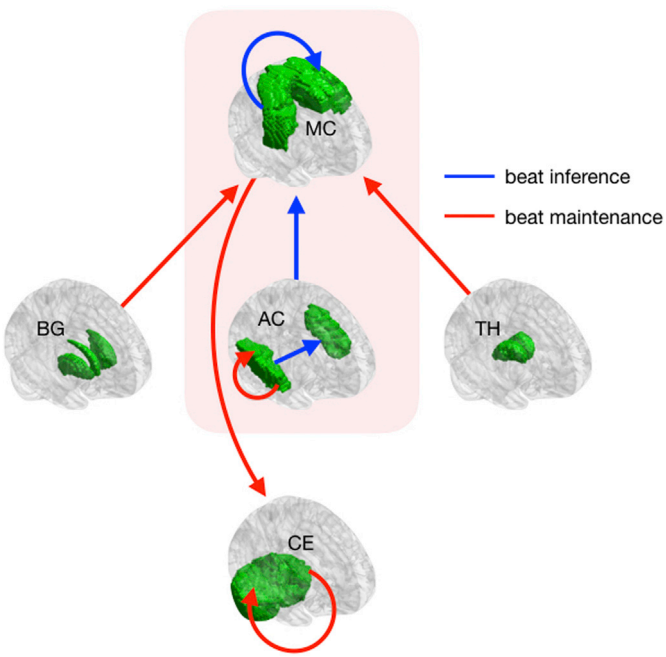

Fig. 7. Schematic representation of the modulation of functional connectivity by beat inference and maintenance within and between motor cortex (MC), auditory cortex (AC), basal ganglia (BG), thalamus (TH), and cerebellum (CE). Blue and red arrows denote increased functional connectivity during beat inference and beat maintenance, respectively. Cortical regions of interest are denoted by colored background. The arrows are pointing from seed to target areas used in each respective PPI analysis and are not assumed to indicate effective connectivity.

(2017) found similar results using multivariate analysis (ICA). It is noteworthy that we evidence greater inter-hemispheric auditory connectivity during low beat salience whereas greater intra-hemispheric connectivity during high beat salience. This is in line with previous findings of increased inter-hemispheric connectivity during high cognitive task demands (Banich, 1998; Welcome and Chiarello, 2008).

4.2.3. Sub-cortical seeds: BG (caudate) and TH

Sub-cortical seeds of the BG and TH display mutually similar connectivity modulation patterns in both low and high beat salience conditions. Specifically, both seeds show positive interaction with the SMA during high beat salience conditions indicating increased connectivity to this area during beat maintenance. In addition, similar positive interaction is observed with the posterior cerebellum (Crus II), the role of which has been indicated in providing internal timing models (Doya, 2000). Only positive interaction was observed with bilateral STG. This finding warrants further study. The BG have been implicated in mediating the processes of both beat finding and beat maintenance. Despite this ambiguity in the precise role of the BG in either beat finding when it is less salient or beat processing in high beat salience conditions, it appears that the coupling between the BG and the auditory, motor, thalamic, and cerebellar areas increases as a function of beat salience, but not within the BG (Cameron and Grahn, 2016; Teki et al., 2011). This lack of increased connectivity observed within the BG is in line with Brodal et al.'s (2017) finding of reduced connectivity with the BG while listening to highly rhythmic music. They used Dynamic Causal Modelling to investigate the dependencies and interactions between auditory- and mesolimbic reward systems. When compared to resting-state, naturalistic conditions of listening to highly rhythmic music rendered reduced connectivity in the dopaminergic reward system including the BG.

4.2.4. Cerebellar seed: lobule VI

The high within-region connectivity observed during high beat salience conditions appear to support the existing view of the cerebellum as one of time-keeping of regular intervals, a process crucial for beat maintenance. The lack of significant coupling with the other regions of the striato-cortical motor pathway might suggest its autonomy in beat perception with a focus on encoding timing regularities.

In line with our hypothesis, the present PPI analyses reveal a dissociation between two sub-networks comprising the cerebello-thalamo-striato-cortical pathways, specifically a shift from cortical pathways during beat inference to thalamo-striato-cerebellar motor pathways during beat maintenance.

4.3. Limitations

The present study has a few potential limitations. The first one is the use of only one stimulus thereby limiting the generalizability of the results. A natural extension of this study would be to repeat the same analyses using music from different genres and combining the results in order to draw more statistically powerful and reliable inferences. However, it is important to note that, in naturalistic paradigm, it is vital that the stimulus has sufficient variation in the feature that needs to be studied. Furthermore, it is crucial that the time-course of the feature variation be sufficiently slow to be captured by fMRI given its limited temporal resolution.

Second, we interpreted the finding of increased centrality in the DMN during high pulse clarity as a reflection of decreased cognitive load and decreased attention during highly predictable moments. However, it may be possible that this is also related to decreased attention and boredom in

response to the music. To clarify this, it would be necessary to collect, for instance, eye tracking data while the participants are listening to the musical stimulus.

Third, while the beat salience feature used in the study did not correlate significantly with any of the other 24 features that we extracted from the stimulus, there might still be confounding variables. This is a problem that is to some extent unavoidable with naturalistic experimental settings.

Finally, one could argue that the assumption of low beat salience does not necessarily imply beat inference. It would, however, be difficult to find evidence for the presence or absence of beat inference with a behavioral test, such as tapping tests. This is because nonperiodic tapping or the absence of tapping does not necessarily indicate that the listener is performing beat inference. However, given that entrainment is such a fundamental response to rhythmic stimuli (Phillips-Silver et al., 2010) it is plausible to assume that during music listening, low beat salience automatically induces beat inference.

There is evidence that task-driven local brain activation and connectivity can be modulated in different directions at the same time. This suggests that local (activation) and integrative (connectivity) processes can be considered as separable brain functions (see, e.g., Gerchen and Kirsch (2017). Therefore, the information provided by either analysis is not necessarily overlapping. Additionally, since beat processing is a highly complex cognitive phenomenon it is better characterized using complex network methods. The reason is that cognitive processes are sustained by dynamic interactions across multiple distributed regions rather than by a specialized particular brain region. Hence network analyses are probably best suited to study these cognitive processes.

Overall, connectome studies are just beginning to shed light on what spatial and functional network attributes may represent, therefore interpretation of eigenvector centrality data is not always straightforward. At best, dynamic graph analysis helps capture functional reorganization in brain states, which is indicative of global information flow. High centrality does not necessarily imply the involvement of that particular region or node in a task (such as beat inference) unless there exists prior literature indicating the roles of those nodes as being part of the task-positive-network. In the current study, the follow-up PPI analyses serve to uncover specific roles played by the regions involved in processing beat salience and hence we recommend such follow-up analyses to support and interpret results obtained using any graph-theory based approaches.

5. Conclusion

The present study is the first to evidence the underlying neural mechanisms involved in the processing of musical beat salience in a dynamical naturalistic setting. We demonstrate partial dissociation of functional networks belonging to the cerebello-thalamo-striato-cortical motor pathway wherein the cerebello-thalamo-striato segment plays a more significant role in beat maintenance while the cortical motor regions are key in beat inference.

Data and code availability statement

Data availability

Subject-level statistical data (dynamic eigenvector centrality maps, PPI maps) will be available from the corresponding author upon request. fMRI BOLD time series data will not be available due to restrictions stated in ethical permission.

Code availability

Matlab scripts for dynamic eigenvector centrality analyses and PPI analyses will be available from the corresponding author upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116191.

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