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Common modulation of limbic network activation underlies musical emotions as they unfold

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ABSTRACT

Music is a powerful means for communicating emotions among individuals. Here we reveal that this continuous stream of affective information is commonly represented in the brains of different listeners and that particular musical attributes mediate this link. We examined participants' brain responses to two naturalistic musical pieces using functional Magnetic Resonance imaging (fMRI). Following scanning, as participants listened to the musical pieces for a second time, they continuously indicated their emotional experience on scales of valence and arousal. These continuous reports were used along with a detailed annotation of the musical features, to predict a novel index of Dynamic Common Activation (DCA) derived from ten large-scale data-driven functional networks. We found an association between the unfolding music-induced emotionality and the DCA modulation within a vast network of limbic regions. The limbic-DCA modulation further corresponded with continuous changes in two temporal musical features: beat-strength and tempo. Remarkably, this "collective limbic sensitivity" to temporal features was found to mediate the link between limbic-DCA and the reported emotionality. An additional association with the emotional experience was found in a left fronto-parietal network, but only among a sub-group of participants with a high level of musical experience (>5 years). These findings may indicate two processing-levels underlying the unfolding of common music emotionality; (1) a widely shared core-affective process that is confined to a limbic network and mediated by temporal regularities in music and (2) an experience based process that is rooted in a left fronto-parietal network that may involve functioning of the 'mirror-neuron system'.

Introduction

One of the most intriguing aspects of music is that despite its relatively abstract nature, it is a powerful medium for inducing and communicating emotions across a wide variety of listeners (Juslin and Laukka, 2004; Lundqvist et al., 2008; Dalla Bella et al., 2001; Fritz et al., 2009). During concerts, a crowd of complete strangers can find themselves sharing feelings of joy, tension or transcendence as the music unfolds (Zentner et al., 2008). Alluding to this inter-personal aspect of music, scholars have consistently regarded music's capacity to promote bonding as an important factor of its ubiquity and antiquity (Cross, 2014; Dunbar, 2012). Spanning developmental stages (Dalla Bella et al., 2001) and surpassing cultural borders (Fritz et al., 2009; Egermann et al., 2015), humans seem to recognize the 'emotional message' conveyed in music and even respond similarly to some of its basic acoustic features, such as loudness and tempo (Egermann et al., 2015). In fact, it has been suggested that the 'bonding capacity' of music relies on temporal regularities that promote inter-individual synchronization via resonance or entrainment (Cross, 2014; Rabinowitch et al., 2013), and that

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this rhythmic entrainment plays an important role in shaping musical emotions (Juslin, 2013). Thus, with music, associating between the sensory 'input' and the experience 'output' becomes particularly important, as the communicative aspect of musical emotions necessarily relies on particular information in music that can be reliably traced.

While much is known or conjectured about the neural correlates of music-induced emotions (cf., Koelsch, 2014; Frühholz et al., 2014), it is still unclear what neural mechanism may mediate the *common, widely shared, emotional experience* with music. Determining the neural representations of this common human experience and its musical origins is of great interest, as it may shed light on how music conveys emotions as well as how emotions may be shared across individuals. It is plausible to assume that similarities in neural activation across individuals (hereafter referred to as common activation) during particular moments of music listening, could reflect a basic mechanism for the sharing of emotions. Such similar modulation in neural activation across individuals could possibly emerge in limbic brain areas already implicated in core emotional processing (Kober et al., 2008; Phan et al., 2002), as well as in musical emotions (Koelsch, 2014; Frühholz et al., 2014). This relies on evidence from the last decade, revealing that virtually every known structure implicated in emotional processing is involved in processing of musical emotions. Structures such as the amygdala, hippocampus, ventral striatum (VStr), insula, and Orbito Frontal Cortex (OFC), have been found to be sensitive to the type of emotion induced (i.e., sad vs. happy), or affective dimension (i.e., pleasant vs. unpleasant) of different musical excerpts (Frühholz et al., 2014; Blood and Zatorre, 2001; Blood et al., 1999; Chapin et al., 2010; Koelsch et al., 2006; Menon and Levitin, 2005; Trost et al., 2012, cf., Koelsch, 2014). Limbic regions such as the amygdala have been additionally found to be sensitive to particular musical features that are known to affect music's emotionality, namely dissonance (Koelsch et al., 2006; Blood et al., 1999), expressive variations in timing and loudness (Chapin et al., 2010) or musical pulse (Alluri et al., 2012). Extending to the system-level, it has been recently shown that some of these regions (the OFC, amygdala or Vstr) form a functional network with a wider set of limbic or sensory areas during music listening (Menon and Levitin, 2005; Lehne et al., 2013; Koelsch and Skouras, 2013; Salimpoor et al., 2013).

Another possibility is that the common aspect of musical emotions involves the 'mirror-neuron' system: brain regions in the ventrolateral prefrontal cortex and superior parietal lobule involved in the internal simulation of the motor gestures of another agent (Rizzolatti and Craighero, 2004). This relies on recent theoretical frameworks, suggesting that the emotion in music may be perceived through processes of mirroring (Juslin, 2013; Overy and Molnar-Szakacs, 2009). This could be driven by a psychological process of either the inner imitation of voice-like expressive characteristics in music (i.e., emotional contagion; Juslin, 2013), or the internalization of music as sequences of expressive motor gestures at varying hierarchical levels (Overy and Molnar-Szakacs, 2009). Initial support for the involvement of this system comes from a number of fMRI studies revealing the emotion-related processing of music in regions implicated in the pre-motor representation of vocal sound production (Koelsch et al., 2006), and in regions that are considered a part of the mirror system such as the inferior frontal gyrus and pre-motor cortex (Chapin et al., 2010).

Although the studies reviewed above clearly linked between musical emotions and specific neural system activation, direct evidence for the idea of a common-representation of emotional information in these systems is lacking. That is, it is unclear if the emotional information in music elicits common activation across different people throughout the listening experience or what musical elements may mediate this similarity. To address this gap, the current study shifts from a single- to group-centered approach in order to characterize the neural systems that are similarly modulated among listeners in correspondence with the unfolding of emotions and musical features.

One elegant way that has been abundantly used to test the idea of common neural representations in fMRI is the approach of inter-subject correlation (ISC) analysis. This model-free approach assesses the coupling between different brains in response to naturalistic stimuli such as film excerpts (Hasson et al., 2004; Nummenmaa et al., 2012) or stories (Lerner et al., 2011), using correlations between time-courses of brain activation of different people. Utilizing this approach within the realm of music, studies have demonstrated that neural activation patterns in several cortical areas involved in low- and high-level perception are similarly synchronized across listeners when the musical structure is preserved (Abrams et al., 2013; Farbood et al., 2015). However, as ISC relies on functional correlations to examine 'brain to brain' coupling, it can only be assessed throughout the entire listening period, or within fairly long time windows (~20 s; Nummenmaa et al., 2012). Therefore, it is implicitly assumed that the synchronization across brains is sustained across fairly long time frames. Furthermore, such correlation-based indexing does not capture the actual pattern of common activation. Thus, moments of common decreases or increases in activation will be similarly represented as a positive correlation pattern in fairly low temporal resolution (i.e. on the scale of seconds). Depicting the detailed dynamics of common activation as emotions evolve is especially important in the case of music, which is tightly linked with the temporal domain, as musical emotions are only realized over time and have properties that are in constant fluctuation (Flaig and Large, 2014). Indeed, it has been shown that the limbic and para-limbic responses associated with music-induced emotions may be highly transient (Mueller et al., 2015), change over the course of listening (Koelsch et al., 2006), and correspond to the fluctuations in reported experience (Chapin et al., 2010; Lehne et al., 2013; Salimpoor et al., 2011). We therefore maintain that it is crucial to depict transient rather than sustained common activation modulations with a high temporal resolution in order to expose the true nature of shared musical emotion processing.

To deal with these described shortcomings in the moment-to-moment portrayal of common activation patterns, we propose a novel 'group-centered' analysis approach. This approach is based on calculating a Dynamic Common Activation (DCA) index; that can be calculated at every sampled time point (i.e. repetition time; TR) in a way that reflects both the strength of fMRI activation across subjects and the variation around this average (see methods and Fig. 1a–c). Intuitively, this measure, which relies on a t-statistic, "cleans" contributions of idiosyncratic activations or outliers, thus emphasizes the representation of similar activation in the highest temporal resolution for fMRI. Calculating the DCA index per sampled time point provides a continuous time-course that represents the modulation in common activation throughout music listening. The obtained time-course can be correlated with other continuous measures such as behavioral ratings or musical annotations. Such an approach complements previous 'single-brain' based studies that used a standard two-level regression approach with a continuous model of the responses to naturalistic music (Chapin et al., 2010; Alluri et al., 2012; Lehne et al., 2013). This, in contrary to the DCA approach, is more affected by the idiosyncratic neural dynamics underlying the ongoing musical emotional experience.

In the current study we aimed to portray the common representations of distributed brain activation dynamics in response to two musical excerpts with different emotional content. This was achieved by asking participants to passively listen to two 8 min long pieces of contemporary music while scanned in the fMRI. The extended length and naturalistic nature of the musical excerpts enabled the depiction of the emerging dynamics of emotions as they evolved throughout the piece. To assess the on-going affective group experience following scanning, participants were requested to continuously rate their experience using a two dimensional scale of valence and arousal (Nagel et al., 2007; Schubert, 2004; Coutinho and Cangelosi, 2011; Eerola and Vuoskoski, 2010). Closing the input-output loop, we further used a comprehensive set of carefully annotated musical features to predict the DCA in the emotion-dependent networks and expose how they relate to the common emotional experience. As growing evidence indicates that a more robust approach for verifying and referencing dynamic variations in

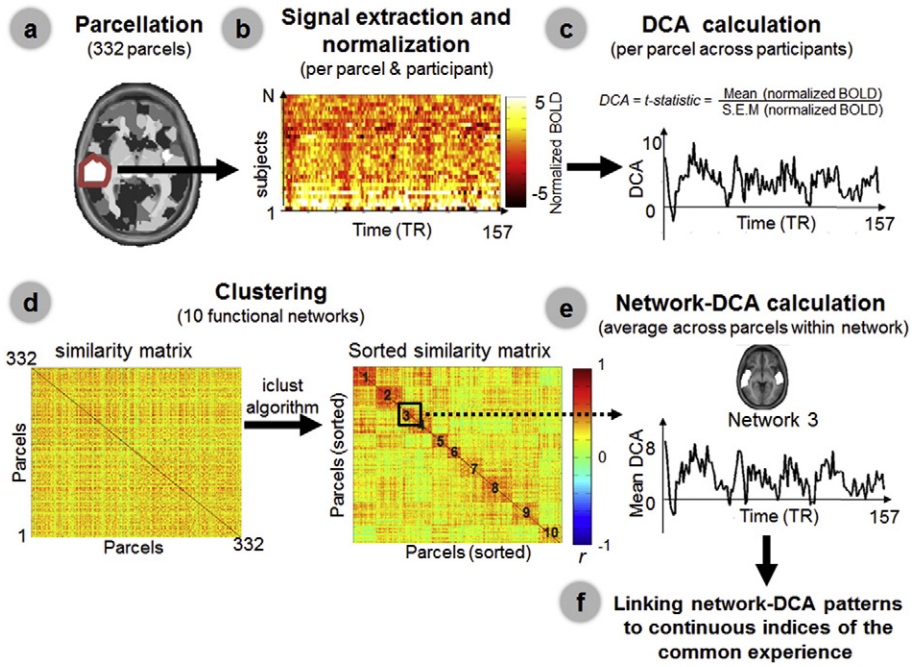

Fig. 1. *Overview of the analysis approach.* (a, b) BOLD signals were extracted from 332 distinct parcels per participant and normalized to baseline. (c) Estimation of the common activation was obtained by calculating the Dynamic Common Activation (DCA) index in each parcel and time point as the one-sample t-statistic across participants. (d) Ten distinct networks were extracted by applying iClust algorithm using the mean of DCA similarity (i.e., correlation) matrices from the two listening sessions. (e) The mean DCA within each network was used in subsequent analyses and referred to as the network-DCA. (f) The resulting temporal patterns of network-DCA were then compared with the corresponding time courses of emotional reports and musical features. The analysis pipeline is demonstrated using data obtained for the parcel marked in white in a. and in response to the musical piece by Ligeti. S.E.M = standard error of the mean.

the brain may require a network view (Raz et al., 2014; Raz et al., 2012; Bullmore and Sporns, 2009), we adopted a system-level perspective for the DCA calculation. In specific, we extracted ten networks using a data driven clustering approach (Fig. 1d–e) and further inspected how the DCA within these extracted networks is associated with either the continuous depiction of the group's ratings of emotional experience or the musical annotations (Fig. 1f).

We hypothesized that limbic and paralimbic brain areas that have been repeatedly implicated in the processing of musical emotions (Koelsch, 2014; Frühholz et al., 2014) would form a functional network and that the DCA time-course modulation within this network will correspond with the ongoing group affective experience. We additionally expected the 'mirror-neuron system', hypothesized as important in the processing of musical emotions via motor simulation, to reveal a similar association with the group affective modulation (Juslin, 2013; Mueller et al., 2015). Lastly, we conjectured that musical parameters known to modulate a listener's basic ability to move (Overy and Molnar-Szakacs, 2009) or synchronize (Cross, 2014) to music, such as beat (Alluri et al., 2012) or tempo (Chapin et al., 2010), would be associated with the affective modulation of the limbic-DCA time-course.

Materials and methods

Participants

Forty healthy volunteers (22 females) between the ages of 19 and 33 ($M = 25.5 \pm 3.6$ years) participated in the entire experiment, which included listening to two musical pieces, termed hereafter Ligeti or Glass (see details below). The participants had no known history of neurological or psychiatric disorders, and provided written informed consent according to the Tel Aviv Sourasky Medical Center institutional review board (IRB) committee guidelines prior to the experiment. Thirteen of the participants had more than five years of experience playing music, ranging between 7 and 22 years ($M_{\text{experience}} = 12.31 \pm 4.75$ years) and were thus categorized as having high levels of musical experience. The remaining 27 participants were categorized as having low levels of musical experience, ranging between 0 and 5 years ($M_{\text{experience}} = 1.94 \pm 1.67$ years). This cut-off was chosen to correspond with the study by Chapin and colleagues (Chapin et al., 2010) who demonstrated an effect of expertise on the neural processing of emotional music and had a similar subject-profile. The cutoff was solely based on prior experience with music playing and *not* listening. This division defined two groups, hereafter termed high- and low- musical experience, which not only differed in the number of years of music-playing, but also in the proportion of participants that are currently playing an instrument, or that have undergone formal or theoretical training. There were no differences between the low- and high- playing experience groups in age or male/female ratio (see details in Table S4). Data from one/two participants were not included in the behavioral rating analysis of the Ligeti/Glass, respectively because of equipment failure. Data of two additional participants were eliminated from the behavioral rating analysis of the Ligeti/Glass piece because they were detected as outliers, as described below in Behavioral measures section. As a result, the behavioral ratings data relied on 37 participants for Ligeti ($M_{age} = 25.85 \pm 3.47$; 20 females; 12 high musical experience) and 36 participants for Glass ($M_{age} = 25.88 \pm 3.55$; 20 females; 12 high musical experience). Data from 11/14 participants were not included in the fMRI analysis of the Ligeti/Glass piece for the following reasons: (1) termination of scanning due to claustrophobia (two participants, both pieces); (2) technical issues during data acquisition (one participant, Glass piece); (3) excessive or abrupt head movements (i.e.>2 mm; 7/9 participants in Ligeti/Glass) (5) evidence for a highly noisy signal (two participants, both sessions). As a result, complete fMRI analysis was available for 29 participants for Ligeti ($M_{\text{age}} = 25.9 \pm 3.8$, 17 females; 9 high musical experience) and 26 participants for Glass ($M_{\text{age}} = 25.6 \pm 3.7$, 16 females; 11 high musical experience).

Sound stimuli

The music stimuli included two recorded piano pieces: (1) Ricercatas no 1 & 2 from *Musica Ricercata* by György Ligeti (7:41 min) and (2) a piano arrangement of the "Hours" from the soundtrack to the film *The Hours,* by Phillip Glass (7:03 min). *Ligeti*'s Ricercatas are a series of 11 piano pieces exploring different compositional possibilities using an increasing number of pitch classes ranging from only two (A and D as the final tone) in the first Ricercata, three (E#, F#, G#) in the second Ricercata (used in the current study) and up to 12 pitch classes in the final 11th piece. While the first Ricercata uses a play on different groupings, accent locations (i.e. a complex temporal structure) and octave shifts, the second Ricercata is much more ordered in the temporal domain, using contrasts of register, loudness, texture and consonance versus dissonance. Nonetheless, it too displays a certain degree of temporal irregularity due to the long periods of silence in between its phrases. The *Glass* piece, in contrast to the Ligeti Ricercatas, is clearly based on harmonic progressions creating a clear harmonic rhythm contrasting major and minor sections. It is highly structured with exact and varied repetitions of phrases or whole sections. In addition, it presents contrasts between successive or simultaneous duple and triple meter. The two musical pieces were selected because they are characterized by distinct affective tones (Fig. 2b) and were shown in a pre-test to elicit clear, yet qualitatively different affective experiences in terms of their valence (i.e., negative for Ligeti and positive for Glass, $n = 17$; Man Whitney U test, $z = 3.12$, $p = 0.002$) but not in terms of their arousal ($z = -1.26$, $p = 0.2$). This enables a good sampling of the two-dimensional affective space, thus strengthening external validity.

Although both musical pieces were used as soundtracks for famous films - Ligeti: *Eyes Wide Shut* (Kubrick, 1999); Glass: *The Hours* (Daldry, 2002), the familiarity of these musical pieces was generally low among our group sample for both pieces (median ratings ≤ 2 on the scale from 1 to 5, corresponding to the labeling of "to a little extent") and did not differ between pieces (Wilcoxon matched paired test, $Z = 1.04$, $p = 0.29$, $n = 38$). In addition, although they differ on many dimensions, both pieces are relatively simple to characterize musically. To further enhance the precision of the characterization of the musical features, both pieces were recorded using a Yamaha Disklavier upright piano. This is an acoustic piano with a MIDI output, allowing the storage of the exact details of each keystroke (e.g., pitch and velocity). The recorded sound files were passed through a music compression procedure using a built-in multiband compressor of Cubase 5 software (Steinberg Media Technologies, Germany). The recordings are available in the supplementary materials.

Experimental design and procedure

A schematic description of the study design can be found in Fig. 2a. The fMRI experiment included a passive music listening task and was followed by a behavioral rating task outside the scanner.

fMRI task

Each of the participants listened to both musical pieces during the same fMRI session in a counter balanced fashion across subjects. Each musical piece was preceded and followed by a 1 min epoch of silence. The musical pieces were presented at an average sound level of 100 dB using Presentation software (Neurobehavioral Systems, Albany, CA) through MR compatible headphones (50–15,000 Hz frequency response) with about 25 dB of passive gradient noise attenuation and over 20 dB active noise cancellation (Optoacoustics, Israel). For further attenuation of gradient noise, participants used earplugs. The participants were instructed to lay still with their eyes closed and to naturally experience the piece. To familiarize the participants with auditory stimulation in the scanner, a short chromatic scale was presented 30 s prior to the presentation of the musical piece.

Behavioral task

Continuous ratings. Immediately following the fMRI session, the participants were presented with the same musical pieces and continuously rated their felt emotional experiences using EMuJoy software (Nagel

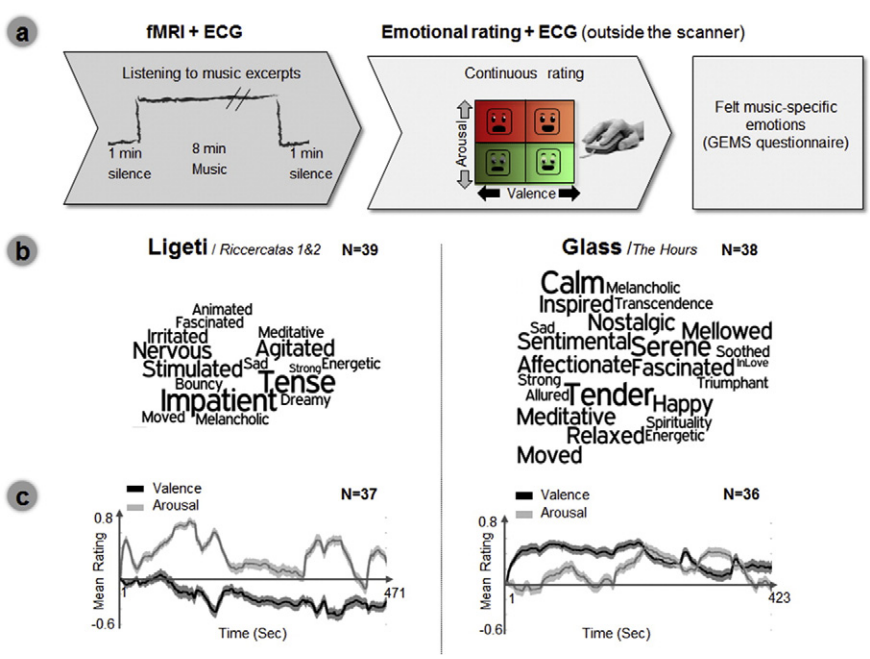

Fig. 2. Experimental design and behavioral characterization of the stimuli. (a) Schematic description of the experimental procedure, which included an FMRI scanning session of passive music listening, followed by a behavioral ratings session of the induced emotional experience during scanning. (b) Emotion label ratings of the listening experience using the GEMS-45 questionnaire (Zentner et al., 2008). Font size is proportional to the median value of the intensity of ratings. Maximal size equals to level 4 out of 5. Only labels rated with a median value higher than 1 are presented. (c) Continuous ratings on the scales of valence and arousal. Thickness of shading represents 1 deviation from the mean (S.E.M). ECG = electrocardiography. GEMS = Geneva Emotional Music Scale-45.

et al., 2007). Specifically, by moving a cursor via computer mouse, the subjects indicated their real-time subjective feeling on the two dimensional emotion response space that encompassed *valence* (i.e., pleasantness, horizontal axis) and *arousal* (i.e., activation, vertical axis). Each cursor movement was recorded by the software at a maximal rate of 20 Hz. The participants were explicitly instructed to indicate their own felt (and not perceived; 10) emotions and to relate as they can to the experience they had during scanning. The participants were given an opportunity to practice the use of the software and to familiarize with the concepts of valence and arousal in a separate practice session. The continuous rating session was conducted separately from fMRI scanning to avoid influence of the rating task on the neural responses associated with naturalistic listening (Lieberman et al., 2007). Such post-scanning rating approach was successfully applied using musical (Chapin et al., 2010) or cinematic materials (Raz et al., 2012) and was further validated in this study by continuously monitoring the participants' heart rate both inside and outside the scanner using electrocardiography (ECG; see details in supplementary materials). The analysis revealed that the patterns of continuous arousal ratings and heart rate – a known index of physiological arousal (Stemmler, 2003) - were positively correlated across the group of listeners both outside and inside the scanner ($p < 0.05$ for all effects; see Table S3).

Musical-emotion label ratings. Immediately following the continuous ratings, the participants were requested to fill out the 45 items of the Geneva Emotional Musical Questionnaire (GEMS-45; Zentner et al., 2008), translated into Hebrew and delivered via Google docs. This questionnaire includes 45 labels that were shown to consistently reflect musically induced emotional states among a wide range of listeners. Participants indicated according to each label how strongly they experienced the depicted feeling during listening on a Likert scale ranging from 1 to 5 for each of the musical pieces. This step was done to obtain a fine-grained characterization of the affective tone of the piece and the range of music-specific emotions that they evoked in the listeners.

MRI data acquisition

Structural and functional scans were performed using a GE 3 T Signa Excite echo speed scanner with an 8-channel head coil. Functional whole-brain scans were performed in an interleaved top-to-bottom order, using a T2*-weighted gradient-echo echo-planar imaging sequence (TR/TE = 3000/35 ms, flip angle = 90°, 128 × 128 matrix, FOV = 220 × 220 mm, 39 slices per volume with 3 mm thickness and no gap). Functional images of two participants were acquired using 38 slices per volume due to a technical limitation. Positioning of the image planes was performed on scout images acquired in the sagittal plane. A total of 200 volumes were acquired for the Ligeti session and 184 for the Glass session. Subsequent to the functional scanning, a T1-weighted 3D axial spoiled gradient echo (SPGR) pulse sequence (TR/TE = 8.9/3.5 ms, flip angle = 13°, voxel size = 1 ∗ 1 ∗ 1 mm, FOV = 256 × 256 mm, slice thickness = 1 mm) was applied to provide high-resolution structural images.

Data analysis and preprocessing

Musical measures

Feature annotation. We annotated several musical features that are considered important for emotional expression in music (Schubert, 2004; Coutinho and Cangelosi, 2011; Eerola, 2011; Eerola et al., 2009; Gabrielsson and Lindström, 2010). The features were extracted in two manners: (1) automatically, based on the MIDI and sound files that were obtained from the DiskLavier recordings; (2) by relying on the judgment of a completely different group of 20 highly-trained musicians that had at least 7 years of regular music training (none participated in the current experiment; $M_{age} = 26.15 \pm 5.04$; 8 females; hereafter termed musicians). Full details about the demographics of this group of musicians, annotation procedure and the extracted features are provided in the supplementary materials. Briefly, the automatic annotation was carried out using the MIR toolbox (Lartillot et al., 2008), PsySound 3 toolbox (Cabrera et al., 2007) and an in-house software and included the depiction of the following features: *spectral centroid, brightness, roughness, dynamic loudness, median velocity, minimum, maximum and mean pitch, pitch range, number of chords (event-density) and the presence of sound*. The 'musician-based' annotation was used to extract several higher order musical features: *tempo, beat strength and musical surprises* (i.e., moments where musical expectations were violated). For extracting rhythmic information, which is considered an important factor in musical emotions (Juslin, 2013; Overy and Molnar-Szakacs, 2009; Trost and Vuilleumier, 2013), each of the musicians listened to the same Ligeti and Glass recordings that were used in the study and was asked to tap to the beat using the "Sonic Visualizer" (version 1.7.2; Cannam et al., 2010). The tapping data were used to extract indices of (1) *tempo* - the frequency of beat-synchronized taps; (2) *beat strength* - the extent of synchronization of taps across the different musicians. To further depict musical surprises, theorized as important in inducing emotions when a certain musical event disconfirms the listener's expectations about the continuation of the music (Meyer, 1956), the musicians heard each piece again and were asked to mark online any musical event that sounded surprising to them. The musicians could adjust their surprise markings if necessary in an additional session so as to fit exactly the point in time at which the surprising event took place. These data were used to annotate musical surprises by depicting, per second, the number of musicians that pointed to a surprising event in that particular moment. The annotation was carried out by a group of musicians in order to maximize the accuracy and specificity of the depiction. More specifically, the assignment of annotation requires not only fine auditory capabilities, but also the capacity to selectively attend to particular elements while disregarding others. These required cognitive abilities, such as auditory attention, working memory, and extraction of relevant information from incoming sounds, have been shown to be strengthened in musicians (Kraus and Chandrasekaran, 2010). Furthermore, the task of synchronizing to musical rhythms has also been found to be more accurate among musicians than non-musicians (Franěk et al., 1991).

Factoring musical features into musical dimensions. To reduce dimensions, principal component analysis (PCA) was applied separately for each musical piece, using a varimax rotation (Alluri et al., 2012). The first six resulting principal components were selected as they accounted for >90% of the variance. The profile of the highest factor loadings (>0.6) within each principal component of the two pieces was highly similar (Fig. S3). The six factors were segregated into the following domains, according to their highest loadings: (1) Pitch information: maximum, minimum and mean MIDI notes (2) Loudness and timbre: median velocity, dynamic loudness, roughness, spectral centroid and brightness; (3) Tempo: number of chords (MIDI) and frequency of beat-synchronized taps (tapping data) (4) Beat strength: inter-subject tapping coherence (5) Pitch Range; and (6) Musical surprises. The time-course of these six resulting components, hereafter termed musical features, were used in all further analyses for explaining the common activation (see details below).

Behavioral measures

The continuous ratings of valence and arousal were extracted per subject and down-sampled into a resolution of 1 Hz and subsequently averaged across subjects. The time courses of rating were checked for outliers by examining the ISC - the correlation of each individual time-course with the average over subjects of all other time-courses. Participants with an ISC of two standard deviations below the overall ISC were removed from analyses. This resulted in the removal of two participants from each ratings data set. The average time-courses of the continuous

ratings of valence and arousal or their combination, as described in the Results section below (Common limbic dynamics correspond to the continuous report of musical emotional experience section), were used in all further analyses for explaining the common activation.

fMRI measures

Preprocessing. The data were preprocessed using BrainVoyager QX version 2.3 software (Brain Innovation, Maastricht, The Netherlands) and in house software developed in Matlab. The first 10 volumes of the acquisition were discarded to allow for stabilization of the magnetic field. Slice scan time correction was performed using sinc interpolation. Head motion correction was performed by spatially aligning all volumes to the middle volume via rigid body transformations using sinc interpolation. Linear trend removal and temporal high-pass filtering were applied to each voxel's time-course to remove linear and nonlinear low-frequency drifts of 3 or fewer cycles per time course (high pass filter of 0.005 Hz). A spatial smoothing with a 6 mm FWHM Gaussian Kernel was used. The structural and functional images were manually co-registered and transformed into the same Talairach space. To account for non-neural fluctuations within the Blood Oxygenation Level Dependent (BOLD) signal, the mean signal changes in white matter (WM) and cerebrospinal fluid (CSF) were regressed out of each voxel using linear regression. Abrupt sharp changes in the signal (i.e., spikes) that exceeded 5 standard deviations (SD) from the average local signal strength (as assessed in sliding windows) were additionally identified and substituted with the value of the moving average. To directly account for the effect of physiological noise, we applied an additional nuisance elimination approach in a sub-group of participants, for whom we had recordings of ECG (n = 22 in Ligeti, n = 23 in Glass). Specifically, we applied the retrospective image-based correction (RETROICOR; Glover et al., 2000) method to regress out the contribution of the cardiac cycle to the BOLD signal at the level of each parcel (Payzan-LeNestour et al., 2013). This was achieved by using second order Fourier models of the phase of the cardiac cycle as four nuisance regressors. Analyses using these sub-set of cleaned data yielded similar results, maintaining the statistical significance of the whole-group effects reported in our paper ($p < 0.05$ for all reported effects). This is despite the reduction in the number of subjects.

Extraction of dynamic common activation (DCA) index within large scale networks. Fig. 1 summarizes the analysis approach for estimating the dynamic fluctuations in the common neural representations within distinct functional networks. The analysis pipeline included the extraction and normalization of BOLD signals from pre-defined parcels (Fig. 1a–b), calculation of a DCA index at the level of parcels (Fig. 1c) and then at the level of 10 large-scale networks of DCA (hereafter termed network-DCA; Fig. 1d–e). The resulting network-DCA could be then linked to continuous indices of the common listening experience (Fig. 1f). The details of each processing step are provided below:

(1) *Parcellation.* We used a whole brain functional parcellation that was generated based on an independent fMRI data set and partitioned the gray matter voxels into 400 non-overlapping parcels (Fig. S4a). This is basically a dimension reduction step, which allows for using clusters rather than voxels for the calculation of DCA and for the subsequent extraction of large-scale DCA networks as described below in this section. The parcels, which covered the entire gray matter in a non-overlapping fashion, were generated by clustering neighboring voxels based on time series similarity. This procedure was performed on an independent fMRI data set, acquired from a group of 72 participants who viewed a five-minute-long anger-provoking scene from the film "Avenge but One of My Two Eyes" (Mograbi, 2005). Specifically, an *iClust* algorithm (Slonim et al., 2005) was used to cluster the voxels based on the mean Pearson correlation between each pair across participants. It was applied separately to the left and right hemispheres to ensure that homologous interhemispheric regions were separated. The obtained parcels were used as the regions of interest for the subsequent analyses. To further enhance data quality, parcels with a signal to noise ratio lower than 1 SD than the overall estimated signal to noise ratio were identified and removed from further analysis. This resulted in the elimination of 68 parcels (Fig. S4b).

(2) *Signal extraction and normalization.* For each subject and listening session, the parcel's time series was obtained by averaging the BOLD signal across all voxels of each parcel at each time point. The signal from each parcel was then normalized (z-scored) in relation to a 24 s rest period prior to music presentation (i.e., baseline) by applying the following transformation (Eq. (1)):

$$X_z(p,t) = \frac{X(p,t) - \overline{X}_{base}(p)}{S_{base}(p)} \tag{1}$$

Where $x(p,t)$ is the BOLD signal intensity of parcel p at time point t of music presentation, $\overline{X}_{base}(p)$ and $S_{base}(p)$ are the average and standard deviation of the BOLD signal in parcel p during baseline, respectively.

(3) *DCA calculation.* In order to estimate the dynamics of common group activation, we applied a novel index, entitled DCA. This continuous indexing approach is based on a simple t-statistic, applied on the set of normalized BOLD values in each time point, across subjects. The DCA is defined as (Eq. (2)):

$$\mathrm{DCA}(p,t) = \frac{\overline{X_z}(p,t) - \mu_0}{S(p,t)/\sqrt{n}} \tag{2}$$

Where $\overline{X_z}(p,t)$ is the sample mean (across subjects) of normalized BOLD signal in parcel p, at time point t, μ_0 is the population mean (assumed to be zero under the null hypothesis of zero change in group activation), $S(p,t)$ is the estimate of the population's standard deviation of normalized BOLD signal in parcel p and time point t, and n is the sample size. This measurement, which is inspired from the reverse inference approach for inter-subject correlation (Hasson et al., 2004), summarizes the activation across the entire group by taking into consideration both the average and variability around the mean signal across subjects. This measure is thus sensitive to the extent of similarity in activity across the group, while controlling for the effect of outliers. The result of this procedure is a time course that represents the cohesiveness in group activation at the resolution of fMRI acquisition that can be further associated with other continuous measures, such as behavioral reports. We preferred this indexing approach over the ISC approach (Hasson et al., 2004; Nummenmaa et al., 2012) for depicting collective activation patterns since it can be extracted per time point and is thus more sensitive to transient moments of group behavior, even when they sparsely occur during listening. ISC, on the other hand, requires well more than one time point for its estimation (~10; Nummenmaa et al., 2012). Additionally, unlike in the case of correlations, this index preserves the original activation or deactivation pattern. In ISC, on the other hand, joint decreases or increases in activation may similarly be represented as positive values (see Fig. S5). These mentioned benefits of the DCA, along with a comparison to a standard two-level approach, are demonstrated using synthetic data in Fig. S5. The importance of temporal correspondence across participants for DCA performance is demonstrated using permutation testing in Fig. S6.

(4) *Clustering of parcels based on DCA.* Having depicted the DCA within the pre-defined parcels, we next turned to apply a data-driven approach to portray how the DCA within these regional parcels organizes in large scale networks. We applied the *iclust* clustering

algorithm (Slonim et al., 2005) to segregate the parcels into ten non-overlapping clusters based on the functional similarity of their DCA. This algorithm searches for a partition, based on a predefined number of clusters, which maximizes the homogeneity (i.e. intra-cluster similarity) within each cluster. Since the iClust algorithm is based on iterative optimization of an initial randomly defined partition, the algorithm was run 100 times and the final optimized partition that yielded the maximal average homogeneity out of the 100 runs was selected. For similarity measure between parcels, we used the Pearson correlation between the parcel's DCA time courses throughout listening, calculated separately per listening session (Ligeti or Glass) and averaged over both sessions. As every clustering algorithm requires to a-priori set the number of clusters, here we heuristically set the number of clusters to 10, based on a well cited paper that found ten reproducible resting state networks (Damoiseaux et al., 2006).

(5) *Network-DCA calculation.* The clustering algorithm segregated the whole brain into distinct networks - fairly homogenous groups of brain regions that present similar temporal patterns of DCA. Such clustering allowed us to inspect the data at the system level - moving from segregated parcels into large-scale networks. Therefore, a network-DCA index was calculated separately per cluster as the averaged DCA time-course over all parcels in that particular cluster. The resulting network-DCA time courses were used for subsequent analyses.

Linking network-DCA patterns to continuous indices of the musical experience. To assess how the network-DCA is related to different indices of the common musical experience, one-level multiple regression analyses were applied. In these analyses, the continuous behavioral reports or musical features that were described above in sections Musical measuresand Behavioral measures (containing six or two different time series, respectively) were used as predictors for the network-DCA time-series. Applying a one-level regression analysis on the continuous group data precluded the use of standard parametric approaches to test the statistical significance of the regression coefficients given the temporal dependence between subsequent samples. To address this issue, we adapted the bootstrap (Efron's) approach (Lunneborg, 1985) for reconstructing the distribution of the regression coefficients within the population and deducing from its dispersion the statistical significance of the observed coefficient. For further details, see supplementary materials.

To note, in all analyses, the first and last 30 s recorded during music listening were excluded to allow for signal stabilization and to avoid the non-reliable responses associated with the beginning or ending of music presentation as suggested by (Schubert, 2013). To allow for comparison with the fMRI data, the time series of musical and behavioral data that were used as regressors were initially convolved with a canonical double-gamma hemodynamic response function (HRF) and downsampled into 1/3 Hz. Further, to enable generalization across musical pieces (external validity), only effects that were found in response to both pieces were reported. This restriction was motivated by our aim to unveil a principle neural correlate of common musical emotions, surpassing particular musical exemplars. Thus, effects that were evident in response to just one piece were regarded as music-specific and were not pursued here. Finally, we adjusted for multiplicity over each line of investigation across the two musical pieces by controlling the false discovery rate (FDR) at a level of 0.05 using the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995).

Effect of music-expertise. To examine the effect that prior musical training has on the common representation of the emotional experience, DCA was separately extracted for the high- and low- musical experience groups (see details in Table S4). The distinction between the groups was made based on a cut-off of 5 years of experience with music playing. To highlight group-specific effects, we applied the same one-level multiple regression analysis as described above (with the same predictors and statistical inference approach) on each of the resulting normalized DCA time courses of the two distinct groups. To further compare between the groups' regression coefficients, bootstrapping procedure was applied. This procedure included the assessment of the percentile location of the real observed value (i.e., difference between regression coefficients of the two groups) in relation to a null distribution of such pairwise group comparison. The null distribution was reconstructed by repeating 5000 times the same pipeline of analysis that yielded the observed data, with the important exception that the subjects-assignment into the different groups was randomly shuffled.

Mediation analysis. To examine the contribution of a certain musical feature to a discovered link between the DCA and a behavioral index, mediation analysis was applied. Using the INDIRECT procedure for SPSS (Preacher and Hayes, 2008), a standard three-variable path model with the time series of behavioral ratings, musical features and DCA was used. The indirect effect was considered to be significant if its 95% bootstrap confidence interval (based on 10,000 iterations) did not include zero at $p = 0.05$. To minimize the dependency between the consecutive time series that were sampled at a rate of 0.33 Hz, the data used for these analyses was down sampled by a factor of three.

Results

Emotional experience

The overall tone of the emotional experience elicited by each piece was characterized using the GEMS-45 questionnaire (Zentner et al., 2008), which includes 45 labels that reflect musically induced emotions. Fig. 2b presents, via font size, the relative intensity of the emotions that were reported to be experienced during the listening to each of the pieces. The most commonly reported labels for Ligeti's piece were “tense” and “impatient” (4 out of 5 in median, corresponding to the category of high intensity). On the other hand, the most commonly reported labels for Glass' piece were “tender” and “calm” (3.5 and 4 out of 5 in median, corresponding to the category of high intensity). This depiction illustrates the qualitative difference in the overall affective tone of each distinct piece.

The dynamic aspect of the subjective musical emotional experience was characterized by obtaining continuous ratings on the scales of valence and arousal during a second listening session outside the scanner. Fig. 2c depicts the temporal pattern of the mean and standard errors of the reliable continuous ratings on the scales of valence and arousal (Glass, $n = 36$; Ligeti, $n = 37$). This depiction reveals that the musical pieces elicited qualitatively different affective experiences with a distinct temporal pattern; a negatively valenced and more arousing experience for the piece by Ligeti, and a positively valenced experience with more variations in arousal for the piece by Glass. Indeed, the Glass piece was rated overall as more pleasant (i. e, positively valenced) and less arousing than the Ligeti piece (paired t-test, valence: $t(34) = 8.7$, $p < 0.001$; arousal: $t(34) = -2.25$, $p = 0.03$). This indicates that the two chosen pieces sufficiently cover the two-dimensional affective space eliciting both positive and negative arousal and valence.

Assessment of the ISC across reliable participants' ratings further verified that that the patterns of subjective ratings were reproducible across the different subjects of this sample for both musical pieces (single sample t-test of Fisher normalized ISC: Glass - valence: mean ISC $r = 0.44$, $t(35) = 6.8$, arousal: mean ISC $r = 0.47$, $t(35) = 7.88$; Ligeti - valence: mean ISC $r = 0.36$, $t(36) = 5.9$, arousal: mean ISC $r = 0.56$, $t(36) = 12.66$; $p < 0.001$ for all).

Networks of common brain activation during music listening

We applied a data driven approach to segregate the DCA data into ten distinct functional networks (mean homogeneity = 0.483;

Fig. 1d–e). The spatial configurations of each of the clustered networks and their corresponding homogeneity values for both listening sessions are depicted in Fig. 3 and in Fig. S1. Remarkably, many of the data-driven clusters of group activation bear resemblance to the well-established resting state networks (Damoiseaux et al., 2006; Yeo et al., 2011). Notably, one of the clustered networks (cluster 10) comprised most of the structures considered to be part of the *limbic network*, such as the amygdala, hippocampus, PHG and OFC and para-limbic regions such as the temporal pole (hereby termed the limbic network; Kober et al., 2008; Yeo et al., 2011; see Table S1 for detailed anatomical information). Additional networks included: (1) *lateralized fronto-parietal networks* (left and right; clusters 7 and 9, respectively; Yeo et al., 2011), encompassing frontal and parietal regions, such as the inferior frontal gyrus (IFG), the premotor cortex (PMC) and the inferior parietal lobule (IPL). The right lateralized network included additional structures such as the bilateral anterior insula and dorsal ACC, considered part of the salience network (Bressler and Menon, 2010); (2) The so-called *default mode* network (Bressler and Menon, 2010), encompassing midline cortical and lateral parietal structures (cluster 8); (3) Symmetric cortical sensory and somato-motor networks (Yeo et al., 2011): visual (cluster 2), auditory (cluster 3), dorsal somato-motor (cluster 1) and ventral somato-motor (clusters 4) (4) *Sub-cortical areas*, encompassing the *basal-ganglia and thalamus* in one network (cluster 6) and the *cerebellum, mid-brain and brainstem* in another (cluster 5). The later cerebellar brain-stem network was excluded from further analyses out of concern that it may be highly susceptible to physiological noise (Boubela et al., 2013).

Common limbic dynamics correspond to the continuous report of musical emotional experience

We next sought to identify the networks that their DCA pattern corresponds with the reported emotional experience. We thus used one-level multiple regression analysis to identify the networks in which the DCA was significantly explained by the continuous behavioral reports during both listening sessions. We first used the average reported valence and arousal as independent explanatory variables, corresponding with the circumplex model of emotion, positing that emotions are distributed in a two-dimensional orthogonal circular space (Russell, 1980). Surprisingly, no network was consistently explained by valence and arousal for both listening sessions (Fig. S2). We therefore examined an alternative representation of the emotional space, corresponding with the vector model (Bradley et al., 2001). This model suggests that the arousal dimension best distinguishes experiences along the valence dimension - becoming more pronounced as activation increases. We therefore extracted two separate indices for valence, which were categorically distinguished based on the concurrently reported arousal level - low or high (i.e. values below or above zero; Fig. 4a). Using these Arousal-gated Valence Indices (AVI), we found that mean fluctuations in valence during moments of *high* arousal (high-AVI) significantly predicted the mean DCA within the limbic network in response to both musical pieces (Fig. 4b; Ligeti: $B = 0.24$, $95\%CI = 0.08$ to 0.42, $t_{(bootstrap)} = 2.83$, $p = 0.002$; Glass: $B = 0.24$, $95\%CI = -0.32$ to -0.08, $t_{(bootstrap)} = -3.18$, $p = 0.0007$). The index of valence under *low* arousal (low-AVI) fell short in predicting any of the network DCA in a consistent manner (Fig. 4b).

Limbic network dynamics relate to changes in the temporal features of music

We next inquired whether the common limbic activation could be explained by a set of music attributes: loudness, pitch-height, tempo, pitch range, beat strength and musical surprises (see Musical measures section, supplementary materials and Fig. S3). We thus performed multiple regression analysis of the limbic-DCA using a continuous depiction of the six extracted musical components as explanatory variables. The DCA within the limbic network was significantly explained by the component of beat strength in Ligeti ($B = 0.3$, $95\%CI = 0.18$ to 0.45, $t_{(bootstrap)} = 4.47$, $p < 0.0001$) and tempo in Glass ($B = -0.34$, $95\%CI = -0.52$ to -0.1, $t_{(bootstrap)} = -3.94$; $p < 0.0001$; FDR-corrected; Fig. 5).

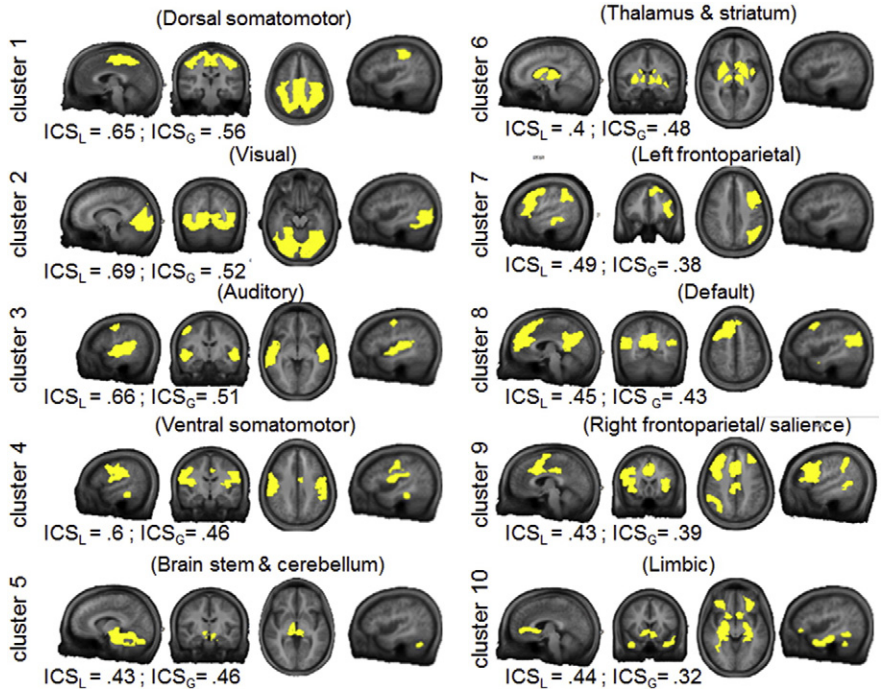

Fig. 3. Spatial distribution of the 10 data-driven extracted networks of the DCA index. The configuration of each network is separately depicted onto MRI-T1 images that were normalized into Talairach space and averaged across subjects. Mean intra-cluster similarity (ICS) is denoted per cluster and each listening session; Ligeti (ICS_L) and Glass (ICS_G). The assigned names of the networks were provided in parentheses based on their common names in the literature. This nomenclature should not be taken to mean that the extracted networks exactly correspond with those reported in the literature nor regarding their functionality.

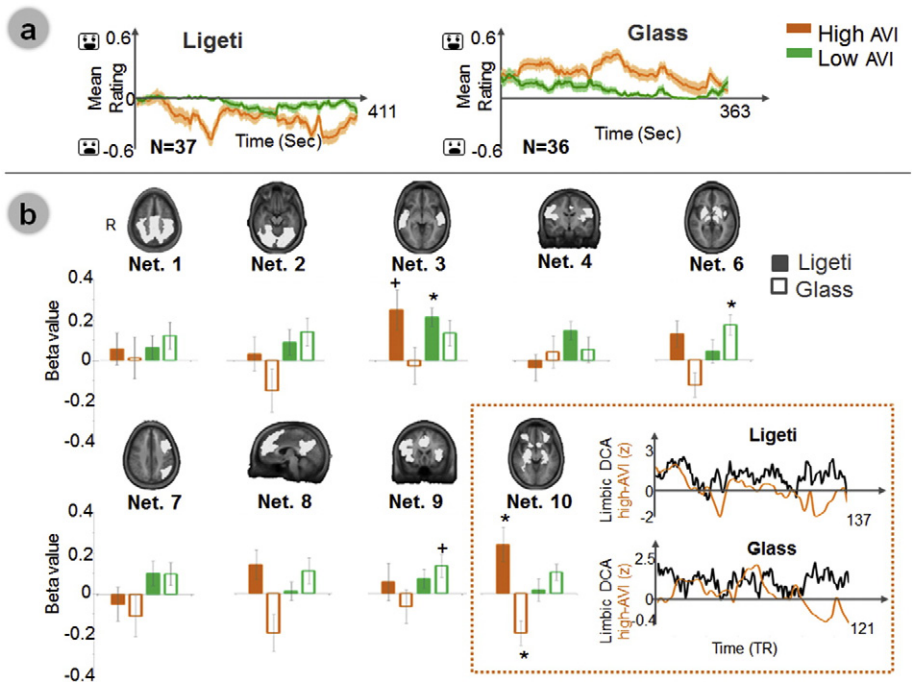

Fig. 4. DCA and the common reported experience. (a) Arousal- dependent valence index (AVI), corresponding to fluctuations in valence when arousal was either above (high-AVI, orange) or below (low-AVI, green) zero. Thickness of shading represents 1 deviation from the mean (S.E.M). (b) DCA regression coefficients for high-AVI and low-AVI per network and musical context. Inset. For both musical pieces, the DCA within network 10 (i.e. limbic-DCA, black line) was associated with the mean high-AVI ratings (orange line). The time series are presented without the opening and ending 30 s of music presentation, which were removed from all analyses to account for nonspecific responses as noted in (Schubert, 2013). Bars ±1 SEM [Reconstructed by bootstrapping ($n_{rand} = 5000$)]. $^{*}p < 0.05$, $^{+}p < 0.06$, FDR corrected. Net. = Network.

Searching for similar effects within other networks, we found only the auditory DCA to be consistently associated with the musical surprises during both listening sessions ($p < 0.05$; FDR corrected; see Table S2 for details).

Connecting the dots: the temporal features of music mediate common limbic-emotion association

The demonstrated limbic sensitivity to both affect and variations in temporal information in music raise the possibility that the association between the limbic-DCA and ongoing reported experiences is mediated by its sensitivity to the temporal aspects of music. To test this, we performed a separate mediation analysis (Preacher and Hayes, 2008; Gilam et al., 2015; Lin et al., 2015) for each musical piece. A significant indirect path between the limbic-DCA and the mean high-AVI was mediated by fluctuations in beat strength for Ligeti (indirect effect = 0.27**, 95% CI = 0.07 to 0.53; Fig. 6a) and tempo for Glass (indirect effect = −0.3*, 95% CI = −0.59 to −0.11; Fig. 6b).

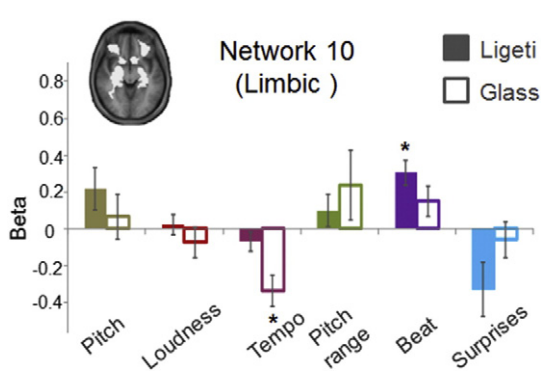

Fig. 5. Regression of Limbic-DCA with musical features. DCA regression coefficient depicted per musical feature and musical piece for network 10 (i.e., limbic). The DCA within the limbic network was associated with tempo for Glass and beat strength for Ligeti. Bars ±1 SEM [Reconstructed by bootstrapping ($n_{rand} = 5000$)]. $^{*}p < 0.05$, FDR corrected.

The effect of musical expertise on the relation between DCA and experience

Contrary to our initial hypothesis, none of the networks encompassing regions considered part of the mirror system (i.e., fronto-parietal networks) were found to be associated with the common emotional experience. We thus exploited the natural variability of our sample in terms of their musical experience and tested whether the common sensitivity to affective information within these networks is more pronounced among a group of individuals with prior musical training (Overy and Molnar-Szakacs, 2009). Participants were divided based on their music playing experience into two groups of high musical experience (>5 years of musical training) and low musical experience (see details in sections Participants & Effect of music-expertise). Multiple regression analyses revealed that the DCA was consistently and significantly associated with the common high-AVI within the default-, left fronto-parietal- and right fronto-parietal-salience networks (i.e., clusters 8, 7 and 9) for both pieces, but only among the groups of listeners with high musical experience (Fig. 7). The implied divergence between groups in their 'brain-behavior' association pattern was further tested by using a permutation based approach. This analysis revealed that the chances of obtaining the observed difference between the groups when they are randomly assigned were lower than 5% for the left fronto-parietal network (Ligeti: $\beta_{diff} = 0.31$, $p = 0.047$; Glass: $\beta_{diff} = -0.35$, $p = 0.042$, one tailed). No such significant difference was found for the additional networks (default mode network: Glass: $p = 0.23$, Ligeti: $p = 0.06$; right fronto-parietal-salience: Glass: $p = 0.1$, Ligeti: $p = 0.1$, one tailed).

Conversely, both groups of high- and low- musical experience showed similar and significant associations between the limbic-DCA and behavioral reports (Fig. 7) as well as between the limbic-DCA and

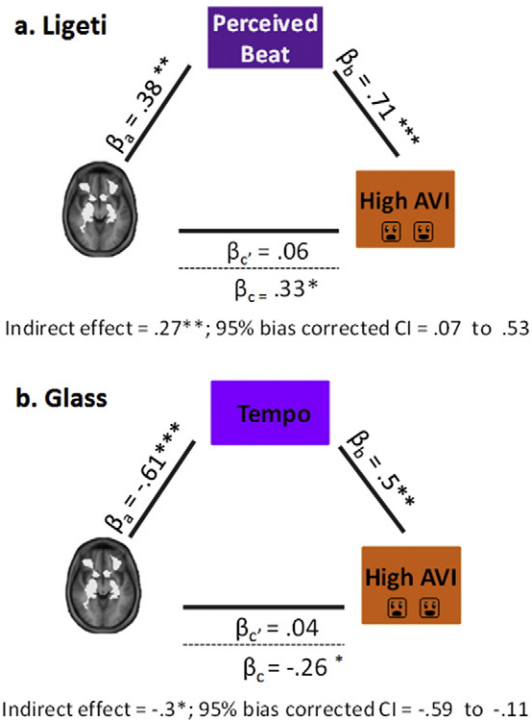

Fig. 6. Models of the relationship between DCA, musical features and the reported musical emotional experience. The illustrated mediation model depicts a significant indirect path from Limbic-DCA to reported experience of valence under high arousal through the processing of (a) beat strength in Ligeti and (b) tempo in Glass. These timing related musical features significantly mediated the relation between limbic activation and reported behavior. β values are shown next to the arrows, indicating each link in the analysis. *p < 0.05; **p < 0.01; one tailed. CI = confidence interval.

the musical indices (i.e., beat strength for *Ligeti*: $\beta = 0.42$; $t_{(bootstrap)} = 6.04$; $p < 0.001$; $\beta = 0.33$; $t_{(bootstrap)} = 4.82$; $p < 0.001$; Tempo for *Glass*: $\beta = -0.34$; $t_{(bootstrap)} = -3.02$; $p = 0.003$; $\beta = -0.55$; $t_{(bootstrap)} = -5.16$; $p < 0.001$, respectively). This strengthens the notion of the commonality of limbic processes that surpasses expert knowledge.

Discussion

The current study examined the inter-personal aspect of music-induced emotions, inquiring if and how affective information in music is commonly shared across the brains of different listeners. To attain our goal, we used a novel 'group-centered' fMRI analysis approach to characterize the common dynamics of distributed brain activity and instances during which the brains of different listeners 'tick' together. We demonstrated that the common group activation (i.e. DCA) within a network of limbic regions corresponded with modulations in both the ongoing emotional experience (Fig. 4) as well as with temporal information in music, namely beat strength and tempo (Fig. 5). Intriguingly, the functional relationship between the musical 'input' and the emotional 'output' was depicted by mediation analysis, revealing that the changes in temporal features of music mediated the common limbic representation of the reported emotional experience (Fig. 6). This mediation result directly links 'behavior, brain and music', offering a mechanistic framework to explain how emotions may be shared through music. An additional layer of processing, uniquely shared among a sub-group of listeners with a high level of music-playing experience, was discovered among a left fronto-parietal network whose major nodes are considered to be part of the 'mirror neuron system' (Fig. 7). This demonstrates how prior experience may shape the way a group of individuals share affective information in music.

Our study delineated a system level organization using a data-driven whole brain approach and characterized the functionality of these revealed networks with regards to music and emotions. In accordance with our prediction, the association between dynamics of common activation and emotions was found for a data-driven network consisting of core limbic regions, such as the amygdala, hippocampus, sgACC and OFC - all previously identified as involved in musical emotions (Frühholz et al., 2014; Blood and Zatorre, 2001; Blood et al., 1999; Chapin et al., 2010; Koelsch et al., 2006; Menon and Levitin, 2005; Trost et al., 2012, cf., Koelsch, 2014). Supporting a system level point of view of emotions (Kober et al., 2008; Raz et al., 2012; Barrett and Satpute, 2013), these neural nodes are known to be functionally

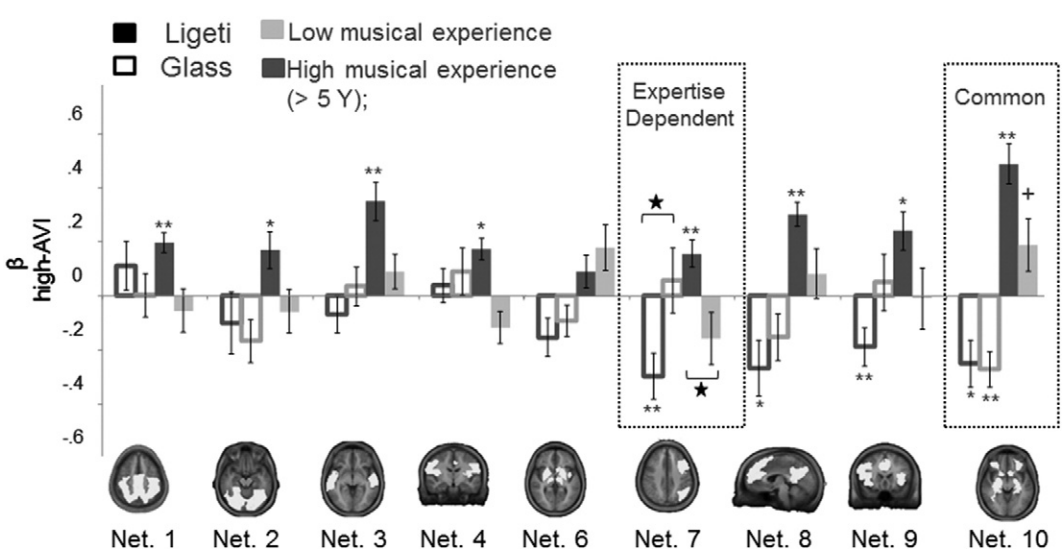

Fig. 7. Effect of musical expertise on the common listening experience. DCA beta coefficients for high-AVI depicted per group (high- and low-musical experience), network and musical piece. The DCA in network 7 (left fronto-parietal) is more strongly associated with the mean high-AVI among the high-experience- than the low-experience group. The DCA in network 10 (limbic) is similarly associated with the mean high-AVI ratings for both groups. Low-experience: N = 20 (Ligeti); N = 15 (Glass); High-Experience: N = 9 (Ligeti); N = 11 (Glass); Bars ±1 SEM [Reconstructed by bootstrapping ($n_{rand} = 5000$)]. *p < 0.05, **p < 0.01, FDR corrected, +p = 0.05. Net. = Network. Stars denote a significant difference between the groups, p = 0.05 (one tailed).

connected (Yeo et al., 2011) and consistently co-activated during emotional stimulation (Kober et al., 2008), as well as within the context of music listening (Menon and Levitin, 2005; Lehne et al., 2013; Koelsch and Skouras, 2013; Salimpoor et al., 2013). Importantly, we extend the previous findings to include a system level group-centered perspective - by pointing to the common fluctuations of limbic network activation across listeners.

We further found that these common neural modulations correspond with the average emotional experience. This is in accordance with a recent fMRI study in which fluctuations in ISC (estimated using a sliding window) in regions related to emotional processes were correlated with the participants' reported valence during emotional cinematic episodes (Nummenmaa et al., 2012). The authors suggested that such inter-subject coupling may provide the neural platform for emotion sharing among individuals. Accordingly, our findings may suggest that the online common representation of musical emotions via limbic circuitry may serve as a basis for the suggested role of music in the communication of emotional meaning and inter-group bonding.

But what kind of musical information does the limbic system commonly represent? Our findings suggest that temporal information in music plays an important mediating role in such common limbic representations of affect in music. These findings correspond with recent fMRI findings that limbic areas, such as the left amygdala, hippocampus and OFC, are sensitive to rhythmic information in music, namely pulse clarity (Alluri et al., 2012), expressive variations in tempo (and loudness; Chapin et al., 2010) and beat regularity (Grahn and Rowe, 2013).

So, why do temporal variations play a role in the common affective experience? Variations in the temporal aspects of music may significantly affect the predictability of the subsequent musical events (Chapin et al., 2010), thereby determining the ability to synchronize to the musical pulse and each other, possibly via predictive coding (Chapin et al., 2010; Vuust and Witek, 2014). This further relates to well established theories regarding the important role of musical expectations and their violations in musical emotions (Meyer, 1956; Huron, 2006). The link between beat strength and the common experience found in our study may be further viewed within a framework that assigns rhythmic entrainment an important role in inducing musical emotions (Juslin, 2013; Trost and Vuilleumier, 2013), possibly affecting social facilitation (Cross, 2014) and pleasure (Vuust and Witek, 2014). More directly relating to the common experience, the joint entrainment of different individuals to a regularly perceived beat was recently suggested to be important, even developmentally crucial, in enabling shared experiences between individuals (Cross, 2014; Tarr et al., 2014; Feldman, 2007). Finally, our findings are consistent with the predictions of the shared affective motion experience (SAME) model (Overy and Molnar-Szakacs, 2009), suggesting that temporal features in music, which embody the core elements of movement within the music, should be similarly represented by all individuals, even the musically untrained.

Contrary to our expectation, the common activation within a left fronto-parietal network that includes major nodes of the mirror-neuron system; IFG, PMC and IPL, was associated with the reported experience only in a sub-group of participants with a high level of musical experience (>5 years). This is in line with findings from previous fMRI studies that reported enhanced sensitivity to emotionality in music among similar fronto-parietal regions (Chapin et al., 2010; Park et al., 2014). Interestingly, as in our case, these studies found that this sensitivity was more pronounced among musically experienced relative to inexperienced participants. Such an expertise-dependent effect is also consistent with the predictions of the SAME model stating the importance of the 'mirror neuron system' in the "sharing of a musical experience between agents and listeners" (Overy and Molnar-Szakacs, 2009, p.1). The model further suggests that this depends on the process of mirroring through an internal representation of the motor gestures and intentions of the performer, which is augmented in people with prior musical experience. However, one should bear in mind that mirroring is just one of several possible mechanisms that underlie the observed effect for expertise, as some of the nodes included in the fronto-parietal network have been implicated in several other cognitive functions such as auditory attention and working memory (Gaab and Schlaug, 2003), speech comprehension (Pulvermüller and Fadiga, 2010) and cognitive control (Vincent et al., 2008). Interestingly, musical training has been found to enhance these high-level auditory functions, such as auditory working memory and has been associated with heightened recruitment of related brain regions (Gaab and Schlaug, 2003; Baumann et al., 2007). Accordingly, our observation may support the idea that experienced listeners share an additional level of representation of affective information in music, possibly by relying on more elaborated auditory or auditory-motor mappings of affective gestures conveyed by musical patterns. Since this study was not originally designed to examine the effect of musical experience and therefore relied on rather small heterogeneous groups, further studies should be conducted to elaborate on this initial finding and unveil its underlying mechanism.

The findings of this study further elucidate the manner by which ongoing musical emotions are commonly represented. Specifically, common activation was explained by valence *under high arousal*, suggesting a more pronounced difference between representations of pleasant and unpleasant states in moments of *high arousal* (Bradley et al., 2001). This is in line with previous studies, suggesting a differential fMRI (Trost et al., 2012) or EEG (Sammler et al., 2007) brain patterns as a function of pleasantness in states of high arousal induced by music. Such pronounced differences between positive and negative valence under high arousal have also been shown in psychophysical experiments using affective pictures, implying a V-shape relation between these dimensions, whereby valence intensifies with increasing arousal (Bradley et al., 2001; Cuthbert et al., 1996; Simola et al., 2015). The use of two musical contexts with distinct affective tones, positive and negative (Glass or Ligeti, respectively), surprisingly revealed that the nature of association between common activation and the reported experience was opposite for each piece (a positive association for Ligeti and a negative for Glass; Fig. 4b). This could imply that the absolute rather than the relative value of the valence of the experience is encoded. Such a v-shaped relation, whereby activation is manipulated by the intensity of valence, be it positive or negative, accords with neuroimaging studies that have shown a similar trend of processing within the amygdala (Gerber et al., 2008), OFC (Lewis et al., 2007) and hypothalamus (Viinikainen et al., 2010) in response to affective stimuli. This form of processing may explain the seemingly conflicting evidence for amygdala and hippocampus responsiveness to joyful or pleasant music in some studies and sad or unpleasant music in other studies (cf. Frühholz et al., 2014). Furthermore, when considering a v-shaped processing mode, it appears that the DCA *decreases* with increased intensity of (absolute) valence under high arousal. This unexpected pattern of inverse relation corresponds with previous findings within the realm of musical emotions pointing, for example, to deactivation within the amygdala and hippocampus with increasing levels of pleasantness (Blood and Zatorre, 2001; Koelsch et al., 2006) or in the OFC and sgACC for increasing levels of unpleasantness (Blood et al., 1999). Note that a phenomenon of deactivation rather than augmented activation may be more common than previously reported due to the abundant use of contrasts between two conditions in imaging studies of musical emotions. Such contrasts tend to focus on the difference between activation trends, without considering changes from baseline, which may hold valuable information regarding the importance of deactivation vs. activation (see example in Koelsch et al., 2006). It should also be mentioned that by inspecting the limbic-DCA and behavior time courses (Fig. 4b), it is possible to detect local dynamics in the pattern of their association, which may indicate a transient divergence from the general pattern of negative association. However, the quantification and interpretation of these local temporal dynamics is beyond the scope of the paper. Lastly, similar trends of association with limbic-DCA were found for beat in the Ligeti and tempo in the Glass

sample, and can be explained in a similar manner. This resonates with the idea that temporal information in music is an important mediator of the emotional experience in music (Eerola, 2011; Trost and Vuilleumier, 2013; Vuust and Witek, 2014), likely by affecting the intensity of the experience in a given affective context.

The findings of this study should be viewed within the context of its strengths and limitations. As this study focused on the most common aspect of musical emotions across different individuals and distinct musical contexts, the issue of individual differences and unique responses to specific musical contexts, or features is beyond the scope of this paper and calls for further research. Furthermore, the use of full-length musical pieces to depict the emerging activation dynamics prevented the use of a large number of musical pieces. Although we sampled two distinct musical pieces and focused on effects that generalize across both pieces, these findings should be affirmed and expanded in future studies using musical pieces from additional genres and with different affective tones than those used here. Finally, taking a system level perspective, this study focused on activation within distributed networks of regions, thus excluding functional effects that are highly modular and limited to a particular region or sub-region (Overy and Molnar-Szakacs, 2009; Ball et al., 2007).

Conclusions

Using a novel analytic approach for capturing the universal nature of the unfolding affective experience that occurs when listening to music, this study offers a new avenue for investigating the communicative aspects of musical emotions. Our findings highlight a multi-layered processing of affective information in music, one that could be attributed, at the most common level, to temporal variations in music, and at a more differential level to musical training experience. This implies a distinction between a core process, common among individuals and rooted in the limbic network, and a more elaborated process that relies on prior experience with music and is governed by a higher order fronto-parietal network. Future studies could use our group-centered approach to distinguish between normal and abnormal representation of emotions, thus guiding new brain-based interventions for neuropsychiatry.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.07.002.

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