





RESEARCH ARTICLE

The early adolescent brain on music: Analysis of functional dynamics reveals engagement of orbitofrontal cortex reward system

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Abstract

Music listening plays a pivotal role for children and adolescents, yet it remains unclear how music modulates brain activity at the level of functional networks in this young population. Analysing the dynamics of brain networks occurring and dissolving over time in response to music can provide a better understanding of the neural underpinning of music listening. We collected functional magnetic resonance imaging (fMRI) data from 17 preadolescents aged 10–11 years while listening to two similar music pieces separated by periods without music. We subsequently tracked the occurrence of functional brain networks over the recording time using a recent method that detects recurrent patterns of phase-locking in the fMRI signals: the leading eigenvector dynamics analysis (LEIDA). The probabilities of occurrence and switching profiles of different functional networks were compared between periods of music and no music. Our results showed significantly increased occurrence of a specific functional network during the two music pieces compared to no music, involving the medial orbitofrontal and ventromedial prefrontal cortices—a brain subsystem associated to reward processing. Moreover, the higher the musical reward sensitivity of the preadolescents, the more this network was preceded by a pattern involving the insula. Our findings highlight the involvement of a brain subsystem associated with hedonic and emotional processing during music listening in the early adolescent brain. These results offer novel insight into the neural underpinnings of musical reward in early adolescence, improving our understanding of the important role and the potential benefits of music at this delicate age.

KEYWORDS

adolescence, dynamic functional connectivity, music listening, orbitofrontal cortex, pleasure

Elvira Brattico and Morten L. Kringelbach are shared last authors.

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1 | INTRODUCTION

Music listening is an important source of enjoyment and entertainment for children and adolescents (Erkkilä & Saarikallio, 2007; Giacometti et al., 1981; Miranda & Claes, 2009; North et al., 2000; Roberts et al., 2009). The increased tendency to listen to music during adolescence coincides with the delicate transition from childhood to adulthood—a critical life phase characterized by developmental and psychosocial challenges and reward-seeking behaviors (Miranda & Claes, 2009; Steinberg & Lerner, 2004). While the bottom-up limbic structures including nucleus accumbens and amygdala, implicated in incentive and emotional processing, undergoes dramatic development during adolescence (Ernst et al., 2005; Galvan et al., 2006; Laviola et al., 2001), top-down control systems residing in prefrontal regions matures slowly, generally up to the mid-20 years of age (Asato et al., 2010; Giedd, 2008; Gogtay et al., 2004; Kringelbach, 2005; Tamnes et al., 2010). Accordingly, the interval between childhood and adolescence is characterized by heightened sensitivity to rewards paired with minimal cognitive control and emotion regulation (i.e., inability to delay rewards), and thus high impulsivity (Bacter et al., 2021; Chein et al., 2011; Dahl & Gunnar, 2009; Fasano et al., 2019; Perry, 2000; Steinberg et al., 2010; Whelan et al., 2012; Winstanley et al., 2006). Age differences in reward-seeking follow indeed a curvilinear pattern, increasing between preadolescence and mid-adolescence, and declining thereafter (Steinberg et al., 2010). In line with this, pleasure-inducing activities, such as music listening, peak in pre- and mid-adolescence (Bonneville-Roussy et al., 2013; North et al., 2000). But, apart from being a source of pleasure, some studies showed the importance of music listening at this age for developmental tasks and psychosocial adaptive functions, such as self-actualization, individual and cultural identity, socialization and integration with peers, and, above all, emotion regulation (Berns et al., 2010; Giacometti et al., 1981; Madjar et al., 2020; North et al., 2000; Russell, 1997; Schwartz & Fouts, 2003; Tarrant et al., 2000). This is particularly relevant considering that, giving the rapid changes in physical development, behavior, and relationships with others, preadolescents are at risk of developing emotional problems (Bacter et al., 2021). A recent study focused on the effects of music making in a young population suggested that the rewarding experience of music per se may play a crucial role in modulating and stimulating impulse control and emotion regulation (Fasano et al., 2019).

While it is often reported that music listening can be rewarding and, at the same time, have positive effects on these regulatory functions in children and adolescents, the neural basis of such potential effects remains relatively unexplored. In particular, none of the previous neuroimaging studies has so far investigated the neural underpinning of naturalistic music listening (i.e., not interrupted by behavioral tasks) in this young population. The lack of studies on music listening in children and adolescents might be due to the fact that employing functional magnetic resonance imaging (fMRI) for research involving young participants raises many challenges, not least of which is the fact that children can find it difficult to remain still and attentive for long periods of time. However, considering both the challenges that children, and in particular adolescents, go through in terms of emotion

regulation due to the developmental imbalance of the neural circuits mentioned above, and the proposed ability of music to affect emotional control thanks to the hedonic power of music pleasure, it is of high relevance to understand the neural underpinnings of the rewarding experience that music listening represents from an early age. As such, investigations can potentially shed more light on to what extent the ability of music listening to be rewarding may rely on the stimulation of specific neural networks also associated to emotional control.

Recently, the *free listening* paradigm has been introduced in fMRI music research, allowing for the investigation of the neural underpinnings of music listening in a naturalistic situation (Abrams et al., 2013; Alluri et al., 2012; Burunat et al., 2014; Fasano et al., 2020; Hasson et al., 2004; Jola et al., 2013; Silbert et al., 2014; Toiviainen et al., 2014) highlighting the recruitment of auditory, parietal, frontal, subcortical, and motor areas. More recently, the advent of network neuroscience has brought insights into the functional connectivity (FC) between brain regions during the listening of musical pieces (Alluri et al., 2017; Karmonik et al., 2016; Toiviainen et al., 2020; Wilkins et al., 2014), showing that real-world music listening is associated with connectivity patterns rather than activity in isolated regions (Pfeifer & Allen, 2012; Reybrouck et al., 2018). However, the scarce research on FC during music listening has been focused on “static” FC (i.e., correlations computed over the entire scanning period), missing meaningful information contained in the dynamics of functional connections (Cabral, Kringelbach, & Deco, 2017; Deco et al., 2011; Hansen et al., 2015; Vohryzek et al., 2020). From the wide range of methods available to characterize the temporal evolution of FC, including dynamic inter-subject FC (ISFC) (Simony et al., 2016), spatial ICA-based methods (Allen et al., 2012), innovation-driven co-activation patterns (iCAPs) (Karahanoğlu & Van De Ville, 2015) among others, we chose the Leading Eigenvector Dynamics Analysis (LEiDA, Cabral et al., 2017) because it has the advantage of not relying on a sliding-window and is sensitive to patterns of phase relationships rather than correlation or co-activation, which has previously shown high sensitivity to changes associated to behavioral tasks and emotional conditions (Larabi et al., 2020; Martínez et al., 2020; Stark et al., 2020; Wong et al., 2021).

Therefore, in the present study, we aimed to investigate how naturalistic music listening affects resting-state brain activity in children entering adolescence. In more detail, we searched for specific functional networks that change their probability of occurrence when listening to music and investigated their switching behavior. Furthermore, under the hypothesis that these functional networks may relate with the hedonic experience of music listening, we compared their occurrence and transition probabilities with the music reward sensitivity of the young participants.

2 | METHODS AND MATERIALS

2.1 | Participants

Participants were part of a longitudinal study addressing the impact of music training on psychological, pedagogical, and neural functions and were recruited from public elementary schools in Aarhus district

(Denmark). We recruited 17 preadolescents 10–11 years of age (mean age: 10 years and 7 months; SD: 5.8 months) including 10 girls and 7 boys, all with normal hearing. Exclusion criteria included any history of developmental or neurologic disorders. Written informed consent for participation in the study was obtained from the parents/guardians on behalf of the child participants and verbal assent was obtained from all children individually. Parents/guardians received voucher compensations for their child's participation.

2.2 | Experimental procedure

Study protocols were approved by the official Midtjyllands Regional Science Ethics Committee (1-10-72-122-16). All preadolescents were tested individually at Aarhus University Hospital. A child-friendly protocol that included a 30-min preparation prior to the actual scanning was designed. Participants were carefully informed about what a scanner is, what they would do during the whole scanning time, and how important it was to stay still. Before starting the scanning session, participants practiced staying still and were exposed to some of the sounds made by the scanner. To avoid any distress for the child, the parents were given the possibility to accompany the child in the MR room and, eventually, remain in the scanner room and hold their hand. Preadolescents watched a cartoon movie during the anatomical scan to assist them with staying still.

2.3 | Behavioral assessment

The administration of psychological tests and questionnaires had a total duration of 45 min. Only the questionnaires relevant for this study are reported and discussed here.

2.3.1 | Barcelona Musical Reward Questionnaire

We used a Danish version for children and adolescents of the Barcelona Musical Reward Questionnaire (BMRQ). The BMRQ (Mas-Herrero et al., 2013) is a psychometric instrument known to be a reliable indicator of interindividual variability in music-induced reward. Consistently with previous neuroimaging studies (Martínez-Molina et al., 2016), we considered the BMRQ overall scores for our analysis.

2.3.2 | Music training

We collected information about the individual level of music experience by asking the participants and their parents to indicate the number of months of music training received.

2.3.3 | Socio-economic status

Parents were asked to indicate their highest level of education and annual household income on a questionnaire. Responses to education

level were scored on a five-point scale: (1) Elementary/Middle school; (2) High school; (3) College education; (4) Master's degree; (5) Professional degree (PhD, MD, and JD). Annual household income was scored on a five-point scale. A final socio-economic status (SES) score was calculated as the mean of each parent's education score and annual income, consistently with previous studies (Habibi et al., 2014; Sachs et al., 2017).

2.4 | Stimuli

The stimuli used for the fMRI paradigm were two medleys of violin themes for children (referred to as piece 1 and piece 2 in the rest of the manuscript), each with a duration of 3 min and 50 s, for a total of 7 min and 40 s, used for the condition “music.” The themes included in the two pieces were: “Winter time in Russia” by Joanne Martin; “Lift off,” “Tiptoe boo!,” “Here it comes,” “In flight,” and “Clare's song” by K. & D. Blackwell, “E-, A-, D-, G-Strängläten” and “Birgers blues” by Eva Bogren. We selected violin pieces for children because this study was the first part of a longitudinal project including two fMRI measurements and looking at the effect of music learning, therefore requiring the music stimuli to be unfamiliar to all participants and easy to be learned over half a year (for more details regarding the selection of the pieces, see Supplementary Material). The two pieces were unfamiliar to the participants and matched as much as possible for complexity, tempo, genre, and accompaniment (see Supplementary Material). The order of piece 1 and piece 2 was counter-balanced across subjects. Before the presentation of the two selected music pieces, participants were familiarized with the *free listening* task by listening to a brief excerpt of music with a duration of 30 s that was not used for the analysis. All the audio stimuli were preceded and followed by 30 s intervals without music, for a total of 2 min per scan without music (Figure 1d, middle) used for the condition “no music.” At the end of the *free listening* paradigm, the participants were asked how much they liked each of the two pieces of music on a 5-point Likert scale and we then calculated for each participant a total liking score by calculating the average of the scores given for the two pieces.

2.5 | Functional magnetic resonance imaging image acquisition

All preadolescents underwent anatomical, diffusion weighted, and fMRI of their brain. Data collection parameters only for the structural and functional scans are described here.

A 3 T scanner (Siemens Magnetom Tim Trio), equipped with a 32-channel head coil, was used to obtain the images. To prevent postural adjustments and to attenuate the noise and vibration of the scanner, foam cushions were placed around the arms of the participants. Music was presented through audio headphones with active noise control (OptoACTIVE, Optoacoustic).

Blood oxygen level dependent (BOLD) weighted fMRI data were acquired using a gradient echo-planar imaging (EPI) sequence. The

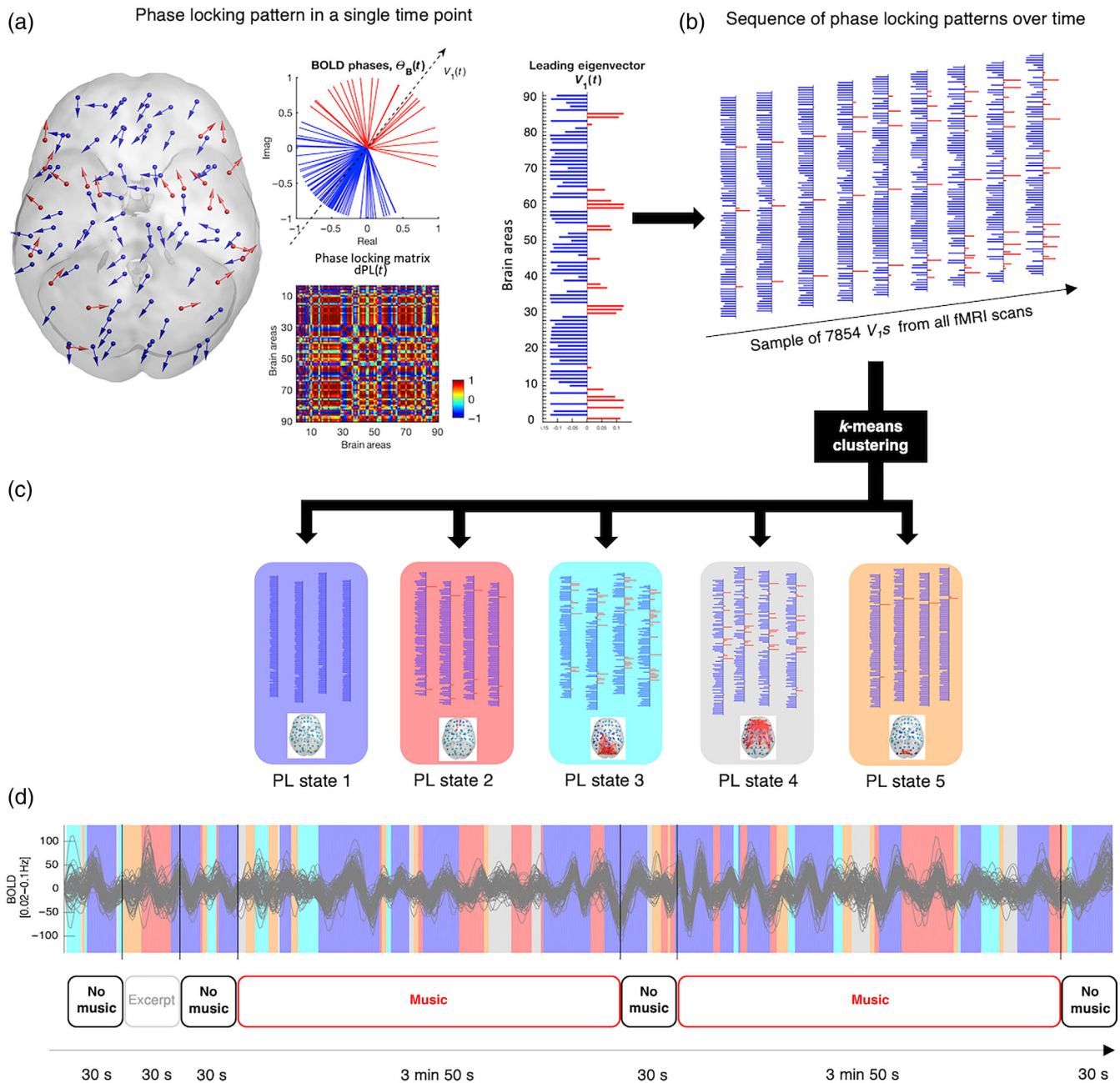


FIGURE 1 Illustration of the methodology to detect the occurrence of PL patterns over time. (a) *Left and middle*: At each time point, the BOLD phases in all $N = 90$ brain areas are represented both in the cortical space (arrows placed at the center of gravity of each brain area) and in the complex plane, centered at the same origin. The PL matrix at time t captures the phase relationship between each pair of brain areas. *Right*: The leading eigenvector of the PL matrix, $V_1(t)$, is the vector that best captures the orientation of all BOLD phases, where each element in $V_1(t)$ corresponds to the projection of each area BOLD phase into $V_1(t)$. The signs of the elements in V_1 (red/blue) are used to divide brain areas into communities. (b) The leading eigenvectors (V_1 s) are obtained for each time point from all fMRI scans in all subjects, resulting in a large sample of 7854 leading eigenvectors. (c) This sample is partitioned into a reduced number of K clusters. For illustration, a random example of partition into five clusters is considered, where each cluster centroid represents a recurrent pattern of BOLD PL, or PL state, illustrated as a network in cortical space by plotting links between elements with positive sign. (d) *Top*: The clustering assigns each time point to the cluster to which $V_1(t)$ is the most similar. The cluster time courses (illustrated as color-shaded bars, over a single fMRI session) are then used to calculate the probability and the state switching probabilities of each PL state in each condition (e.g., music, no music). *Bottom*: Paradigm used in our study. BOLD, blood oxygen level dependent; fMRI, functional magnetic resonance imaging; PL, phase locking

scans comprised 469 volumes of 48 axial-slices (TR: 1300 ms; TE: 27.32 ms; FOV: 192×192 ; voxel size 2.50 mm^3). During the fMRI recording, participants listened to the stimulus presented at an

average sound level of 80 dB. A high-resolution T1-weighted 3D structural image was acquired for anatomical reference (176 slices; TR: 2420 ms; TE: 3.7 ms; FOV: 256×256 ; voxel size:

$1 \times 1 \times 1 \text{ mm}^3$). An MRI-compatible eyetracker (EyeLink 1000—SR research) was used to monitor the preadolescents and ensure they did not fall asleep.

2.6 | Preprocessing

The initial preprocessing of the fMRI data was performed with FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) using the MELODIC tool (version 3.14). The following standard steps were performed within MELODIC: (1) removal of the first five EPI volumes to allow for signal stabilization; (2) high-pass filtering with a cut-off frequency of 0.01 Hz, removing signal components with periods longer than 100 s; (3) spatial smoothing of the EPI volumes with an FWHM of 4 mm (Smith & Brady, 1997); (4) motion correction with MCFLIRT (Jenkinson et al., 2002).

Registration of the EPI data to standard MNI space was performed through a dual linear registration process using default settings in MELODIC. This included a transformation between the EPI data and a structural T1 scan of the same participant, using the BBR algorithm in FSL with 6 degrees of freedom, and a transformation between the same structural T1 scan and an average brain template in MNI space for children ranging in age between 7.5 and 13.5 years (Fonov et al., 2011), using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001) with 12 degrees of freedom. Prior to the registration process, participants' T1 brain images were extracted using FSL's brain extraction tool (BET) (Smith, 2002). Registrations between native spaces and MNI were visually inspected for each participant to ensure satisfactory anatomical alignment between the standard brain and the native structural image.

Noise removal was performed by using probabilistic spatial independent component analysis (ICA) decomposing each participant's fMRI session into $N_{\text{components}} \times \text{time}$, with the number of components, $N_{\text{components}}$, being estimated automatically through Bayesian dimensionality estimation techniques (Beckmann & Smith, 2004). The ICA decompositions were reviewed independently by two raters (experimenters MCF and AS) and classified into noise or signal based on criteria outlined in Griffanti et al. (2017) for the frequency content and appearance of the timecourse and for the pattern of the spatial map of each component. Following this hand classification, the FSL function *fslregfilt* was used to recombine the data to $N_{\text{voxels}} \times \text{time}$ while regressing out the contribution of the components labeled as noise.

After this pre-processing, we extracted the time courses of BOLD activity in 90 cortical and subcortical regions-of-interest (ROIs) defined using the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). This was done through a registration between the AAL template and the standard Fonov brain (Fonov et al., 2011), both of which were defined in MNI space. FLIRT was used to perform an affine registration with nearest neighbor interpolation between the standard 152 MNI brain and the standard Fonov brain. The resulting AAL atlas of the standard Fonov brain (Figure S4) was then readily

translated to each participant's native space through the individual transformation matrix generated using FLIRT as described in point 5 of this section. Representative timecourses were estimated using the FSL function *fslmeans* as the mean across the voxels included in each of the AAL ROI's. The BOLD signals in each of the 90 brain areas were subsequently band-pass filtered between 0.02 and 0.1 Hz (using a second order Butterworth filter as in Lord et al., 2019), discarding in this way the high frequency components associated to cardiac and respiratory signals (>0.1 Hz), and focusing on the most meaningful frequency range for detecting FC in BOLD signal fluctuations (Biswal et al., 1995; Cabral et al., 2017; Glerean et al., 2012).

2.7 | Dynamic phase-locking analysis

To evaluate the temporal dynamics of recurrent functional networks, we first estimated the phase of the bandpass filtered BOLD signals in all $N = 90$ areas over time, $\theta(n,t)$, using the Hilbert transform (Cabral et al., 2017; Deco et al., 2017; Deco & Kringelbach, 2016; Glerean et al., 2012; Ponce-Alvarez et al., 2015). Previous works have shown that the range of frequencies considered in the preprocessing step (0.02–0.1 Hz) is sufficient to return meaningful phase locking (PL) patterns overlapping with known resting-state networks (Lord et al., 2019). In Figure 1a, we represent all $N = 90$ BOLD phases at time t in the complex plane, where the real axis corresponds to $\cos(\theta(n,t))$ and the imaginary axis corresponds to $\sin(\theta(n,t))$.

To obtain the pattern of BOLD PL between all brain areas at each single time point t , we compute a dynamic PL matrix $dPL(n,p,t)$, with size $N \times N \times T$, where $T = 464$ is the number of recorded frames in each scan, using the following equation:

$$dPL(n,p,t) = \cos(\theta(n,t) - \theta(p,t))$$

$dPL(n,p,t)$ is 1 if two areas n and p have synchronized BOLD signals at time t , and is -1 if they are in anti-phase.

2.8 | Leading eigenvector of phase locking

To characterize the evolution of PL patterns over time, we employed the LEiDA (Cabral et al., 2017). The leading eigenvector of the dPL matrix at time t , $V_1(t)$, is a $N \times 1$ vector that captures the main phase orientation over all areas, where each element in $V_1(t)$ represents the projection of the BOLD phase in each brain area into the leading eigenvector (Figure 1a) (Lord et al., 2019; Vohryzek et al., 2020).

When all elements of the leading eigenvector, $V_1(t)$, have the same sign, it means all BOLD phases are following the same direction with respect to the orientation determined by $V_1(t)$, which is indicative of a global mode governing all BOLD signals (Figueroa et al., 2019; Lord et al., 2019; Vohryzek et al., 2020). If instead the leading eigenvector $V_1(t)$ has elements of different signs (i.e., positive and negative), the BOLD signals follow different directions with respect to the

leading eigenvector, dividing brain areas into two “communities” according to their BOLD phase relationship (Figure 1a) (Figueroa et al., 2019). Notably, the network formed by the smallest community of brain areas has been found to reveal meaningful functional networks (Larabi et al., 2020; Lord et al., 2019; Vohryzek et al., 2020). This arises from the fact that the subsystems forming functional networks represent a small subset of areas synchronizing together while simultaneously desynchronizing from the rest of the brain (where “the rest of the brain” is the largest portion).

2.9 | Detection of phase-locking states as recurrent patterns of phase locking

To explore whether there are specific functional networks that differentiate between music listening and no music, we first clustered the whole sample of PL patterns into a varying number of clusters, applying a k -means clustering to all leading eigenvectors $V_1(t)$ across all preadolescents (7854 leading eigenvectors corresponding to all 462 TRs of all 17 preadolescents) (Figure 1b). The clustering divides the sample into a k number of clusters (each representing a recurrent PL configuration), with higher k revealing rarer and finer-grained network configurations. The centroids of each cluster c are vectors with size $N \times 1$, which we use to represent recurrent PL states. Importantly, the clustering assigns a single PL state to each fMRI time point, as highlighted by the shaded bars in Figure 1d.

Since the exact number of functional networks is unclear, we ran the k -means clustering algorithm with k ranging from 3 to 15 (i.e., dividing the sample of eigenvectors into $k = 3, k = 4, \dots, k = 15$ clusters) to cover the range of functional networks commonly reported in literature (Damoiseaux et al., 2006; Yeo et al., 2011). Subsequently, we examined, for each k , any PL state that significantly differed in probability between music listening and no music. We note that this methodological approach inherently assumes a common repertoire of PL states during rest and task, with task being characterized by a change in the relative probability of occurrence of the different states (Figueroa et al., 2019; Wong et al., 2021), and not by a single task-specific FC state, as considered in other task studies (Gonzalez-Castillo et al., 2015).

2.10 | Occurrence and switching profiles of phase-locking states

The probability of occurrence is calculated as the number of timepoints assigned to a given PL state divided by the total number of timepoints in each condition of the paradigm. The probabilities were calculated for each subject, in each experimental condition and for the whole range of clustering solutions explored. In addition, we computed the switching matrix, which captures the trajectories of PL dynamics in a directional manner, namely indicating the probability of transitioning from a given PL state to another (Figueroa et al., 2019; Lord et al., 2019).

2.11 | Statistical analysis

2.11.1 | Differences between conditions

Differences in probabilities of occurrence and in probabilities of transition for the different states between music and no music were statistically assessed using a permutation-based paired t test. In more detail, the probabilities in the two conditions are randomly permuted between conditions and a t test is applied to compare conditions. This process is repeated 10,000 times in order to evaluate the probability of the null hypothesis (Cabral et al., 2017).

To evaluate the significance of results taking into account the family-wise error rate (i.e., probability of false positives arising from multiple comparisons), we define two corrected thresholds of $\alpha_1 = 0.05/k$ (green dashed line in Figure 2a,b) and $\alpha_2 = 0.05/\Sigma(k) = 0.05/117$ (blue dashed line in Figure 2a,b). The first one, α_1 , takes into account the number of independent hypotheses tested in each partition model. The second threshold, α_2 , is the most conservative Bonferroni correction considering all hypotheses tested, but since the hypotheses are not independent across k , this threshold can be too conservative, increasing the probability of missing true positives (Figueroa et al., 2019).

In order to verify the robustness of our results, we also compared the probabilities of occurrence of PL states between Music piece 1 and Music piece 2.

2.11.2 | Correlation analysis with individual musical reward sensitivity

As a further analysis, we correlated the overall BMRQ scores with the differences in occurrence and switching profiles of PL states between music and no music to better explore the neural underpinning of music reward sensitivity.

2.11.3 | Correlation analysis for possible confounders

Moreover, we correlated the difference in probability of occurrence of PL states during music vs. no music with the preadolescents' individual level of music training (determined in number of months of music education) and with the SES, with the purpose of understanding if previous music training experience and SES could affect the difference of PL configurations across the two conditions. The results of these additional analyses are presented in the Supplementary material.

2.11.4 | Static functional connectivity analysis

In order to further justify the choice of our methodological approach, we performed a statistical comparison of the static FC between No

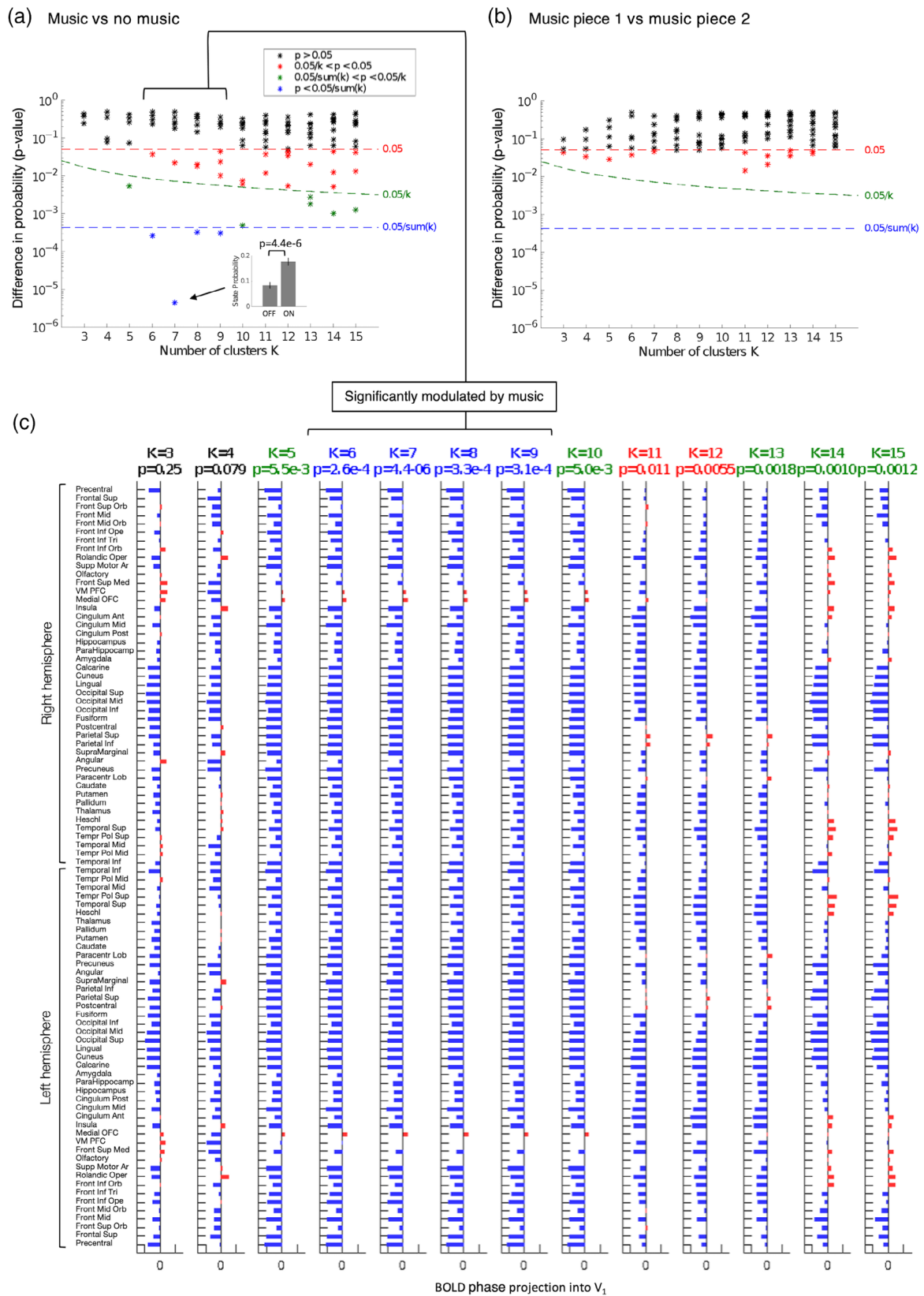


FIGURE 2 Legend on next page.

Music and the two Music Pieces, comparing every functional link (i.e., pairwise correlation) using the same permutation test used for

the LEIDA analysis. None of the 4005 pairwise correlations revealed statistically significant differences between conditions (Figure S1).

3 | RESULTS

3.1 | Detection of phase-locking states modulated by music

We first searched for PL states that significantly differentiated music listening from no music. To do so, for each solution with k PL states (i.e., with number of clusters k varying between $k = 3$ and $k = 15$), we compared the probability of occurrence of each PL state between conditions and obtained the corresponding p -values. In Figure 2a we show all the p -values obtained from the permutation tests performed for each k colored according to the confidence level, where blue means the statistics survive the most conservative correction for positive-dependent multiple comparisons. This analysis reveals that, when clustering the eigenvectors into either $k = 6, 7, 8$, or 9 clusters, the algorithm consistently returns a PL state that significantly differs in probability between music and no music ($p < .0004$).

As a validation step, the same analysis was performed comparing the probabilities of each PL state during the two similar pieces of music that the preadolescents listened to during the scan (Figure 2b). In this case, no difference between piece 1 and piece 2 was detected in the probability of any of the PL states after correcting for multiple comparisons (all $p > .05/k$, for all k between $k = 3$ and $k = 15$, red/black asterisks).

The partition into $k = 7$ states revealed the most significant difference between music and no music, with one PL state showing increased probability of occurrence during music listening with $p < 5 \times 10^{-6}$. Importantly, as illustrated in Figure 2c, this result is not exclusive to the division into seven states, with the partitions into $k = 5, 6, 7, 8, 9$, and 10 states revealing a very similar PL pattern increasing its probability while listening to music. Indeed, the Pearson's correlation between the most significant PL patterns obtained from $k = 5$ to $k = 10$ correlate with $r = 0.98$, which indicates that they refer to the same underlying PL state, with subtle differences arising from the number of output states constrained by k . For finer grained partitions into $k = 13, 14, 15$, other PL states were found to differ in probability (p -values $< \alpha_1$), yet less statistically significant (p -values $> \alpha_2$). For the subsequent analysis, we selected the partition into $k = 7$ states.

Figure 3 illustrates the repertoire of PL states detected when clustering the eigenvectors into $k = 7$. This reveals different network

configurations that reoccur in all participants during the scan. In Figure 3d, we show the mean probability of occurrence (and standard error of the mean, SEM) of the seven PL states in each condition. Except from PL state 2 (described in the following section), none of the other six PL states showed significant differences between music and no music. The global signal has not been regressed out. In alignment with previous studies in adults, a state of global BOLD phase coherence (PL state 1) is found to occur with the highest probability (Cabral et al., 2017; Lord et al., 2019). Moreover, the remaining networks show spatial overlap with previously described functional networks (Yarkoni et al., 2011; Yeo et al., 2011), such as the Default Mode Network (PL state 4), the visual network (PL state 5) or the somatomotor network (PL state 6).

3.2 | Relevant phase-locking state

The PL state that consistently appeared more often while listening to music than without music is shown in detail in Figure 4 (cf. PLstate.mov in Supplementary Material). This PL state consists of a small network including bilateral medial orbitofrontal cortex (medial OFC), bilateral ventromedial prefrontal cortex (VM PFC), and left olfactory cortex. We further refer to this PL state as the "reward PL state" since it involves key brain areas of the reward system (Kringelbach, 2005). For the selected clustering model ($k = 7$), the reward PL state occurred $18\% \pm 1.5\%$ of the time while music was playing compared to $8\% \pm 1.3\%$ when music was off ($p = 4 \times 10^{-6}$ uncorrected, $p = 5 \times 10^{-4}$ corrected by the 117 nonindependent hypothesis tested).

3.3 | Switching probabilities

We examined the transition patterns between PL states in detail for the selected partition model ($k = 7$) by calculating the probability of, being in a given PL state, transitioning to any of the other states for each participant and in each condition. The average switching probability matrices are reported in Figure 5a during music (left) and no music (right) with asterisks denoting the transitions exhibiting changes in probability between the two conditions ($**p < .05$ and $*p < .1$). The transition graph is represented in Figure 5b, with red arrows indicating

FIGURE 2 Detection of PL patterns differing significantly between music and no music but not between similar music pieces, over the range of partition models explored. (a) We compared the probability of occurrence of each PL state between music and no music for each partition model (i.e., with number of clusters k varying between $k = 3$ and $k = 15$) calculating the corresponding p -values. For each k , we obtain k p -values (*), each corresponding to a different PL state. P -value are colored according to the significance level with respect to the different thresholds: (red) $\alpha = 0.05$ (green) $\alpha_1 = 0.05/k$, (blue) $\alpha_2 = 0.05/117$, where 117 is the total number of comparisons performed. (b) No significant differences were detected between the two similar music pieces listened during the scanning session, with red asterisks meaning the p -values $< .05$ can be false positives due to multiple comparisons. (c) For each partition model, we represent the PL state that most significantly differed between music and no music as a bar plot, with the corresponding p -value on the title. As can be seen, there is a robust PL pattern that consistently appears significantly different between conditions when clustering either into $k = 5, 6, 7, 8, 9$, or 10 clusters. In particular, for $k = 7$, one of the seven PL states shows a difference in probability between no music and music with a p -value = .0000044 (shown in Figures 3 and 4). fMRI, functional magnetic resonance imaging; PL, phase locking

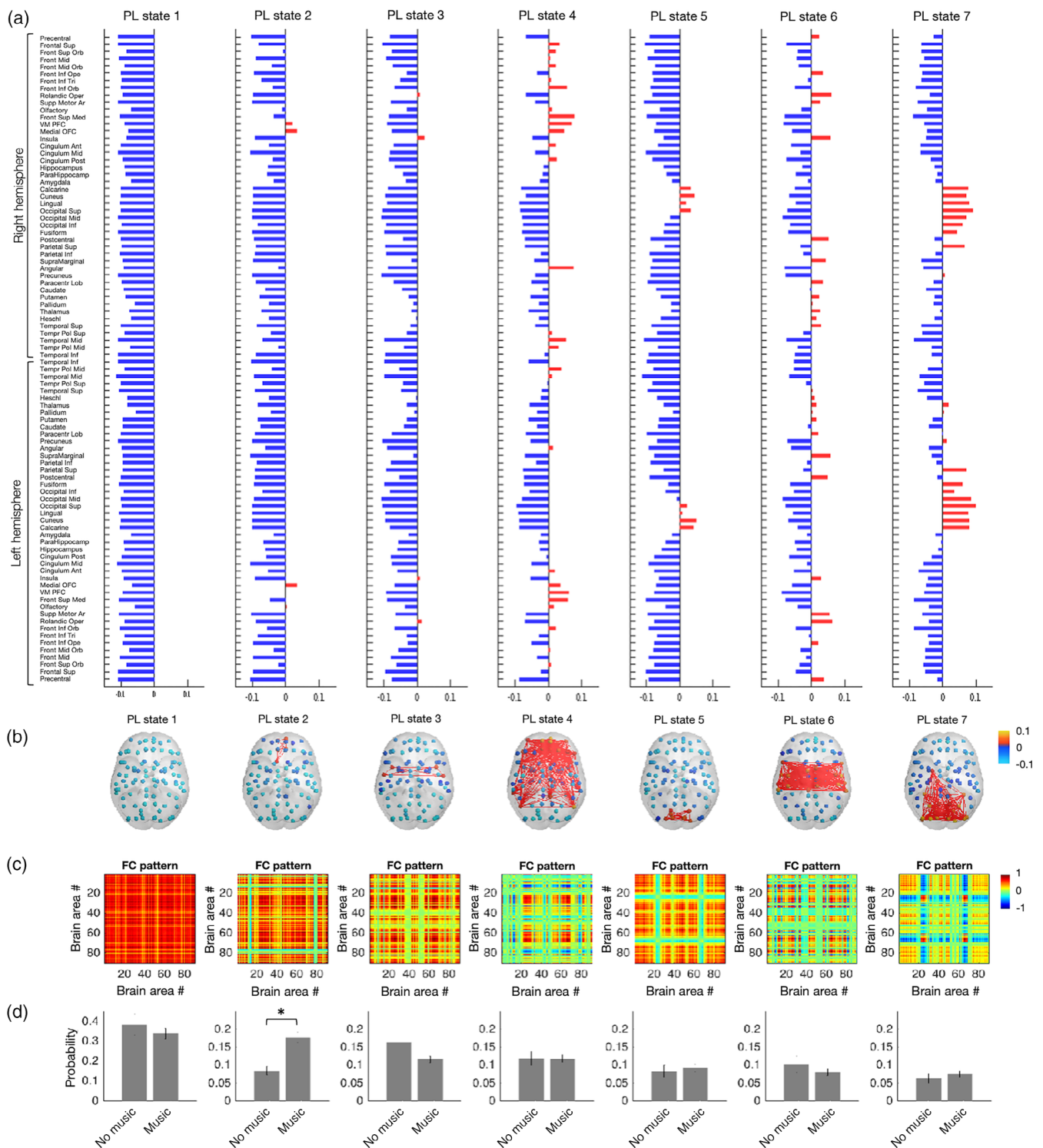


FIGURE 3 Repertoire of PL states assessed with LEiDA (for $k = 7$) and their probabilities of occurrence during music compared to no music. Each PL state is represented by a cluster centroid vector V_c , where each element $V_c(n)$ corresponds to a brain area. (a) Bar charts reporting the centroid vectors and corresponding list of $N = 90$ AAL brain areas ($V_c(n) > 0$ in red, blue otherwise). (b) Each V_c is represented in cortical space by plotting spheres at the center of gravity of each brain area n and coloring them according to the value in $V_c(n)$, and links plotted between elements with $V_c(n) > 0$. (c) Each $N \times N$ matrix (given by $V_c V_c^T$) represents a recurrent pattern of functional connectivity. (d) Probability of occurrence of each PL state in each experimental condition (music and no music), with asterisks (*) denoting statistical significance with $p < .05/k$ in the probability of occurrence between conditions. Only one PL state (2) shows significant difference in probability between music and no music ($p = 4 \times 10^{-6}$ uncorrected, $p = 5 \times 10^{-4}$ Bonferroni corrected by the 117 nonindependent hypotheses tested). AAL, automated anatomical labeling; LEiDA, leading eigenvector dynamics analysis; PL, phase locking

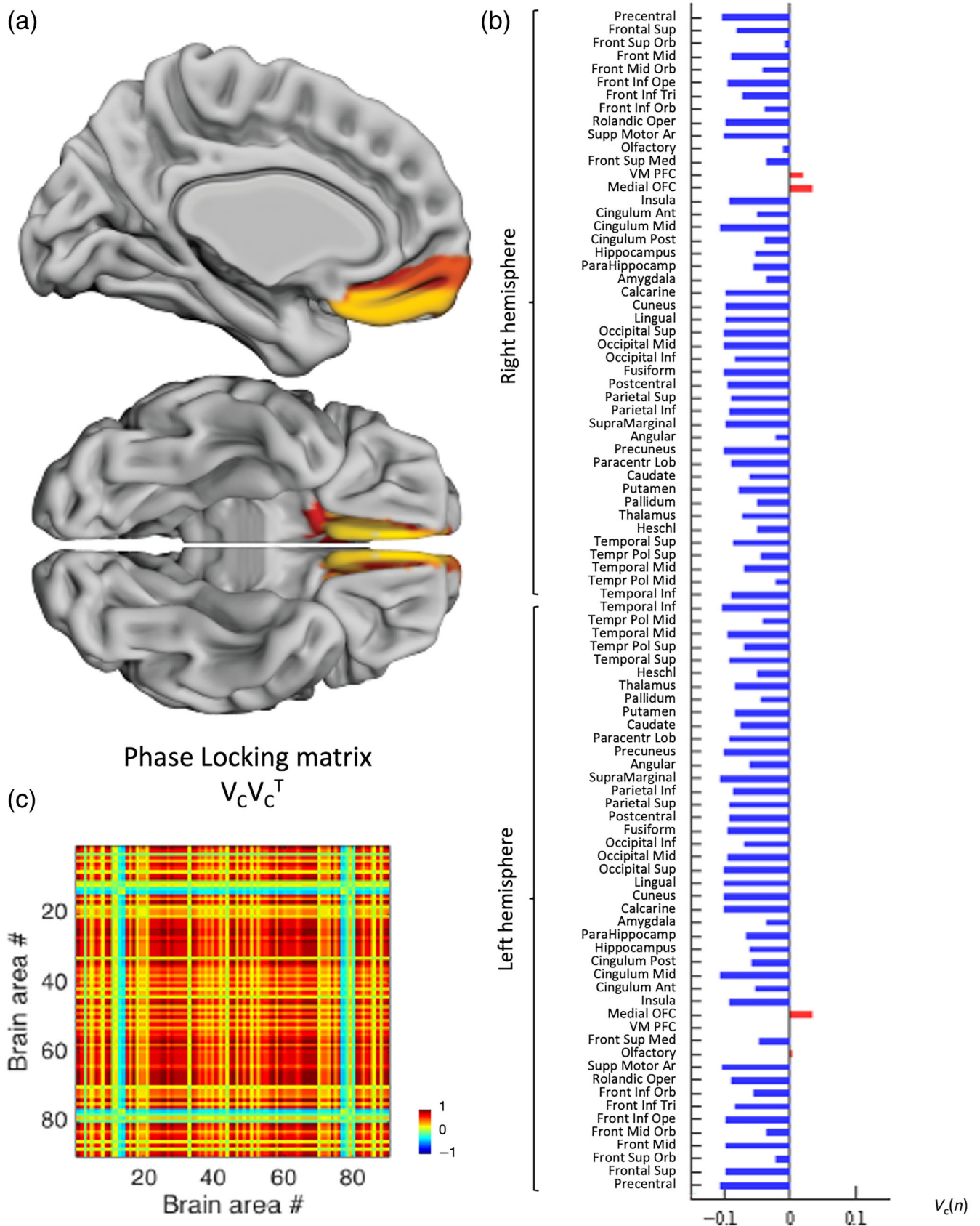


FIGURE 4 Pattern of phase locking occurring significantly more often while listening to music. (a) Representation of the brain regions exhibiting phase-shifted fMRI signals using a heat map on the cortical surface. (b) Bar chart representing, for each brain area n , the corresponding value in the centroid vector $V_c(n)$, with $V_c(n) > 0$ in red and blue otherwise. Values in V_c are normalized such that the norm is 1. (c) PL pattern represented in matrix format as the outer product of the cluster centroid vector $V_c V_c^T$. fMRI, functional magnetic resonance imaging; PL, phase locking

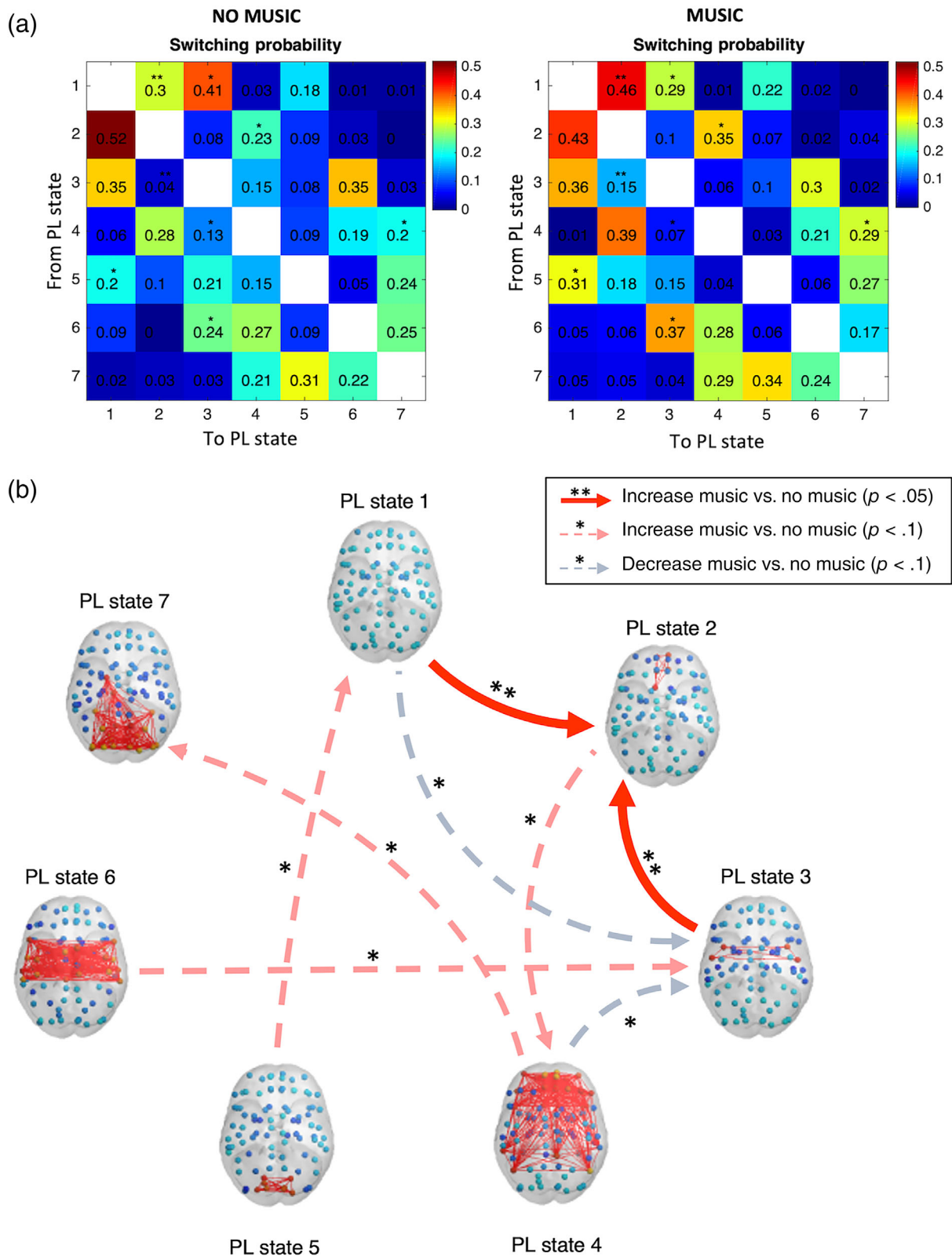


FIGURE 5 Switching probabilities during music listening and no music and differences between the two conditions. (a) Switching matrices showing the probability of, being in a given PL state (lines), transitioning to any of the other states (columns) both during no music (left) and music (right). Between-condition differences assessed via a permutation test are indicated by two asterisks (**) for a significance threshold of $p < .05$ and with one asterisk (*) for a threshold of $p < .1$. (b) Graph illustrating the transitions with stronger changes in probability between music and no music shown in (a). Each arrow represents a state-to-state transition, with red arrows representing an increase, while blue arrows show a decrease in probability of transition in music compared to no music. PL, phase locking

the switches that occurred more often in the music condition than in no music, and in blue the switches that were less frequent during music.

The most significant change was detected in the probability of switching from PL state 3—involving bilateral insula and rolandic operculum—toward the reward PL state (PL state 2), increasing from 4% to 15% when music was turned on ($p = .006$ uncorrected, $p = .04$ corrected by k). Moreover, the state of global coherence (PL state 1) showed a statistical trend of transitioning more often to the reward PL state during music than during no music (46% vs. 30%, $p = .01$ uncorrected). The remaining transitions cannot be considered statistically valid (dashed lines, with $.05 > p > .1$ uncorrected) and are only reported for illustrative purposes.

3.4 | Correlation with individual music reward sensitivity

The music reward sensitivity of the preadolescents, assessed by the BMRQ questionnaire, was correlated with the probability of occurrence of the reward PL state (considering both the absolute probability and the difference in probability between music and no music). However, no significant correlations (Pearson's r) were detected (all $p > .05$) (see Supplementary material). As additional analysis and considering the involvement of the reward PL state in emotional processing, we also correlated the difference in probability of occurrence between music and no music with the BMRQ single subscale *Emotional Evocation* (including items such as “I like to listen to music that contains emotion”; “I get emotional listening to certain pieces of music”; “I sometimes feel chills when I hear a melody that I like”), finding a trend of significance ($r = 0.47$, $p = .055$, uncorrected).

Notably, considering instead the switching probabilities between PL states, the individual BMRQ total scores were found to correlate positively (Pearson's $r = 0.51$, $p = .038$, uncorrected) with the participants change in probability of switching from PL state 3 (bilateral insula and rolandic operculum) toward the reward PL state (PL state 2) between conditions. In more detail, the difference in probabilities of transition was calculated for each subject (matrix values reported in Figure 6, left refer to the average difference across subjects). The BMRQ scores were correlated with the changes in probability of all possible transitions, with only one transition showing a correlation with the BMRQ score with $p < .05$ (not surviving correction for multiple comparisons). The scatter plot of the individual switching probabilities (x axis) versus the individual BMRQ score (y axis) is reported (Figure 6, middle), together with an illustration of the transition (red arrow) from PL state 3 to PL state 2 rendered on the cortical surface to facilitate the neuroanatomical interpretation of the relationship between BMRQ scores and PL state switching (Figure 6, right).

4 | DISCUSSION

We here identified a significantly increased occurrence of a functional network pattern during music listening compared with no music in preadolescents (10–11 years of age), consisting of a pattern where the BOLD signals of bilateral medial OFC and ventromedial prefrontal cortex are phase shifted from the rest of the brain. The OFC involved in this PL state is considered to be a key area of the brain's pleasure system and has been consistently related to musical reward (Blood et al., 1999; Blood & Zatorre, 2001; Salimpoor & Zatorre, 2013; Trost et al., 2012). Similarly to other pleasant activities, music listening has been associated with a cyclical time course of pleasure including: a

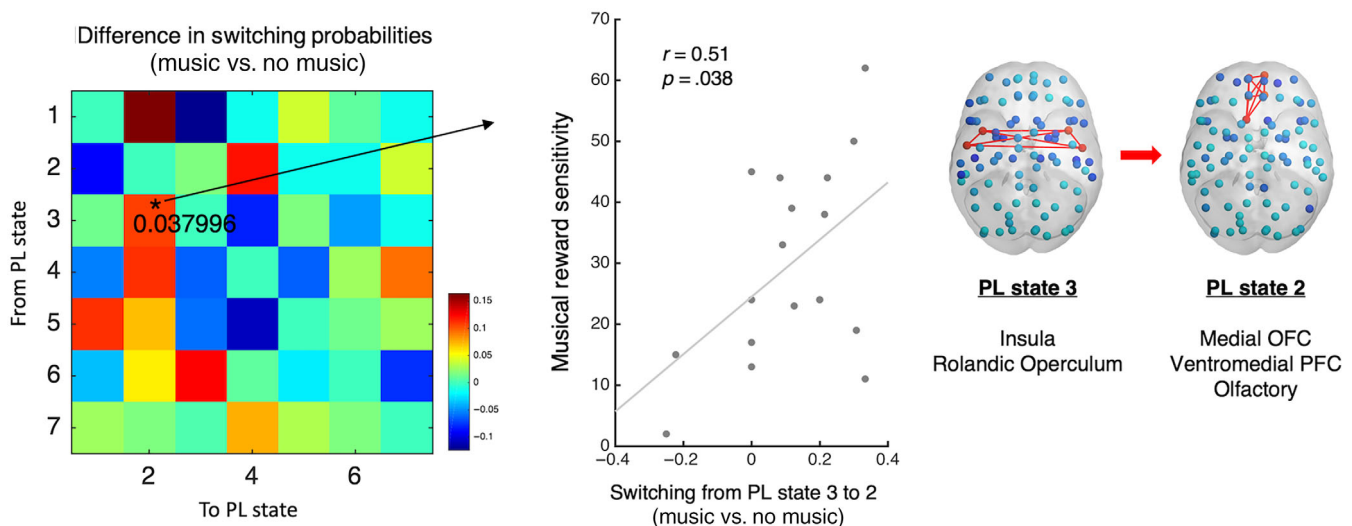


FIGURE 6 Music reward sensitivity correlates with the difference in switching probabilities from PL state 3 to PL state 2 between music listening and no music. *Left*: Matrix showing the average difference in switching probabilities between music and no music across participants. Significant Pearson's correlation with the individual BMRQ scores is indicated by one asterisk (*) for a significance threshold $p < .05$. *Middle*: Scatter plot of individual BMRQ scores and differences between music and no music in the transition probabilities from PL states 3 to 2. *Right*: Graphical illustration of the state-to-state transition (red arrow) occurring with increased probability during music in participants with high BMRQ score than with low BMRQ score. BMRQ, Barcelona Musical Reward Questionnaire; PL, phase locking

phase of expectation or wanting for a specific rewarding musical structure; a phase of consummation or liking of the music reward, which can have a peak level of pleasure (e.g., musical chills); a satiety or learning phase, where one learns and updates musical predictions changing both the wanting phase and the liking phase for future listening experiences (Brattico, 2015, 2019a; Brattico et al., 2013; Gebauer et al., 2012; Georgiadis & Kringelbach, 2012; Kringelbach et al., 2012). These musical pleasure cycles, driven by different mechanisms including musical expectancy, memory associations, evaluative conditions (for a review, see Gebauer et al., 2012; Brattico, 2019b), involve the reward brain system, in particular the OFC, the ventral tegmental area, and the nucleus accumbens (Blood & Zatorre, 2001; Brattico, 2015; Brattico et al., 2016; Brown et al., 2004; Koelsch et al., 2006; Liu et al., 2016, 2017; Menon & Levitin, 2005; Osuch et al., 2009; Reybrouck et al., 2018; Suzuki et al., 2008). Interestingly, all these areas are similarly engaged in other pleasurable experiences involving food (Kringelbach et al., 2012) or sex (Georgiadis & Kringelbach, 2012). Although findings from MEG have indicated that the OFC plays a significant role on many timescales within the pleasure cycle (Kringelbach et al., 2008; Parsons et al., 2013; Young et al., 2016), this region has been proposed to be part of the top-down neural route to conscious liking of music, providing a modulation of the sensory musical pleasure by means of reward value attribution, as complementary to the bottom-up neural route to sensory pleasure in music operating in a fast manner without conscious awareness (Brattico, 2015).

Despite the well-documented impact of music on the brain's pleasure system and the important role that music listening plays in the lives of children and adolescents as a source of enjoyment (Erkkilä & Saarikallio, 2007; Giacometti et al., 1981; Miranda & Claes, 2009; North et al., 2000), the neuroimaging studies focused on music listening conducted thus far have been focused mainly on adults. The only study with music listening in children (as distinguished from simple music discrimination tasks studies) that has been done by now has showed, by means of a general linear model, increased BOLD signal in the OFC in 10-year-old children when exposed to irregular chords (unexpected harmonic functions) versus regular chords (Koelsch et al., 2005), corroborating the hypothesized ability of musical expectancy violation to engage emotional processing (Kraehenbuehl & Meyer, 1957; Krumhansl, 1997). However, the stimuli used in that study consisted of artificial chord sequences, therefore partially missing ecological validity. Our study is the first using a *free listening* task in preadolescents allowing them to listen and to enjoy real music (rather than very brief or artificial sounds) without being interrupted by unnatural behavioral tasks (Alluri et al., 2012; Brattico, 2019b; Haumann et al., 2018; Poikonen et al., 2016).

A second aspect of novelty of this study relies on the employment of a new method of analysis able to measure the dynamic processing of music listening. The temporally extended musical pleasure cycle during music listening (Brattico, 2019a; Brattico et al., 2013; Gebauer et al., 2012; Koelsch et al., 2006), underlines the need of understanding the neural underpinning of music listening using a method that allows to catch the dynamic networks that re-occur and

dissolve over an extended period of time. Using LEiDA, we were able to explore music processing focusing on time-varying whole-brain FC patterns rather than relying on static correlational patterns or seed-based approaches. Without the limitations of sliding windows, LEiDA considers only the phase relationships between brain areas. The fact that significant differences in the relative occurrence of functional networks between experimental conditions are detected irrespective of the signal amplitude reinforces the hypothesis that the phase shifts between brain areas contain meaningful information to investigate brain function (Vohryzek et al., 2020).

The ecologically valid paradigm, in combination with the LEiDA methodology adopted to measure the dynamic processing of music, allowed us to start capturing at least partially the potential neural base hidden behind the well-established tendency of children and adolescents to spend hours listening to music while being emotionally affected by it (Erkkilä & Saarikallio, 2007; Roberts et al., 2009; Tarrant et al., 2000).

We show indeed that music is able to attract recurrently in preadolescents a reward brain network involving a region that is strongly involved not only in musical pleasure cycles but in the general experience of reward and emotional processing and regulation (Kringelbach, 2005). In support of this, a trend toward statistical significance was found when correlating the difference of probability of occurrence of the reward brain network during music as compared to no music with the *emotional evocation* factor of the music reward sensitivity ($p = .055$). The more the preadolescents were scoring high in items such as “I like to listen to music that contains emotion”; “I get emotional listening to certain pieces of music”; “I sometimes feel chills when I hear a melody that I like,” the more the network involving OFC was recruited when listening to music as compared to no music. Our additional analysis comparing the probabilities of PL states between the two similar music pieces listened during the scanning session did not reveal any significant difference, supporting the replicability of our results. After the *free listening* paradigm, the participants indicated an average liking of 3.5 (SD = 0.6) on a 5-point Likert scale of how much they liked the pieces they had listened to, showing to perceive the pieces as overall pleasurable (71% of the children indicated to like the pieces between 3.5 and 4.5). Additionally, we observed a higher probability to switch from both the PL state 1 (global mode) and the PL state 3 (insula and rolandic operculum) to the reward PL state during music listening compared with no music. Interestingly, we found a positive correlation between the music reward sensitivity of the participants, measured by means of BMRQ, and the tendency to switch from PL state 3 to the reward network (PL state 2): the more the preadolescents were inclined to be rewarded by music, the more the state involving the medial OFC reward system was preceded by a state involving the insula and the rolandic operculum. Similarly to our results, Koelsch et al. (2005) found that the rolandic operculum was recruited in conjunction with the anterior superior insula while children were listening to pleasant music and the authors related the activity in this network, together with the ventral striatum, to the emotional perception of the musical stimuli. Considering the strong involvement of insula and OFC in the

pleasure system, it is likely that the bilateral insula played a role in recruiting the activity in bilateral rolandic operculum during emotional perception of the musical stimuli before switching to a PL state involving OFC, especially in the most rewarded-by-music participants. The relationship between this transition and the music reward sensitivity is consistent with a previous study in which greater activity in medial OFC while listening to favorite music was correlated with self-reported capacity to experience pleasure in a range of different situations (Osuch et al., 2009). Overall, the remarkable ability of music to recurrently engage a brain state involving the medial OFC, known to be involved in liking, monitoring, learning, and memory of the reward value of reinforcers, confirms the involvement of this brain region in musical pleasure also in preadolescents, as investigated for the first time through the lens of dynamic FC.

Most importantly, the recruitment of the brain network involving OFC during listening to pleasant music can potentially provide new knowledge in the field of child and adolescent psychiatry. Apart from being intimately involved in all parts of the pleasure cycle, this complex brain region plays indeed a crucial role in emotional processing and regulation, self-reflection, and cognitive control (Kringelbach & Rapuano, 2016), as also confirmed by the correlation we found with the subscale *emotional evocation* of the BMRQ (see above). In line with this, the immaturity of the OFC in adolescence has been related to the increased emotional reactivity that this period is characterized by (Casey et al., 2008; Monk et al., 2003; Thomas et al., 2004). OFC is one of the last brain regions to mature (Gogtay et al., 2004; Kringelbach, 2005; Shaw et al., 2008; Tamnes et al., 2010) and its protracted development, in terms of synaptic pruning and myelination, suggest that it might not be able to provide sufficient top-down control of robustly activated reward and affect processing emotional regions (e.g., nucleus accumbens and amygdala) during adolescence (Casey et al., 2008; Galvan et al., 2006; Steinberg, 2010; Steinberg et al., 2009; Strang et al., 2013). This developmental pattern increases the probability of risky decision making and high emotional reactivity, especially in those adolescents prone to emotional reactivity (Casey et al., 2008). In particular, abnormalities of the volume, the activity, and the connections of OFC with subcortical regions strongly related to emotions such as amygdala, have been shown to be predictive of obesity, internet gambling disorder, cannabis, or alcohol abuse in adolescents (Chai et al., 2011; Cheetham et al., 2017; Maayan et al., 2011; Peters et al., 2015). Therefore, the top-down control function of the OFC in the emotional network, although not yet fully matured in adolescence, and the frequent recruitment of a PL state involving this region during music listening, potentially provides the basis for using music listening as a coping strategy for emotion regulation in adolescence (Arnett, 1995; Giacometti et al., 1981; Miranda & Claes, 2009; North et al., 2000; Schwartz & Fouts, 2003). We may speculate that the capability of music listening to stimulate and strongly attract the OFC reward system during adolescence might make music able to modulate the development and the function of top-down reward regulation of this brain region. This would be consistent with studies showing the effects of music training—and therefore continuous music exposure—on cortical thickness maturation in OFC

and inhibitory control in children and adolescents (Alemán et al., 2017; Fasano et al., 2019; Holochwost et al., 2017; Hudziak et al., 2014; Moreno et al., 2011). If this is the case, this can have important repercussions in the clinical context. Indeed, since orbito-frontal dysregulation appears to be a signature feature across a broader field of psychopathology in adolescence, the potential role of music listening in modulating the functioning of OFC at this age might have potential implications for future therapeutic and/or preventive music intervention. Music listening may represent a low cost, safe, and side-effects-free prevention or intervention tool for stimulating the function of top-down emotion regulation in children and adolescents with or without clinical symptoms related to an impaired emotional and cognitive control.

This raises an urgent need of exploring and understanding with further studies the neural basis of the regulatory effects of music listening in this delicate and vulnerable age extending this investigation to clinical populations.

5 | LIMITATIONS

The selection of the music pieces used as stimuli in our study was limited by the fact that this study was part of a second longitudinal study including two fMRI measurements and looking at the effect of music learning, therefore requiring the music stimuli to be unfamiliar to all children and easy to be learned over half a year. Since our priority was to design a child-friendly protocol including a maximum of 30-min of actual scanning in order to avoid any distress to the young participants, we decided to not include any additional music piece. This did not allow us to select pieces self-chosen by the children as their favorite ones. Even though our participants found our music stimuli overall pleasant, extending this work to include the favorite pieces of each participant as stimuli may enhance the attractive power of music to recruit brain reward systems. However, the presentation of identical and unfamiliar stimuli to all the children allowed us to avoid confounding variables related to different musical features, genre, and level of familiarity of the pieces selected.

The selection of an adequate parcellation scheme is always a subject of debate in neuroimaging analysis. Here, we followed the previous works on LEiDA and used the original version of the AAL parcellation (Tzourio-Mazoyer et al., 2002), which does not adequately segment some of the key regions of the pleasure circuit such as the nucleus accumbens. A new version of the AAL parcellation has been released (AAL3) including brain nuclei such as the nucleus accumbens, substantia nigra, ventral tegmental area, red nucleus, locus coeruleus, and raphe nuclei (Rolls et al., 2020). Future studies using parcellations schemes with better definition of areas in the pleasure circuit would be crucial to confirm its recruitment during music listening in preadolescents.

In the analysis of dynamic FC, some works have found increased sensitivity when subtracting the static connectivity matrix from the time-evolving dFC matrices (Xie et al., 2018). In line with the previous studies using LEiDA, this procedure was not performed here, and it is

unclear how it would affect the results. In any case, not removing the mean PL pattern allows a more direct interpretation of the results in the sense that each pattern detected is a PL pattern, and not the difference in PL with respect to the mean.

Given that we used the cluster assignment returned by the k_{means} algorithm to detect the occurrence of PL states, this approach inherently assumes that only one state is “active” at each time-point (i.e., the closest cluster centroid using a “winner-take-all” approach). It may be argued that it is unlikely that the brain operates only in one network at a time, and other approaches can be used to consider simultaneous activations of different networks. One possibility is to consider the proximity to all the cluster centroids (also returned by the k_{means}), or to use different methodological approaches, such as Principal Component Analysis, Hidden Markov Models, or Dictionary Learning algorithms. However, it is interesting to note that considering only the dominant pattern at each time point provides such a sensitive measure that returns meaningful results such as the ones detected in this work.

Finally, future studies should replicate our results using an active control condition or control group to further strengthen our results. An alternative interpretation of these results may be indeed that the increased probability of a brain state involving phase-coherence with these regions of OFC being separate from all other regions might also be an indication of the underdevelopment of these brain regions, an insufficiency to provide top down control of activated reward, rather than a sign of enhanced reward processing during music listening. Comparing the results to adults or adding an active control could be helpful for excluding these alternative interpretations.

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CONFLICTS OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The codes used in this study are publicly available at: github.com/juanitacabral/LEiDA/tree/master/MUSIC_preadolescents.

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