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Beauty is in the brain networks of the beholder - An exploratory fMRI study

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Abstract

Listening to music while appreciating its beauty is a common activity in daily life. Only few studies have explored the association between such aesthetic processes with brain activity and the related patterns of brain connectivity states. Here, we exploratorily applied a recent algorithm for extracting the dynamic changes in time-varying functional connectivity by measuring functional magnetic resonance imaging (fMRI) responses from 36 participants attentively listening to an entire musical piece. A separate behavioral session served to identify the musical passages that were consistently rated as beautiful or non-beautiful. We found that the FC state that is most recurrent for beautiful musical passages includes the orbitofrontal cortex (OFC) and visual brain regions. In turn, the two FC states that were most recurrent during listening to non-beautiful musical passages included mainly brain structures related to sensory processing plus some associative regions. Moreover, the switching probability of a reward network including OFC, visual, and striatal regions was significantly higher during listening to beautiful musical passages, whereas more frequent transitioning occurred for FC states related to auditory, amygdala, and insula regions during listening to non-beautiful musical passages. These findings of this exploratory study indicate a key contribution of high-order structures implicated in reward evaluation such as OFC and of visual associative areas related to imagery, and revealed an enhanced neural communication during listening to aesthetically valenced music. In turn, the findings obtained during listening to non-beautiful musical passages are interpreted as associated with the neural demands of disentangling its auditory obscurity.

Keywords: music listening, neuroaesthetics, dynamic functional connectivity, functional magnetic resonance imaging, brain

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Introduction

Finding beauty in everyday objects, evaluating them, and deriving feelings of pleasure from the whole process is a cognitive function in humans that has been proven adaptive during species evolution and is universal, namely, it is observed across cultures, ages, and epochs (Elvira Brattico et al., 2009; Volland & Grammer, 2003). This pervasiveness and universality of the function of beauty (along with the related psychological function of aesthetic judgment), suggest the existence of biological substrates regulating it instead of or in addition to cultural constructs that have appeared over the course of human history. The relatively new field of neuroaesthetics adopts such a biological approach to beauty in art and, hence, is dedicated to identifying the psychological and neural correlates of beauty aesthetic judgments of artifacts (Elvira Brattico et al., 2013; Nadal & Vartanian, 2019; Pearce et al., 2016).

One of the most common everyday human artifacts associated with beauty judgments is music. The International Federation of Phonographic Industry has reported that the weekly time spent on music listening per person is 18.4 hours (IFPI, 2021). When listening to music even ordinary people without any formal musical training and without necessarily doing any conscious reflection judge whether a musical piece is beautiful or not, namely issuing an aesthetic judgment. In a questionnaire study, it was found that the layperson's understanding of musical aesthetics has 'beauty' as the primary concept (Istók et al., 2009).

Despite the relevance of aesthetic judgment of beauty in music for the daily practice of music listening and of its universality and putative biological evolutionary role hinting at the existence of a biological brain substrate, up to now, only few studies have focused on elucidating the neural mechanisms that govern this process. Jacobsen et al. (2006) and Kornysheva et al. (2010) systematically analyzed neural substrates of aesthetic processing across content domains and sensory modalities and proposed for the first time that the aesthetic judgment of beauty activates triggered brain networks associated with evaluative judgments, specifically the orbitofrontal cortex (OFC). In a subsequent study by Ishizu and Zeki (2011) investigated the brain determinants of the beauty experience across art domains and found that the A1 field of the medial orbitofrontal region of the frontal lobe is the only brain structure that was recruited both when judging a music clip or a

painting as beautiful (when contrasted to other music or paintings judged as non-beautiful). Brown et al. (2011) proposed a critical network of aesthetic judgments including the anterior insula, OFC, ventral basal ganglia, and anterior cingulate cortex. Another study investigating the perception of beauty in music by Brattico et al. (2020) identified neurological mechanisms for musical intersubjective aesthetic judgments located in the supratemporal-orbitofrontal circuit.

However, these structures do not work alone. When listening to music, several other neural structures are involved (Angulo-Perkins et al., 2014; Ding et al., 2019; Menon & Levitin, 2005; Popescu et al., 2004). Evidence suggests that music listening affects brain regions associated with complex cognitive processing and brain connectivity. Menon and Levitin (2005) found that listening to music strongly modulates the brain networks related to reward autonomic and cognitive processing. Indeed, neural communication between regions is what presumably underlies the issuing of complex judgments such as aesthetic ones. Recent studies on visual aesthetic experience have associated it with connectivity between several brain regions, including the default mode network (DMN) (Belfi et al., 2019; Cela-Conde et al., 2009; Jacobsen et al., 2006), dorsolateral prefrontal cortex (DLPFC) (Kawabata & Zeki, 2004; Ticini, 2017), insula (Di Dio et al., 2007; Vartanian & Goel, 2004), amygdala (Cela-Conde et al., 2004; Di Dio et al., 2007), and hippocampus (Brown et al., 2004; Koelsch, 2014). These brain regions are engaged in cognitive functions containing memory formation and regulation, working memory encoding, emotional learning, and cognitive-emotional processes.

A brain structure whose connectivity seems to be pivotal for eliciting an aesthetic experience of visual art, and with initial findings (Blood & Zatorre, 2001) also for music, is the OFC. Previous research has emphasized the critical role of OFC in reward processing (Kringelbach & Berridge, 2017; O'Doherty et al., 2001; Rolls et al., 2020). Several neuroimaging studies also found that one part of the brain that seems to be particularly associated with pleasure is the OFC (Berridge & Kringelbach, 2013; Blood & Zatorre, 2001). Besides OFC, the insular cortex and the ventromedial part of the prefrontal cortex are also related to pleasure rating (Berridge & Kringelbach, 2013). Furthermore, (Tsukiura & Cabeza, 2011a) reported a positive correlation between medial OFC activity and attractiveness and goodness judgments. Another fMRI study also showed that the activity of OFC is associated with the experience of musical and visual beauty (Ishizu & Zeki, 2011).

Compared with visual arts, fewer connectivity studies investigating aesthetic judgments of music have been conducted and only one specifically focused on beauty judgments (Brattico et al., 2020; for a review, see Reybrouck et al., 2018). Brattico et al. (2020) found that beautiful musical passages were associated with high connectivity between auditory and orbitofrontal cortices, while not beautiful passages showed lack of such connectivity and neural activation restricted to temporal lobes. Moreover, in the study by Brattico et al. (2020) the connectivity analysis in neural activity was limited to the only two brain regions that showed the highest regional activation. Hence, the connectivity analysis was fully hypothesis-driven, drastically reducing the complexity of the phenomenon under scrutiny.

Recent findings on the human connectome have provided new perspectives on brain connections in the field of aesthetics. As for music, dynamic communication between different parts of the orbitofrontal region is visible in preadolescent children listening to music that they found pleasant (Fasano et al., 2020). These functional connections and their individual differences are most likely driven by anatomical white matter paths, as evidenced by MRI studies conducted with adult listeners (Martínez-Molina et al., 2019). For instance, Sachs et al. (2016) found that white matter connectivity between brain regions including the superior temporal gyrus, insula, and medial prefrontal cortex, explained individual aesthetic variations in reward sensitivity to music. In sum, previous human connectome studies have led to a preliminary understanding of how listening to pleasant and/or beautiful music affects functional brain networks. However, still little is known on the connectivity changes over time, which are crucial for music, a temporal art.

In recent connectivity studies of cognitive functions, it has been observed that the patterns of brain connections are not stable over an experimental session but vary over time. This has inspired researchers to develop a new approach for understanding the temporal dynamics of brain network states, called dynamic functional connectivity (dFC). dFC can provide information about time-varying interactions intra- and inter-brain networks (Fong et al., 2019) which is not possible with traditional static FC. The most widely used method used for dFC analysis is sliding window correlation (Allen et al., 2014; Chang & Glover, 2010; Wilson et al., 2015). A limitation of this method, however, is that most of the noise sources in fMRI are non-stationary and may affect the FC network over time (Hutchison et al., 2013). Another limitation is the length of the sliding

window, which can affect the robustness and temporal resolution (Cabral et al., 2017; Shine et al., 2015). A novel approach named Leading Eigenvector Dynamics Analysis (LEiDA) has recently been proposed to overcome the previous limitations (Cabral et al., 2017). The LEiDA method reduces the dimensionality of calculation, enhances the robustness to high-frequency noise, and improves temporal resolution compared to previous approaches (Cabral et al., 2017; Lord et al., 2019).

Previous research has established that the process of listening to music requires the involvement of higher-order cognitive functions and connections in the brain. Moreover, there is a close interaction between the aesthetic experience of music and reward-related brain regions and other functional brain regions. However, the relationship between aesthetic experiences of music and dynamic functional connectivity changes in the brain remains unclear. In addition, it is also crucial to explore how pleasant or unpleasant aesthetic experiences affect dynamic functional connectivity networks, respectively. Therefore, in this explorative study, by using a novel dynamic functional connectivity approach, LEiDA, we aimed to measure if specific FC states emerge in relation to listening to beautiful music that may help us better understand the relationship between brain connectivity and the beauty experience in music. In addition, the dynamic interaction within brain regions and the neural mechanisms associated with aesthetic experience are the main concerns that this article intends to explore.

Method

Participants

The study protocol was approved by the Coordinating Committee of the Helsinki and Uusimaa Hospital District, Finland, and performed in compliance with the Declaration of Helsinki. Informed consent was signed by all participants in this study. This dataset had been previously published so it can be partially found in open repositories in Zenodo. Originally, it was obtained within the large protocol (“Tunteet”), which includes several different datasets (fMRI and MEG paradigms, behavioral measures, and related questionnaires). For a general view of the dataset, see (Alluri et al., 2015, 2017; Bonetti et al., 2018; Brattico et al., 2020; Burunat et al., 2016; Haumann et al., 2021; Niranjana et al., 2019; Toiviainen et al., 2020).

A total of 36 healthy volunteers (mean age 28.75 ± 9.21 SD, 17 males) with varying levels of musical expertise were recruited in this fMRI experiment. The detailed information was listed in Table 1. None of them reported any hearing, neurological or psychological disorders. Participant inclusion criteria were no metal in the body, no tattoo or recent permanent coloring, no pregnancy or breastfeeding, no chronic pharmacological medication, and no claustrophobia.

Table 1. Detailed information of the participants of this study.

Subject	Age	Hand	Gender	Education
1	20	Right	Female	Missing
2	18	Right	Female	Missing
3	20	All	Male	Secondary school
4	33	Right	Male	Bachelor's degree
5	21	Right	Male	Secondary school
6	25	Right	Female	Missing
7	31	Right	Male	Master's degree
8	44	Right	Male	Music graduate
9	40	Right	Male	Master's degree
10	27	Right	Female	Bachelor's degree
11	34	Right	Female	Master's degree
12	35	Right	Female	Bachelor's degree
13	26	Right	Male	Master's degree
14	24	Right	Male	Bachelor's degree
15	22	Right	Female	Bachelor's degree
16	29	Right	Female	Music graduate
17	21	Right	Male	Secondary school
18	39	Right	Female	Missing
19	27	Right	Female	Bachelor's degree
20	19	Right	Male	Secondary school
21	34	Right	Male	PhD
22	23	Right	Female	Secondary school
23	28	Right	Female	Bachelor's degree
24	21	Right	Female	Secondary school
25	24	Right	Male	Missing
26	26	Right	Male	Missing
27	21	Right	Male	Secondary school
28	33	Right	Female	Master's degree
29	23	Right	Female	Missing
30	28	Right	Female	Master's degree
31	52	Right	Male	Master's degree
32	50	Right	Female	Master's degree
33	20	Right	Female	Missing
34	29	Left	Male	Missing
35	19	Right	Male	Secondary school
36	49	Right	Female	Master's degree

Stimuli

While in the fMRI scanner, participants listened without interruptions to three musical pieces: 1) Adios Nonino by the Argentinian composer Astor Piazzolla (1959), (this stimulus will be hereafter referred to simply as Piazzolla); 2) Rite of Spring (comprising the first three episodes from Part I: Introduction, The Augurs of Spring: Dances of the Young Girls and Ritual of Abduction) by

the Russian born composer Igor Stravinsky (1947); and 3) Stream of Consciousness by Dream Theater (2003). Musical stimuli were presented by MR Confon (Magdeburg, Germany), an MRI compatible music-playing system. After screening three pieces of music and their related behavioral and brain responses, we selected Piazzolla as the stimulus dataset for the present study. This instrumental tango contains a great amount of acoustic variation and three contrasting themes varying in rhythm, tonal clarity, timbre, and showed the highest consistency in ratings among participants (Burunat et al., 2014). The duration of Piazzolla is around 8 minutes.

After fMRI scanning, in a separate behavioral session, a separate group of participants evaluated continuously the perceived beauty and non-beauty of the Piazzolla stimulus via a Nintendo Wii motion sensor by vertically moving the sensor up when finding the music beautiful and down when finding it non-beautiful (Brattico et al., 2020). The continuous behavioral ratings Wii data was recorded at 2Hz with WiiData Capture (detailed in Brattico et al. 2020 Study 1). Via a MoCap toolbox (Toiviainen, Burger, 2015, MCT Manual v1.5), the Wii data was parsed and interpolated into 10 ms intervals. In this process, the recoded locations of the rating remote were obtained, including both horizontal and vertical dimensions. The x-axis represented the time point of the music and the y-axis represented the continuous ratings corresponded to each time point. Each participant's signal was analyzed individually and normalized by the maximum value. The average value of the data was seen as zero. Then the maximum rating value for all participants was set to 0.4, while the minimum rating value to -0.4. When the ratings' value was above zero, the rating was considered positive. On the contrary, the value below zero was considered negative. We considered consistency to be 100% when all participants have a positive rating value at the same time point. Only few time points had a 100% agreement. Subsequently, we chose an agreement of 70% as the threshold of rating dataset and an average rating value above 0.15 for the "beautiful" musical passages, while a rating agreement of 70% agreement and an average rating value below -0.15 for the "non-beautiful" musical passages. Afterward, the selected passages were evaluated and revised by two music experts to confirm the consistency between music passages and the ratings and the initial movement delays that participants may incur during rating. Aesthetic experience can include two types of evaluations, one is the attribution of the perceptual attributes of the stimulus, and the other is the subject's response attitude towards the stimulus (Calvo-Merino et al., 2008). In this study,

the aesthetic ratings represent the participants' consensus attitude toward the musical stimulus. The beautiful and non-beautiful musical passages selected for the present study were listed in Table 2. The precise position of the beautiful and non-beautiful musical passages in the entire music piece was shown in the Supplementary information Figure S1.

Table 2. Selected beautiful and non-beautiful musical passages from the Adios Nonino tango piece by Astor Piazzolla. Overall, the passages comprised 98 seconds in the beautiful musical passages and 95 seconds in the non-beautiful musical passages. Each time point below was represented as 'minutes: seconds'.

Piazzolla	
beautiful	non-beautiful
01:30 - 01:50	00:36 - 01:08
03:50 - 04:23	01:57 - 02:12
04:37 - 04:52	02:55 - 03:08
06:22 - 06:40	05:40 - 06:15
07:08 - 07:20	

fMRI data acquisition

The fMRI paradigm was performed with scanning protocol using a standard 20-channel head-neck coil in a 3T Siemens MAGNETOM Skyra whole-body scanner, at the Advanced Magnetic Imaging (AMI) Centre, Aalto University, Finland. A single-shot gradient Echo planar imaging (EPI) sequence (FOV = 192 × 192 mm; 64 × 64 matrix; 33 slices slice thickness = 4 mm, interslice skip = 0 mm; TE = 32 ms; whole brain, TR = 2s, flip angle = 75°) was obtained. The 3D T1-weighted structural images (FOV = 256 × 256 mm; 256 × 256 matrix; 176 slices; slice thickness = 1 mm; interslice skip = 0 mm; pulse sequence = Magnetization-Prepared Rapid Gradient-Echo [MPRAGE]) were also acquired for each participant. During fMRI scanning, participants were asked to listen to the music piece while keeping their eyes open and staying awake. Participants were motivated to listen attentively since they knew that they would answer some questions and rate the music afterward. Analysis of this behavioral data is reported in Alluri et al. (2015) and in Brattico et al (2020). The volume of the music was individually adjusted to a moderately comfortable but hearable level before the start of the session.

Preprocessing

The fMRI data were preprocessed using the MELODIC (Multivariate Exploratory Linear Optimized Decomposition into Independent Components) tool (version 3.15) based on FSL

(FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) (Mark Jenkinson et al., 2012) platform (version 6.0.4). The following standard preprocessing pipeline was used:

- 1) convert the raw fMRI data to Neuro Informatics Technology Initiative (NIFTI) format;
- 2) remove the first 4 time points to allow for signal equilibration;
- 3) spatial smoothing with an 8 mm FWHM Gaussian kernel;
- 4) a high pass filter cut-off of 0.008 Hz;
- 5) slice timing correction;
- 6) motion correction with MCFLIRT (Mark Jenkinson et al., 2002);
- 7) remove non-brain tissue to strip the skull using the brain extraction tool (BET) (Smith, 2002);
- 8) registration of the fMRI data from the functional space to standard Montreal Neurosciences Institute (MNI) (Evans et al., 1994) space through a two-stage process. First, a linear transformation from the functional data to T1 structural using 6 degrees of freedom (DOF) boundary based registration (BBR) by FLIRT (Jenkinson & Smith, 2001). Then, transform structural to the standard template using a 12 DOF BBR by FLIRT and a non-linear registration by FNIRT.

ICA-based noise removal

After basic data preprocessing, Independent Component Analysis (ICA) included in the MELODIC tool of FSL was used to decompose fMRI data into spatial maps, time-courses, and power spectrum in order to remove noise components from the fMRI data deriving from both human physiological activities, such as respiration, heartbeat, blood flow, and cerebrospinal fluid flow, and from other systematic noise such as scanner noise, head movement, susceptibility noise, and other complex noise sources (Beckmann & Smith, 2004; Thomas et al., 2002). ICA components were examined one by one, then categorized as signal or artefact components by hand classification (Griffanti et al., 2017) and the FSL function *fsl_regfilt* was performed to eliminate the noise components and generate the denoised data. Then, the denoised data was transformed into a common space for further data analysis.

Next, the time courses of the BOLD signal were extracted according to Automated Anatomical Labeling (AAL) parcellation into $N = 90$ brain regions. A second-order Butterworth bandpass filter between 0.02 and 0.1 Hz was applied to the time courses of the BOLD signal.

Dynamic Functional Connectivity

We applied Leading Eigenvector Dynamics Analysis (LEiDA) to capture the dominant Functional Connectivity (FC) pattern of BOLD signals for each experimental comparison. First, Phase Coherence Connectivity (Cabral et al., 2017; Glerean et al., 2012; Ponce-Alvarez et al., 2015) of BOLD was calculated to obtain a time-resolved dFC matrix. Phase coherence of BOLD signals between each pair of brain regions was estimated with Hilbert transform (Figuroa et al., 2019; Glerean et al., 2012), which expresses a signal $x(t)$ as $x(t) = a(t)\cos[\varphi(t)]$, where $a(t)$ represents the instantaneous envelope and $\varphi(t)$ represents the instantaneous phase. Subsequently, the dynamic FC matrix, $dFC(n, p, t)$, which represents the phase coherence between brain regions n and p at time t was obtained by the following equation:

$$dFC(n, p, t) = \cos[\varphi(n, t) - \varphi(p, t)]$$

where $n, p = 1, 2, \dots, N$, N represents the numbers of brain regions ($N = 90$) and $t = 1, 2, \dots, T$, T represents the length of the time courses of the BOLD signal. The value $dFC(n, p, t) = 1$ indicates that the two brain regions n and p have an aligned phase at time t , while $dFC(n, p, t) = -1$ indicates that the two brain regions n and p have an anti-aligned phase at time t . Finally, $dFC(n, p, t) = 0$ indicates that the phases of the two brain regions are orthogonal.

Leading Eigenvector of dynamic FC patterns

At each time point t , the dynamic FC matrix $dFC(n, p)$ is an $N \times N$ symmetric matrix since the phase coherence is nondirectional. Therefore, the upper or lower triangular matrix of each $dFC(n, p)$ contains all the meaningful features of the dynamic FC patterns. To further reduce the dimensionality of the $dFC(n, p)$ matrix, a one-dimensional vector named leading eigenvector $V_1(t)$ is calculated using eigenvalue decomposition. The leading eigenvector captures the dominant FC pattern of each $dFC(n, p)$ matrix at time t while effectively reducing the dimensionality (from $N(N - 1)/2$ to N) and computational complexity. The outer product $V_1 V_1^T$ ($N \times N$) can reconstruct the dominant FC matrix.

Each leading eigenvector V_1 contains N elements representing each of the brain regions. The sign (positive or negative) of each element in V_1 denotes whether the elements belong to the same

or different community. For example, if every element in V_1 has the same sign, it indicates the phases of the BOLD signal follow the same direction, and consequently all brain regions are assigned to the same community. If instead, V_1 has components with two different signs (both positive and negative), the phases of the BOLD signal follow opposite directions and the brain regions are divided into two different communities (see Figure. 1a) (Cabral et al., 2017; Figueroa et al., 2019; Newman, 2006). The magnitude of each eigenvector element shows the strength, at which the respective brain region is connected to its community (Newman, 2006). Since V and $-V$ reflect the same relative relationship of the directions of the phases, in this study, we ensure most of the elements in each leading eigenvector have negative signs by multiplying them by -1 if necessary.

FC states

To clearly illustrate the brain connectivity patterns, the FC states were displayed in cortical space. In the visualizations, the sphere located in the center of gravity of each brain region represents the corresponding element in the eigenvector. The magnitude of each element of the eigenvector is indicated by the color of the sphere. More specifically, the spheres colored yellow-to-red indicate the corresponding eigenvector element with positive values, whereas cyan-to-blue indicate elements with negative values. The weakly (cyan/yellow) and strongly (blue/red) saturated colors of the spheres represent weak and strong contributions, respectively (see Figure. 1f) (Fasano et al., 2020; Figueroa et al., 2019).

To investigate specific FC patterns associated with musical beauty, k -means clustering algorithm was applied to the leading eigenvectors across all time points and subjects (8568 leading eigenvectors, 238 time points per person for 36 participants). By this method, the leading eigenvectors were divided into k clusters, with each cluster reflecting a reoccurring FC state. A larger k value categorizes the dataset more precisely, exposing more uncommon and detailed connectivity patterns. In this study, we performed clustering with a range of k between 2 to 20. For each k , the FC states and the switching process between each of the FC states were examined. The k -means clustering results show the most significant differences are reported in the following sections.

To investigate the dynamic pattern of brain states characterizing aesthetic listening to music,

the connectome patterns associated with listening to beautiful vs. non-beautiful were pairwise compared with a t-test (10000 permutations). For each t-test, a total of 10000 permutations are performed.

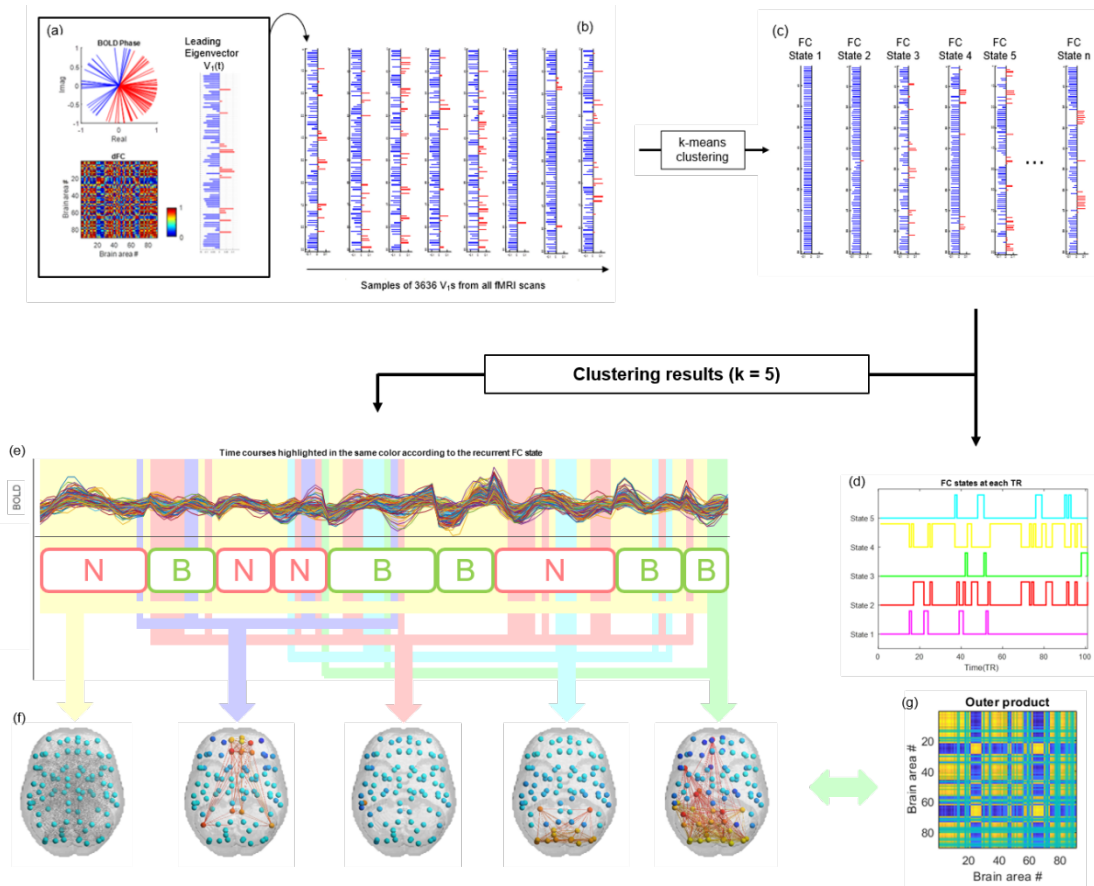


Figure 1. Flow diagram of obtaining FC states with the LEiDA algorithm.

The process of LEiDA algorithm is shown. By calculating the phase coherence of BOLD signals, the leading eigenvectors across all time points were obtained. Then, the k -means clustering was used to calculate the FC states. The details were shown as follows:

- At each time point t , the instantaneous phases of the BOLD signals in the $N = 90$ brain regions (top left; represented in the complex plane) and corresponding dynamic FC matrix (bottom left) are calculated. The leading eigenvector $V_1(t)$ that captures the dominant FC pattern of each dFC matrix is calculated (right). The signs of $V_1(t)$ (blue or red) indicate the phases of the BOLD signal follow different directions and the brain regions are divided into two different communities.
- All leading eigenvectors across all time points and subjects (8568 leading eigenvectors, 238 time points per person for 36 participants) are obtained.
- k -means clustering algorithm is performed on V_1 s to divide all leading eigenvectors into k clusters.
- In the following figures, we use $k = 5$ to illustrate the clustering results and FC states. Each time course has been divided into 5 clusters, representing 5 different FC states (illustrated as colored square-wave pulse), respectively.
- According to the clustering result shown in (e), the FC state for each fMRI section is represented as the same color-shaded bars. B represents the beautiful musical passages and N represents the non-beautiful musical passages.
- The 5 different FC states are represented in cortical space. The magnitude of each element of the eigenvector is indicated by the color of the sphere. More specifically, the spheres colored yellow-to-red indicate the corresponding eigenvector element with positive values, whereas cyan-to-blue indicate elements with negative values. The weakly (cyan/yellow) and strongly (blue/red) saturated colors of the spheres represent weak and strong contributions, respectively.
- The FC states, calculated by $V_1 V_1^T$, can also be expressed as the outer product of V_1 in matrix format.

Results

Detection of the recurrent FC states

To determine FC patterns specifically associated with beauty, we estimated the probability of occurrence of each FC state during listening to beautiful and non-beautiful musical passages for each k ranging from 2 to 20. The result is shown in Figure 2.

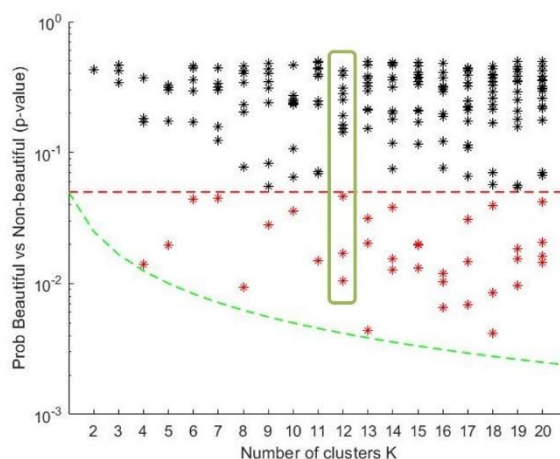


Figure 2. Significance values for the comparisons between the probabilities of the FC states in each k -means clustering model as a function of k for beautiful vs. non-beautiful comparison.

Each dot represents the p-values obtained by the t-test comparison of the probability of occurrence of each FC state associated with beautiful vs. non-beautiful comparison as a function of k . The p-values obtained by t-test comparison of the probability of occurrence of each FC state associated with beautiful vs. non-beautiful comparison were shown. The red dashed line is the uncorrected threshold 0.05. The green dashed line is the threshold corrected by the number of clusters. The green square box represents the cluster solution selected for the comparison, $k = 12$. The dots (p-values) in Figure 2 are marked with different colors depending on their level of significance. In particular, black dots represent states with no significant differences in the probability of occurrence between each comparison. Red dots represented states that passed the standard threshold (<0.05 , uncorrected).

As can be seen, with k greater than 3 and less than 12, only one FC state in each model significantly differentiates listening to beautiful vs. non-beautiful passages. On the other hand, with k from 12 to 20, at least three FC states significantly differ between conditions. Hence, we chose the clustering solution $k = 12$ for this study as this provided the optimal combination of model simplicity and specificity.

FC state with significant differences

With the clustering solution $k = 12$, three FC states were found to differ in their probability between the beautiful and non-beautiful conditions. They are displayed in Figure 3. All 12 FC states are displayed in the Supplementary information Figure S2.

FC state 3 includes the primary and non-primary auditory cortex, namely Heschl's gyrus and

superior temporal gyrus (STG). The probability of occurrence of the FC state 3 for the beautiful ($3.62 \pm 0.16\%$) and non-beautiful ($6.06 \pm 0.22\%$) musical passages ($p = 0.0105$). FC state 4 includes visual regions, namely the occipital gyrus, lingual gyrus, and calcarine gyrus. The probability of occurrence of the FC state 4 for the beautiful ($3.92 \pm 0.12\%$) and non-beautiful ($2.69 \pm 0.07\%$) musical passages ($p = 0.0464$). FC state 10 includes cortical frontotemporal and subcortical striatal and limbic regions, namely STG, putamen, amygdala, supplementary motor area (SMA), and Rolandic operculum. The probability of occurrence of the FC state 10 for the beautiful ($1.06 \pm 0.03\%$) and non-beautiful ($2.31 \pm 0.09\%$) musical passages ($p = 0.0169$).

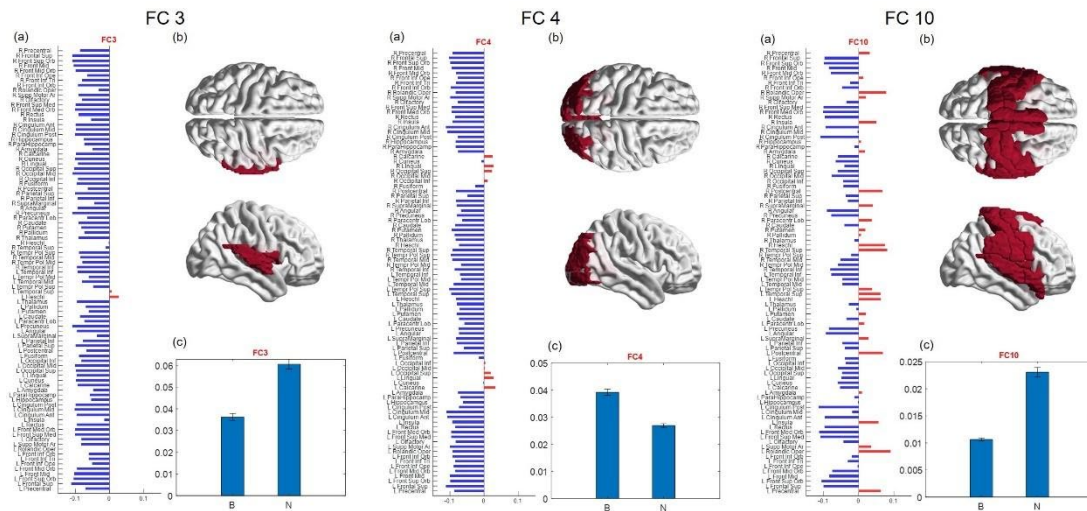


Figure 3. FC states differing in their probability between the beautiful and non-beautiful conditions.
 (a) FC states represented in vector format. The signs of elements (blue or red) indicate the brain regions belonging to each of the two communities. Regions with the same color represent a connected community and each eigenvector element's magnitude shows the strength of each brain region belonging to the FC state. R and L indicate the right or left hemisphere, respectively.
 (b) The cortical space images of the FC states represented in transverse and sagittal planes.
 (c) The error bar charts show the probability of occurrence of each FC state during listening to the beautiful (B) and non-beautiful (N) musical passages.

Switching probabilities

The change in FC state from a previous time point to a later time point was considered a transitioning. Then, we calculated the transitioning probability during beautiful and non-beautiful musical passages, respectively. Finally, we compared the transitioning probabilities between beautiful and non-beautiful musical passages with t-tests. For each t-test, a total of 10000 permutations are performed. The switching probabilities between each FC state during listening to the beautiful and non-beautiful musical passages are shown in Figure 4. The main transition process

between the 12 FC states is shown in Figure 5. The whole transitioning process is shown in the Supplementary information Figure S3.

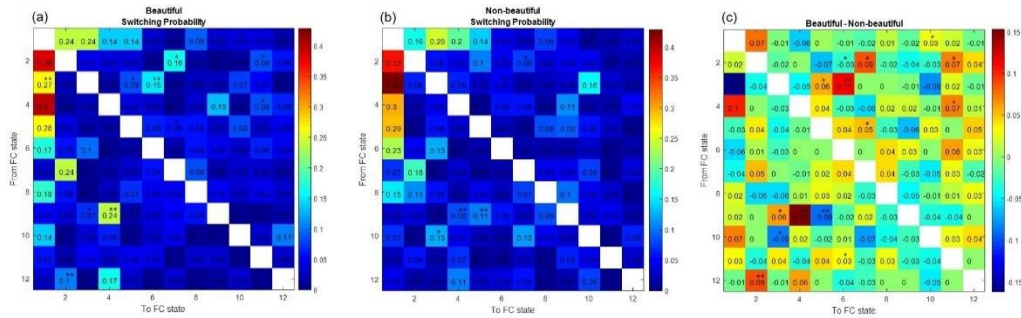


Figure 4. Switching probabilities during listening to beautiful vs. non-beautiful musical passages.

Switching probabilities, calculated as the probability of transitioning from a given FC state to another FC state, during listening to (a) beautiful and (b) non-beautiful musical passages were shown.

(c) The switching probability differences between listening to the beautiful and non-beautiful musical passages. A positive value indicates that the switching probability for the respective transition process was higher during listening to the beautiful musical passages than the non-beautiful musical passages, whereas a negative value indicates the opposite.

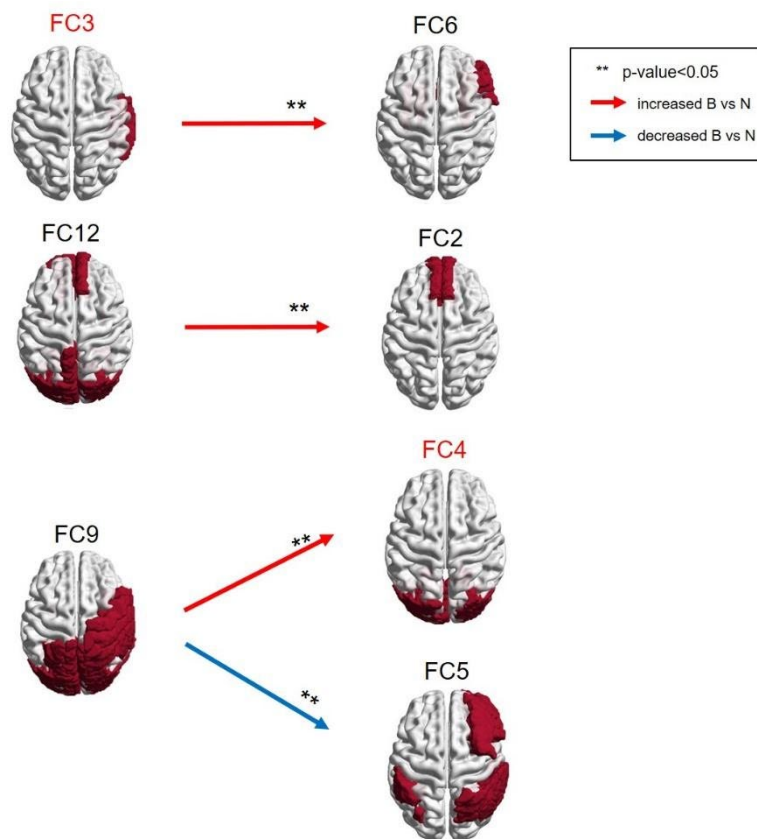


Figure 5. Transitioning process during listening to beautiful vs. non-beautiful musical passages.

Spatial maps of the FC states and the transitioning processes with significant probability differences during listening to the beautiful vs. non-beautiful musical passages were shown. The red arrows represented transitions with increased probability during listening to the beautiful musical passages compared to the non-beautiful musical passages, whereas the blue arrows represented those with decreased probability during listening to the beautiful musical passages compared to the non-beautiful musical passages. B and N in the legend represented the beautiful and non-beautiful musical passages, respectively. Significant differences during listening to the beautiful vs. non-beautiful musical passages were indicated with asterisks (*). Two asterisks represent the significance threshold $p < 0.05$.

In Figure 5, the transitioning probability from FC 3 (auditory) to FC 6 (basal ganglia), from FC 12 (visual, OFC, and frontal) to FC 2 (OFC), and from FC 9 (visual and parietal) to FC 4 (visual) increase significantly during listening to beautiful musical passages compared to non-beautiful ones. The transitioning probability from FC 9 (visual and parietal) to FC 5 (left DMN and OFC), on the other hand, increased significantly during listening to the non-beautiful musical passages compared to the beautiful musical passages.

Discussion

In the explorative study, we investigated the temporal dynamics of the brain connectome related to freely listening to musical passages commonly judged as beautiful or non-beautiful. By means of a novel analysis method for extracting the dynamic FC states from fMRI signals, we evidenced the predominance and switching of sensory and motor networks to limbic and reward-related areas during listening to beautiful musical passages as opposed to mainly auditory networks involved during listening to non-beautiful music.

Pleasant aesthetic experience

During listening to beautiful musical passages, the FC state related to visual regions, which was one of the three most recurrent states, were more recurrent during listening to beautiful. More specifically, this FC state includes the bilateral occipital gyrus, lingual gyrus, and calcarine sulcus. The occipital gyrus, lingual gyrus, and calcarine sulcus play a vital role in processing vision. Liu et al. (2017) reported two clusters of brain regions that communicate with each other during liking judgment conditions. One cluster is related to cognitive processing and the other is related to visual processing. The following topology interaction analyses showed that naturalistic listening displays a similar functional connectivity pattern with liking judgment.

We also calculated the switching probabilities, namely the probability of transitioning from a given FC state to another FC state, during listening to beautiful vs. non-beautiful musical passages. We observed more frequent switching related to auditory and visual brain regions, OFC, and DMN areas during listening to beautiful music passages compared to non-beautiful passages. Recent neurological studies have demonstrated that OFC is linked to aesthetic judgment including beauty

in arousal (Blood et al., 1999; Brattico et al., 2020; Fasano et al., 2020; Trost et al., 2012), visual preference (Bray & O’Doherty, 2007; Ishai, 2007; Kawabata & Zeki, 2004; O’Doherty et al., 2003), memory (Tsukiura & Cabeza, 2011b), and even imaging reward (Bray et al., 2010). The pleasurable experience of musical chills or frissons (shivers down the spine and goose bumps in relation to a very pleasurable listening experience) has been found to be associated with brain circuitry related to pleasure and reward, which includes OFC, amygdala, ventral striatum, and ventral medial prefrontal cortex (Blood & Zatorre, 2001). Trost et al. (2012) reported that music emotion evoked brain regions including the striatum, insula, OFC, and sensory and motor areas. Recent studies have also emphasized the importance of OFC in the reward systems during positively valenced music listening experiences in both adults (Brattico et al. submitted) and early adolescents (Fasano et al. submitted). Furthermore, the core region of frontal DMN overlaps with the hedonic network, which is related to brain regions that are responsible for pleasant sensations and feelings (Kringelbach & Berridge, 2009; Reybrouck et al., 2018). This suggests that when listening to beautiful music brain states related to vision, audition and reward recurrently switch between each other. This extends previous FC findings (Martínez-Molina et al., 2019; Salimpoor et al., 2013) indicating that the information exchange between perceptual, integrative, and reward systems is essential to a positive musical aesthetic experience. Hence, our findings, while confirming the role of the orbitofrontal and visual regions for aesthetic music appreciation, provided a dynamic perspective in which those regions interact with each other continuously over the course of a listening session.

Unpleasant aesthetic experience

Our study also examined the brain connectivity states during listening to non-beautiful musical passages: the FC state related to left STG and Heschl’s gyrus are involved in auditory processing, whereas the other FC state related to bilateral temporal gyrus, putamen, amygdala, postcentral gyrus, precentral gyrus, supramarginal gyrus, SMA, insula, and Rolandic operculum includes areas related to auditory processing, motor control, sensorimotor processing, and emotion processing. Both states were most recurrent as compared to listening to beautiful musical passages. As compared to the states that were more recurrent during listening to beautiful musical passages, a negative listening experience involved brain regions related to auditory processing and high-level cognitive

processing. When listening to non-beautiful musical passages, we found more frequent switching from the auditory state to the global state and from the FC state encompassing frontostriatal regions as well as limbic ones such as the amygdala and insula, possibly associated with the activation of a negative emotional response. We can speculate that the predominance in this FC state of brain structures that are responsible for auditory processing is related to the higher need for resolving uncertainties and broken expectations when listening to non-beautiful musical passages. Such speculation is supported by empirical evidence obtained in our previous study with music experts that non-beautiful musical passages were rated as more complex regarding their harmonic, executive, and rhythmic structure. According to predictive coding theory, our brain actively anticipates upcoming sensory input, rather than passively registering it (de-Wit et al., 2010). Auditory experiences that widely differ from the expected sensory input, and that require additional auditory processing might induce unpleasant aesthetic responses and be judged negatively (Brattico, 2021; Koelsch et al., 2008; Vuust et al., 2022b).

Moreover, dissonant music induces more unpleasant feelings and has been observed to evoke a negative auditory experience used in various studies related to music aesthetics (Dellacherie et al., 2011; Fritz et al., 2009; Koelsch et al., 2006; Pallesen et al., 2005). The amygdala has been reported to be the core component of processing fear and threatening emotions (Baxter & Crosson, 2012). Several neuroimaging studies have implicated the relationship between unpleasant music and the amygdala (Brattico, 2015; Brattico et al., 2011; Koelsch et al., 2006, 2008). A similar phenomenon was also found in a visual and auditory stimulation experiment by Gaiseanu (2021), who reported increased amygdala activity in response to non-beautiful signals. In addition, we observed more frequent transitioning from a brain state involving parieto-occipital visual and attentional structures to a brain state related to DMN and including medial prefrontal and parietal cortex. The parietal lobe integrates and processes sensory input such as hearing, smell, and touch. The precuneus, a part of the parietal lobe, is involved in several high-order brain functions including memory tasks, cue reactivity, and emotional responses to pain. Blood et al. (1999) found that activation of the precuneus was associated with increasing dissonance in music. Suzuki et al. (2008) also found activity in the parietal lobe during listening to non-beautiful dissonant chords. Similarly, Brattico et al. (2016) obtained activation in the precuneus when contrasting attentive listening to liked musical

passages vs. disliked ones. Furthermore, the medial prefrontal cortex was associated to dissonant music listening (Bravo et al., 2019). Flores-Gutiérrez et al. (2007) also highlighted the role of the prefrontal cortex and paralimbic regions during unpleasant musical experiences.

To date, only few studies have attempted to investigate how the negative experience of music affects the human brain. Most of the time, researchers identify the negative experiences of music as unpleasant, dissonant, or rough. Previous studies have linked dissonant music to the activation of several limbic regions including the amygdala, hippocampus, precuneus, and temporal lobe (Blood et al., 1999; Koelsch et al., 2006). Pallesen et al. (2005) also reported increased brain responses in the amygdala, retrosplenial cortex, brain stem, and cerebellum induced by dissonance. Additionally, Kawabata and Zeki (2004) reported that the motor cortex is activated when watching non-beautiful pictures. This was explained by the withdrawal reaction triggered by non-beauty or threat. Overall, our findings indicate that an unpleasant aesthetic experience of music recruits more auditory regions and connections than a positive aesthetic experience and calls into action limbic areas that have been previously robustly associated with negative emotions.

While the findings are promising, they should be considered exploratory since this study explored the application of the novel LEiDA approach to the naturalistic free listening paradigm and the FC states obtained from the contrast between listening to beautiful vs. not-beautiful passages did not survive Bonferroni or FDR corrections for the multiple comparison problems. On the other hand, the obtained FC states were highly consistent across model solutions indicating the likelihood of not false findings. The only previous study applying LEiDA to fMRI time series associated with music listening by Fasano et al. (2020) reported one FC state including OFC regions that survived Bonferroni correction. However, Fasano's study looked into a more obvious contrast, between music listening for 4 minutes and no-music rest for 30 seconds, hence between two conditions highly different in length and in acoustical content. The current study focuses on conditions that are comparable in acoustic features and fully balanced in length, without obtaining robustly significant findings. That either suggests that the statistical power is not sufficient or that LEiDA is not a sensitive methodology for nuanced cognitive tasks. As Ahrends et al. (2022) explored in the study, the robustness and stability of the time-varying FC methods, such as LEiDA, can be affected by several factors including processing, time course extraction, and model complexity. Therefore,

further research should address this open question.

In sum, via investigating the relationship between beauty in music and dynamic brain connectivity by using a naturalistic free-listening paradigm, we extended the evidence of the essential contribution of OFC and visual regions for an aesthetic experience and revealed the dynamic interaction of OFC, visual, and reward networks for eliciting a positive aesthetic response to music. Moreover, our findings on the dynamics of states further support the complexity of the aesthetic musical experience requiring high-order cognitive processes that continuously alternate with sensory processing and emotion regulation.

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