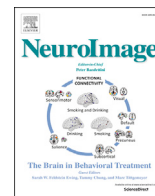




Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Dynamic intersubject neural synchronization reflects affective responses to sad music

Matthew E. Sachs^{a,b,*}, Assal Habibi^a, Antonio Damasio^a, Jonas T. Kaplan^a

^a Brain and Creativity Institute, University of Southern California, 3620A McClintock Avenue, Los Angeles, CA, 90089-2921, USA

^b Center for Science and Society, Columbia University in the City of New York, 1180 Amsterdam Avenue, New York, NY, 10027, USA

ARTICLE INFO

Keywords:

Naturalistic stimuli
Emotion
Music
Enjoyment
Intersubject synchronization

ABSTRACT

Psychological theories of emotion often highlight the dynamic quality of the affective experience, yet neuroimaging studies of affect have traditionally relied on static stimuli that lack ecological validity. Consequently, the brain regions that represent emotions and feelings as they unfold remain unclear. Recently, dynamic, model-free analytical techniques have been employed with naturalistic stimuli to better capture time-varying patterns of activity in the brain; yet, few studies have focused on relating these patterns to changes in subjective feelings. Here, we address this gap, using intersubject correlation and phase synchronization to assess how stimulus-driven changes in brain activity and connectivity are related to two aspects of emotional experience: emotional intensity and enjoyment. During fMRI scanning, healthy volunteers listened to a full-length piece of music selected to induce sadness. After scanning, participants listened to the piece twice while simultaneously rating the intensity of felt sadness or felt enjoyment. Activity in the auditory cortex, insula, and inferior frontal gyrus was significantly synchronized across participants. Synchronization in auditory, visual, and prefrontal regions was significantly greater in participants with higher measures of a subscale of trait empathy related to feeling emotions in response to music. When assessed dynamically, continuous enjoyment ratings positively predicted a moment-to-moment measure of intersubject synchronization in auditory, default mode, and striatal networks, as well as the orbitofrontal cortex, whereas sadness predicted intersubject synchronization in limbic and striatal networks. The results suggest that stimulus-driven patterns of neural communication in emotional processing and high-level cortical regions carry meaningful information with regards to our feeling in response to a naturalistic stimulus.

1. Introduction

Emotions and feeling enrich and color our everyday lives. They are also a key element of human survival in that they motivate adaptive behaviors and aid in homeostatic regulation (Damasio, 1999). Over the last several decades, neuroscientists have provided evidence that numerous brain regions that serve a variety of functions not exclusively related to affect, are involved in representing a diverse range of emotional states (Lindquist et al., 2012). This has led to the hypothesis that the resplendent tapestry of emotions that we experience emerge from communication between a system of brain regions that tend to function together, such as the amygdala, ventral striatum, insula, anterior cingulate cortex (ACC), thalamus, hypothalamus, and the orbitofrontal cortex (OFC) as well as regions typically thought to be part of the default mode network (DMN), i.e., the posterior cingulate and medial prefrontal cortex (MPFC; Kober et al., 2008). The traditional neuroimaging studies

that inform this theory tend to use static affective stimuli, such as pictures, faces, smells, sounds, and short film or music clips. Because of this, our understanding of the patterns of co-functioning and neural communication that generate various aspects of affect, such as the recognition of emotion, the subjective experience of that emotion, and subsequent feelings of pleasure or displeasure, is limited.

Music is a useful tool for answering key questions related to specific aspects of emotions and feelings. While basic emotions, such as happiness, sadness, fear, and anger, can be perceived within musical structure (Balkwill and Thompson, 1999; Fritz et al., 2009), because of its temporal nature, music can also induce a wide-range of feelings, from the everyday to the aesthetic (Zentner et al., 2008), that morph and evolve over time (Brattico et al., 2013). Indeed, neuroimaging studies that evaluate brain activity associated with music-evoked emotions have shown a high degree of overlap between the regions that respond to musical emotions and those that respond to everyday emotions (Koelsch, 2014), including

* Corresponding author. Center for Science and Society, Columbia University in the City of New York, 1180 Amsterdam Avenue, New York, NY, 10027, USA.
E-mail address: ms5924@columbia.edu (M.E. Sachs).

<https://doi.org/10.1016/j.neuroimage.2019.116512>

Received 19 June 2019; Received in revised form 14 November 2019; Accepted 31 December 2019

Available online xxx

1053-8119/© 2020 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

the amygdala, caudate, ventral striatum, cingulate, orbitofrontal cortex, as well as Heschl's and superior temporal gyri in the auditory cortex.

Moreover, music can convey an emotion that is, at times, distinct from the emotion that the listener experiences (Gabrielsson, 2001). Emotional responses to sad music provide an intuitive and elegant exhibition of this disconnect. Many people who listen to sad music report that while the piece of music is clearly conveying negative emotions, they do not experience such negative emotions while listening and, in fact, often experience positive emotions such as enjoyment (Sachs et al., 2015). While not everyone enjoys listening to sad music, recent evidence suggests that personality traits such as empathy may modulate one's emotional response to negative valence when expressed through music (Eerola et al., 2016; Vuoskoski et al., 2012). This raises the question of whether separate neural mechanisms are engaged during the perception of an emotion, the experience of that emotion, and the overall hedonic experience (Brattico et al., 2013). Enjoyment of art associated with positive vs. negative emotions has been shown to activate different brain regions (Brattico et al., 2016; Ishizu and Zeki, 2017; McPherson et al., 2016; Wilson-mendenhall et al., 2015). Furthermore, it has been proposed that subjective feelings and intensity of emotional responses involve regions of the brain known for viscerosensory processing, such as the insula, ACC, amygdala, and striatum, whereas enjoyment, pleasure, and aesthetic appreciation involve regions that monitor and integrate cognitive and sensory information, such as the orbitofrontal cortex and posterior cingulate (Brattico et al., 2013). However, this hypothesis has not yet been empirically tested. Assessing the brain regions that are altered in response to full-length pieces of music that convey complex emotions like pleasurable sadness can help unravel the unique role that the spatial and temporal patterns of neural activity serve in representing affective experiences.

One limitation with previous fMRI studies, which may have contributed to this gap in our understanding of emotional responses to music, is that traditional experimental designs typically require time-locked and repeated presentations of mostly static, or relatively short, stimuli in order to model the expected hemodynamic response. While these models provide strong experimental control, the constraints also make it difficult to assess responses to more dynamic stimuli that convey emotions over a longer period of time and are therefore more akin to the types of experiences we have in everyday life, outside of the lab. To gain a more complete picture of the involvement of various brain networks in the neural basis of feelings, it becomes necessary capture the time-varying patterns of the fMRI signal in response to more ecologically-valid stimuli.

Recently, a variety of analytical techniques have been developed that do not impose an expected model on the data and therefore allow neuroscientists to image activity from the brain continuously during the presentation of more realistic and naturalistic stimuli, such as full-length movies and pieces of music. These analyses involve calculating correlations between the neural signal across participants' brains and matching moments of high correlation with events in the stimulus, allowing researchers to link a unified, collective experience to changes in neural signal over time. One such method, termed intersubject correlation (ISC), for instance, involves calculating the correlation in the BOLD signal between all participants one brain parcel at a time (Hasson et al., 2010). The advantage of this approach is that idiosyncratic fluctuations in BOLD signal that are unrelated to the naturalistic stimulus are essentially cancelled out and therefore voxels that show highly correlated activity across people are assumed to be stimulus-driven: no modelling of the BOLD signal according to the onset of some external event is required.

ISC has been used previously to identify neural patterns in response to music (Trost et al., 2015), films (Hasson et al., 2004), and narrative stories (Nummenmaa et al., 2014). The synchronized patterns that emerge have been shown to be time-locked to the events of the stimulus, highly reliable across multiple scanning sessions with different stimuli, and identifiable in brain regions that may not be significantly activated when averaging across participants, as is done with more traditional

neuroimaging procedures (Hasson et al., 2010). It also has been employed to uncover neural differences that may account for the ways that individuals process complex, socioemotional stimuli. For example, by comparing ISC in response to a movie between a cohort of individuals with autism spectrum disorder (ASD) and typically-developed individuals, researchers found that synchronization of activity in primary sensory and associated areas was more variable and less reliable in the ASD group, which may underlie some of atypical socio-emotional behaviors associated with this developmental disorder (Hasson et al., 2009).

While it is often concluded from these types of studies that the regions that show high synchronization in response to a stimulus are somehow involved in its processing, it is still unclear what aspects of the stimulus these patterns are attending to. To begin to understand the meaning behind these synchronized brain patterns, it becomes necessary to identify how these patterns change in tandem with certain aspects of the stimulus. Several methods have been developed for assessing the dynamic quality of synchronization. *Sliding window* ISC, for instance, involves calculating correlations across individuals in short, temporal windows that shift in time by a pre-specified "step" size. What results is a continuous measure, with each point representing the synchronization of a particular voxel or region in that window of time, which can be subsequently correlated with an additional continuous measure that reflects a psychological or behavioral concept of interest. This approach has been used previously to identify time-varying patterns of activity that map onto changes in expressed valence in music over time (Trost et al., 2015). In this study, it was shown that the regions that show high ISC, i.e., the ACC, amygdala, and caudate, were activated by continuous ratings of negative valence in music; that is, as negative emotions increased, so did activation in these subcortical regions. The dynamic method provides a necessary balance between stimulus-dependent and stimulus-free analyses without requiring strong assumptions with regards to the shape, amplitudes, and timescale of the expected neural responses.

One complication with regards to sliding window ISC approach is the choice of appropriate window and step size for analysis. Previous studies have shown that different window sizes have profound effects on the temporal structure of the synchronization patterns (Shakil et al., 2016). An alternative that was recently developed to avoid this issue involves comparing two signals by first statistically separating the instantaneous amplitude from the phasic information with signal processing filters, and then comparing only the phasic component across people at each moment in time (Glerean et al., 2012). Because this method measures intersubject similarity in phasic rather than in correlational terms, it can be calculated at each volume and thus, no averaging across windows is necessary. Instantaneous phase synchronization (ISPS), as it is called, has been shown to be more sensitive than sliding window ISC at revealing synchronization effects (Nummenmaa et al., 2014). For example, in this paper, continuous self-report ratings of valence during the presentation of 45-s narratives was associated with ISPS in the thalamus, anterior cingulate, lateral prefrontal, and orbitofrontal cortices; an association was not found with ratings predicting sliding-window ISC in these regions.

In light of evidence suggesting that the brain is organized into functional networks (Yeo et al., 2011), it is highly likely that the dynamics of feelings are additionally represented by time-varying patterns of communication *between* brain regions (Touroutoglou et al., 2014). Indeed, recent dynamic functional connectivity studies with naturalistic stimuli have shown that connectivity between regions involved in affect, including the insula, putamen, ACC, OFC, amygdala, and striatum, were predicted by changes in affective experience (Raz et al. 2016; Singer et al., 2016). Furthermore, the patterns of communication between regions may reflect separable aspects of affective processing. A recent functional connectivity study showed that attentional resources allocated to emotional stimuli was associated with connections between the dorsal anterior insula and dorsal ACC, whereas momentary experiences of arousal in response to the stimuli were associated with connections

between the ventral anterior insula and ACC (Touroutoglou et al., 2012).

Both dynamic ISC and ISPS can be adapted to assess stimulus-driven inter-regional changes by correlating the signal (or comparing the phasic component of the signal, as is the case with ISPS) of a single participant's brain region with the signal (or phasic component) of other regions across participants (Glerean et al., 2012; Simony et al., 2016). This approach has been shown to more fully remove the effects of intrinsic activity on functional connectivity, as compared to averaging across participants (Kim et al., 2018).

While studies that utilize these data-driven, multivariate methods have clarified the role of specific brain regions in socioemotional processing, few of them that have employed to specifically investigate the dynamic quality of complex feeling states that are likely to emerge in response to music and art. In particular, the brain regions involved in representing the intensity of an emotion as well as the pleasantness or unpleasantness of that experienced emotion, which can be distinct in response to something like music, has yet to be addressed. Answering this question will likely reveal a more profound and nuanced picture of the interactive quality of the human brain as a reflection of fluctuations in mood, motivations, wants, desires, and behaviors.

By specifically using a piece of music is negatively valent and yet enjoyable, as well as model-free analytical techniques, this study aimed to uncover stimulus-driven patterns of neural activity and connectivity that are driven by two related, yet distinct aspects of emotional experience: feelings of sadness and feelings of enjoyment. We first assessed how continuous subjective ratings of emotional experience and enjoyment covary during the presentation of a full-length piece of music that conveys sadness. We then evaluated neural synchronization of brain activity across participants as they are listening to a sad piece of music, using ISC and ISFC, and test how a trait measure of empathy known to be related to emotional responding to music (Kawakami and Katahira, 2015) modulates the resulting ISC maps. This analysis provides a neural explanation for the ways in which sad music is experienced differently across people. We next evaluated the temporal dimension of the musically-driven neural synchronization by calculating intersubject phase synchronization at each moment in time. Continuous ratings of emotional experience were used to assess how changes in intensity of sadness and enjoyment predict time-varying patterns of intra-regional and inter-regional synchronization. To our knowledge, no study to date has assessed how the intensity of feelings of both sadness and enjoyment are related to stimulus-driven patterns of brain activation and connectivity. Based on findings from previous univariate neuroimaging studies (Koelsch, 2014) we predicted that listening to a sad, aesthetically-pleasing piece of music would be associated with neural synchronization of regions within the auditory cortex as well as in regions involved in processing affective stimuli, including the striatum, insula, ACC, and OFC. We further predicted that trait measures of empathy would modulate the patterns of synchronization in these regions, with more empathic people displaying greater ISC in brain regions involved in understanding and resonating with the emotions of others, such as the medial prefrontal cortex (Krämer et al., 2010). Finally, we predicted that self-reported tracking of enjoyment would be associated with time-varying patterns of synchronization within and between networks involved in reward monitoring, reward prediction, and aesthetic judgment, such as the DMN (MPFC, precuneus, posterior cingulate) and the OFC, whereas self-reported tracking of sadness would be associated with time-varying patterns of synchronization within and between networks involved in viscerosensory processing of emotion, such as the striatal (caudate, pallidum, and putamen) and limbic/paralimbic networks (amygdala, cingulate, hippocampus, parahippocampal gyrus, thalamus, and insula; Kober et al. (2008).

2. Methods

2.1. Stimuli selection

To find pieces of music that reliably induced the intended emotion of

sadness, we started by exploring online music streaming sites, such as Spotify and Last.fm, as well as social media sites such as Reddit and Twitter for social tags that included the word "sad" as well as synonyms. We also included a piece of music used in several previous studies to induce feelings of sadness (Eerola et al., 2016; Vuoskoski and Eerola, 2012). As a comparison set, we additionally searched for pieces of music that reliably conveyed happiness, using social tags with the word "happy" and its synonyms. This resulted in a list of 120 pieces (60 sad and 60 happy with a mix of lyrics and non-lyrics). Eight coders then listened to 60-s clips extracted from these pieces and rated whether it conveyed either happiness or sadness. All clips in which 75% (6/8) coders agreed on the intended emotion were then used in an online survey that asked participants to rate how much they enjoyed the clip, what emotion they feel in response to the clip (sadness, happiness, calmness, anxiousness, boredom), and how familiar they were with the clip, using a 5-point Likert scale. The survey was completed by 82 adult participants via Amazon's Mechanical Turk. The final survey included 27 pieces of music, though because we believed that listening to 27 1-min clips of music would have been too cognitively demanding, each participant was only presented with 12 clips selected at random. The number of presentations of each clip was counterbalanced across participants.

Based on the results from the survey, we excluded pieces that were rated as highly familiar, and selected the pieces that had the highest ratings of the intended emotion (sadness or happiness) and low ratings on all other emotions. To avoid any potential confounds associated with semantic information conveyed through the lyrics of a song (Brattico et al., 2011), we additionally decided to only select pieces that were instrumental. This resulted in three pieces of music to be used during neuroimaging: (1) one longer piece that reliably induced sadness without lyrics [*Discovery of the Camp* by Michael Kamen, performed by the London Metropolitan Orchestra, a classical piece written for the HBO miniseries *Band of Brothers* and used in previous studies of music-evoked sadness (Eerola et al., 2016; Vuoskoski and Eerola, 2012)] (2) one shorter piece that reliably induces sadness without lyrics [*Frysta* by Ólafur Arnalds, an ambient piece written for piano and strings], and (3) one piece that reliably induced happiness without lyrics [*Race against the sunset* by Lullatone, a pop song featuring the ukulele and bells]. While the focus of this paper is on the responses to the longer piece of sad music, we collected behavioral and neural responses to this second, shorter sad piece of music in order to be able to validate and assess the generalizability of potential results. Additionally, we collected responses to a piece of happy music so that we assess if similar or distinct patterns of neural synchronization emerge with enjoyment in a happy emotional context. The methods and results presented here, however, focus on responses to the longer, sad piece of music only.

2.2. Pilot behavioral study

To assess the feasibility and reliability of continuous ratings in responses to the three selected pieces, before the commencement of the fMRI portion of the study, an independent group of 51 healthy adult participants were recruited from USC's undergraduate population to participate in a behavioral version of the fMRI paradigm. During this study, participants were instructed to listen attentively to the three full-length pieces described above and to simultaneously monitor changes in their affective experience and report these changes using a fader with a sliding scale. Each participant listened to each piece twice in two separate conditions. In one condition, participants continuously reported the intensity of their felt emotional response, from 0-not at all sad/happy to 10-extremely sad/happy. Participants were only asked to rate the intensity of their feelings of sadness for the pieces that were intended to convey sadness and happiness for the pieces that were intended to convey happiness and never both. In the second condition, participants continuously rated their momentary feelings of enjoyment from 0-not enjoyable to 10-extremely enjoyable. As participants moved the fader, a real-time visualization of their responses was presented on a computer screen via

Psychtoolbox for MATLAB (Kleiner et al., 2007). The order of ratings was counterbalanced across participants. During all music-listening trials, heart rate and skin conductance were continuously monitored and collected using a BIOPAC MP150 system. The results from this pilot study were used to inform and adjust the behavioral paradigm for the fMRI study and were published in two separate papers (Greer et al., 2019; Ma et al., 2019).

2.3. fMRI participant selection

Separate from the pilot study (see above), an independent cohort of adult, right-handed participants ($N = 40$, 21 female, $M_{\text{age}} = 24.1$, $SD = 6.24$) were recruited from the greater Los Angeles community based on responses to the online survey in which they listened to a 60s clip of the three final pieces. Only participants who was not familiar with the pieces of music and reported feeling the intended emotion in response to the clip (either happiness or sadness) were invited to participate in the fMRI portion of the study. All participants had normal hearing and normal or corrected-to-normal vision with no history of neurological or psychiatric disorders.

2.4. fMRI scanning procedure

All data was collected at the University of Southern California Dana and David Dornsife Neuroimaging Center. After participants gave consent, they completed a questionnaire in which they reported their current emotional state using the Positive and Negative Affective Scale (PANAS; Watson et al., 1988).

During scanning, participants listened to full-length recordings of the three pieces of music, the order of which was be counterbalanced across participants. As the music played, participants were instructed to pay attention to the music, to lie as still as possible, and to keep their eyes open and focused on a fixation point continually presented on a screen. An eye-tracking camera was monitored to ensure that the participants were awake and alert during scanning. The auditory stimuli were presented through MR-compatible OPTOACTIVE headphones with noise-cancellation (Optoacoustics). Skin conductance, respiration rate, and pulse were simultaneously recorded during scanning (see *MRI data acquisition* section for additional details).

At the conclusion of each piece, participants were presented with a series of questions on the screen and were instructed to respond using an MRI-safe button box with four buttons. Specifically, participants were asked how much attention they paid to the music, how intense was their emotional reaction to the piece, how much they enjoyed the music, and how familiar they were with the piece. The three pieces were presented in three separate functional runs with a brief rest period between runs. After music listening, a 5-min resting scan was additionally collected.

2.5. Post-scanning continuous ratings

Immediately following scanning, continuous ratings of the intensity of felt emotions and enjoyment were collected while listening to the same pieces of music. We chose to have participants rate their experience with the music outside of the scanner to avoid the influence of the task on the neural responses to the stimuli (Taylor et al., 2003). This data was collected exactly as described above in the pre-fMRI behavioral study. Briefly, all participants listened to each piece twice and continuously rated (1) the intensity of felt sadness or happiness and (2) the intensity of their feelings of enjoyment using a fader connected to a laptop computer. The order of pieces and conditions was completely randomized.

2.6. Survey measures

After the continuous music ratings, participants completed an online survey designed to assess their musical background and experience

(Goldsmith Musical Sophistication Index; Mullensiefen et al., 2014) and general aesthetic responses to music (Aesthetic Experience Scale in Music; Sachs et al., 2016). Additionally, the survey included a trait measure of empathy (Interpersonal Reactivity Index; Davis, 1983), a measure of depressive symptomology and severity (PHQ-9; Martin et al., 2006), and a measure of generalized anxiety disorder severity (GAD-7; Löwe et al., 2008). General enjoyment of sad music was also evaluated using a modified version of the Like Sad Music Scale (Garrido and Schubert, 2013).

2.7. MRI data acquisition

Imaging was conducted using a 3-T Siemens MAGNETOM Trio System with a 32-channel matrix head coil at the Dana and David Dornsife Neuroscience Institute at the University of Southern California. Functional images were acquired using multiband and a gradient echo, echo-planar, $T2^*$ -weighted pulse sequence ($TR = 1000$ ms, $TE = 25$ ms, flip angle = 90° , 64×64 matrix). Forty slices covering the entire brain were acquired with a voxel resolution of $3.0 \times 3.0 \times 3.0$ mm with no interslice gap. A $T1$ -weighted high-resolution ($1 \times 1 \times 1$ mm) image was also obtained using a three-dimensional magnetization-prepared rapid acquisition gradient (MPRAGE) sequence ($TR = 2530$ ms, $TE = 3.09$ ms, flip angle = 10° , 256×256 matrix). Two hundred and eight coronal slices covering the entire brain was acquired with a voxel resolution of $1 \times 1 \times 1$ mm.

During scanning, psychophysiological measures were collected using the BIOPAC MP150 system. Skin conductance responses (SCRs) were acquired with two MRI-compatible electrodes placed on the participants left foot. Heart rate was measured indirectly by recording pulse using the BIOPAC TSD200 pulse plethysmogram transducer, which records the blood volume pulse waveform optically. The pulse transducer was placed on the participant's left index finger. Respiration was measured using BIOPAC TSD201 respiratory-effort transducer attached to an elastic respiratory belt, which was placed just below the participant's sternum and measured changes in thoracic expansion and contraction during breathing. All physiological signals were sampled simultaneously at 1 kHz using RSP100C and PPG100C amplifiers for respiration and pulse, respectively, and were recorded using BIOPAC AcqKnowledge software (version 4.1.1). SCR was connected to a grounded RF filter.

2.8. MRI preprocessing

Functional data were preprocessed using FSL (www.fmrib.ox.ac.uk/fsl). Steps included correction for head motion and slice-acquisition time, spatial smoothing (5 mm FWHM Gaussian kernel), and high-pass temporal filtering (0.005Hz, 128s period). To account for non-neural fluctuations of the BOLD signal, mean signal changes in white matter (WM) and cerebrospinal fluid (CSF) were regressed out of each voxel using linear regression. Additional motion scrubbing was conducted to regress out abrupt sharp changes in the signal using framewise displacement as a measure of how much the brain moved from one data-point to the next and a cutoff of 0.50 mm (Power et al., 2012). Additional artifact filtering was conducted using an ICA-based procedure for removal of non-neuronal variance from BOLD data (AROMA; Pruim et al., 2015). After all filtering, the preprocessed data were nonlinearly warped to a standard anatomical (MNI152) brain. Finally, to account for the initial response to the onset of the music, the first 20 s of the pieces of music were deleted before further analyses.

Upon inspection, multiple participants had significant artifacts in the psychophysiological data recorded during scanning. In order to avoid potentially reintroducing artifacts into the BOLD signal during preprocessing, we decided to not include these measures as regressors, but, rather, to account for non-neural signal via the ICA-based approach described above.

2.9. Analysis of continuous affective ratings

Continuous affective ratings collected after scanning were sampled at 10Hz. To align the time series across participants, spline interpolation was used to align time points to the nearest 10th of a second. Ratings were then downsampled to match the TR of the brain data (1Hz). The interpolated, downsampled ratings were demeaned and averaged across participants for each piece and each condition (emotion or enjoyment) separately. Intersubject coherence in the enjoyment and emotion ratings were calculated by correlating each participant's ratings with the average rating of the rest of the group. Any participant whose intersubject rating was less than 2 standard deviations below the average intersubject rating was removed from subsequent analyses. This resulted in the removal of two participants.

2.10. Voxelwise ISC analysis

Whole-brain intersubject correlation (ISC) of the fMRI data was calculated using the ISCs toolbox (isc-toolbox, release 1.1) developed by Kauppi (2010). Using Pearson's correlation coefficient, temporal correlations in every voxel of the brain between every pair of subjects was calculated and then averaged to create a group-level ISC map. Global ISC maps were computed for each of the pieces separately. Statistical significance of the ISC maps was calculated based on nonparametric voxelwise permutation tests (Pajula et al., 2012). To generate an appropriate null distribution, each participant's voxel time series was circularly shifted by a random lag so that they were no longer aligned in time across the subjects, yet the temporal autocorrelations of the BOLD signal was preserved, and the correlation coefficient was recalculated. This process was repeated 100,000 times. P-values of the r statistic from the non-shuffled data were then calculated based on the permutation distribution and corrected for multiple comparisons with Benjamin-Hochberg False discovery rate (FDR; Kauppi et al., 2014).

2.11. Voxelwise regression with affective ratings

As a complementary analysis to whole-brain ISC, we additionally used continuous ratings of sadness and enjoyment to predict subject-level BOLD signal using a GLM approach. Results are presented in the Supplementary Materials.

2.12. Whole-brain ISC differences between high and low empathy groups

To evaluate differences in ISC during the processing of emotional music between people with high and low empathy, we first divided participants into two groups based on a median split of scores on the 4 subscales of the Interpersonal Reactivity Index (IRI; Davis, 1983). We then used a two-group formulation of a linear mixed-effects (LME) model with a crossed random-effects formulation to identify voxels that had higher ISC values within the high Fantasy group as compared to the low Fantasy group as well as higher ISC values within rather than across groups. The LME approach has been shown to accurately account for the correlation structure embedded in the ISC and provide proper control for false positives (Chen et al., 2017). The model gives voxelwise population ISC values within each group as well as voxelwise population ISC values between the two groups, which reflects the ISC effect between pairs of participants that belong to different groups. We then contrasted the within-group high empathy ISC maps from the within-group low empathy ISC maps as well as within-group high empathy ISC maps from the across-group ISC maps. Minimum cluster size for significance was calculated with AFNI's 3dFWHMx and 3dClustSim and contrasts were thresholded using an initial voxelwise threshold of $p < 0.001$ and controlled for family-wise error (FWE) using the calculated cluster size threshold that corresponded to a p -value of 0.05.

2.13. Intersubject phase synchronization calculation

To avoid issues with selecting an arbitrary window size and to increase the temporal resolution, we opted to use a recently developed approach that evaluates BOLD-signal similarity across participants dynamically by calculating differences in phasic components of the signal at each moment in time (inter-subject phase synchronization; ISPS). The fMRI Phase Synchronization toolbox was used to calculate dynamic ISPS (Glerean et al., 2012). The filtered, preprocessed data was first band-pass filtered through 0.025Hz (33s) to 0.09Hz (~11s) because the concept of phase synchronization is meaningful only for narrow-band signals. Using the Hilbert transform, the instantaneous phase information of the signal was determined and an intersubject phase coefficient was calculated for each voxel at each TR by evaluating the phasic difference in the signal for every pair of participants and averaging. This results in a value between 0 and 1 that represents the degree of phase synchronization across all participants at that moment in time.

A similar method was then used to assess dynamic inter-regional synchronization. Instantaneous seed-based phase synchronization (SBPS) was performed by calculating the difference in the phasic component of two voxels/regions in one participant and then subsequently evaluating phase differences in interregional synchronization across participants. When averaging across all participants, this analysis resulted in a group-level, time-varying connectivity measure between all pairs of regions (Nummenmaa and Lahnakoski, 2018).

2.14. Predicting dynamic synchronization from continuous affective ratings

Continuous affective ratings were then used to predict the ISPS and SBPS time series in order to evaluate how stimulus-driven brain activity reflects changes in emotional responses to the music.

To both focus the scope of our analysis and increase predictive power, we limited this analysis to pre-defined networks that we hypothesized to be involved in affective experiences with musical stimuli. We used results from previously published meta-analyses of fMRI studies with emotions to select 50 ROIs belonging to 1 of 5 networks (Kober et al., 2008; Lindquist et al., 2012; Touroutoglou et al., 2014). The limbic and paralingic network consisted of the amygdala, hippocampus, parahippocampal gyrus, thalamus, and insula. The striatal network included the caudate, putamen, and pallidum. The default mode network included the posterior cingulate, precuneus, inferior parietal lobule/angular gyrus, middle temporal gyrus, and medial prefrontal cortex (Kober et al., 2008; Shirer et al., 2012). We additionally included regions of the primary and secondary auditory cortex, including Heschl's gyrus, the superior, middle, and inferior frontal gyri, and temporal poles, as well as a several regions that constituted the orbitofrontal cortex (Kahnt et al., 2012). All regions were defined using the AAL (Automated Anatomical Labeling) atlas (Tzourio-Mazoyer et al., 2002). A full list of ROIs as well as their coordinates are available in Table 2 and are visualized on a template brain in Fig. 3.

The demeaned, averaged time series for enjoyment ratings and sadness ratings were down-sampled to 1Hz to match the TR of the fMRI data and convolved with a double gamma HRF to compensate for the hemodynamic delay. Two separate GLM models were employed to predict network-based ISPS and SBPS, once with the sadness ratings, regressing out enjoyment ratings and once with enjoyment ratings regressing out sadness. Significance of beta values between affective ratings and ISPS/SBPS, averaged across regions that constituted a singular network, was calculated non-parametrically through permutation testing, phase-scrambling the emotion ratings time course 5000 times by randomizing the phase of each Fourier component (Honey et al., 2012) to create a null-distribution. The resulting p -values were corrected using Benjamin-Hochberg (FDR) with a positive $q < 0.05$ to control false discovery rate across the two models.

2.15. Continuous measure of musical features

To evaluate the contribution of changes in acoustical properties of the sounds to neural synchronization, we extracted continuous measures of loudness and timbre using the MIRtoolbox in Matlab (Lartillot and Toivainen, 2007). We focused specifically on these two aspects of sonic information because we previously showed that these features were most predictive of the sadness and enjoyment ratings overtime (see Ma et al. *under review*). Loudness was extracted using the *mirrms* function and timbre was extracted using the *mirbrightness* function, both with default parameters in sliding windows with a duration of 1s and a step size of 1s to match the sampling rate of the MRI signal (1 Hz).

To determine the unique contributions of changes in affect, as compared to changes in auditory signal, we then ran two additional GLM models to predict region-based intersubject phase synchronization, including either the continuous measure of loudness (RMS) or timbre (brightness), orthogonalized to the rating of interest.

2.16. Code availability

The custom code used to generate the results in this study will be made available on the corresponding author's personal website.

2.17. Data availability

The data supporting the findings of this study will be made available from the corresponding author upon reasonable request. Raw MR data will be uploaded to [OpenNeuro.org](https://openneuro.org).

3. Results

3.1. Behavioral data and continuous ratings

Four out of the 40 participants had to be removed from subsequent analyses, one due to an anatomical anomaly discovered during scanning, one due to high motion-related artifacts, and two due to their ratings of affect being below the two standard deviations cutoff below the average ISC value across people (ISC enjoyment: 0.18, SD = 0.13; ISC sadness:

0.21, SD = 0.14). This resulted in a total of 36 participants (19F, $M_{age} = 24.25$). After removing the first 20 s of the pieces, the average ISC for sadness ratings amongst the final 36 was 0.16 (SD = 0.15) and the average ISC for enjoyment ratings was 0.10 (SD = 0.14).

As has been shown previously with continuous ratings of affect (Upham and McAdams, 2018), the variance across participants with regards to the felt emotional response to music was quite large. Across all participants and all time points, the average enjoyment rating was 4.57 with an average standard deviation of 2.72. The average sadness rating was 4.53 with an average standard deviation across all time points of 2.86. Average ratings for both enjoyment and sadness are presented in Fig. 1. Inside the scanner, the average post-listening ratings were 3.19 (SD = 0.82) for enjoyment, 2.83 (SD = 0.85) for sadness, 1.39 (SD = 0.60) for familiarity, and 3.25 (SD = 0.73) for attention.

A summary of responses to all questionnaires are presented in Table 1 and correlations between personality factors and average ratings for sadness and enjoyment are presented in Supplementary Table 1. To summarize, the Fantasy subscale of empathy was significantly correlated

Table 1
Summary statistics of collected behavioral measures.

Questionnaires		Mean	SD
Age		21.50	6.40
Years of music training		4.86	2.18
Empathy (IRI)	Fantasy	19.28	5.79
	Perspective Taking	18.92	4.86
	Empathic Concern	19.58	4.29
	Personal Distress	10.53	4.27
Music Sophistication Index (Goldsmith MSI)	Active Engagement	40.79	6.61
	Perceptual Abilities	41.31	3.20
	Musical Training	25.82	6.07
	Emotions	30.97	2.91
	Singing Abilities	29.74	4.54
	General Sophistication	78.14	8.94
Mental health status	Anxiety (GAD-7)	5.67	4.10
	Depression (PHQ-9)	5.50	4.06

Note. N = 36.

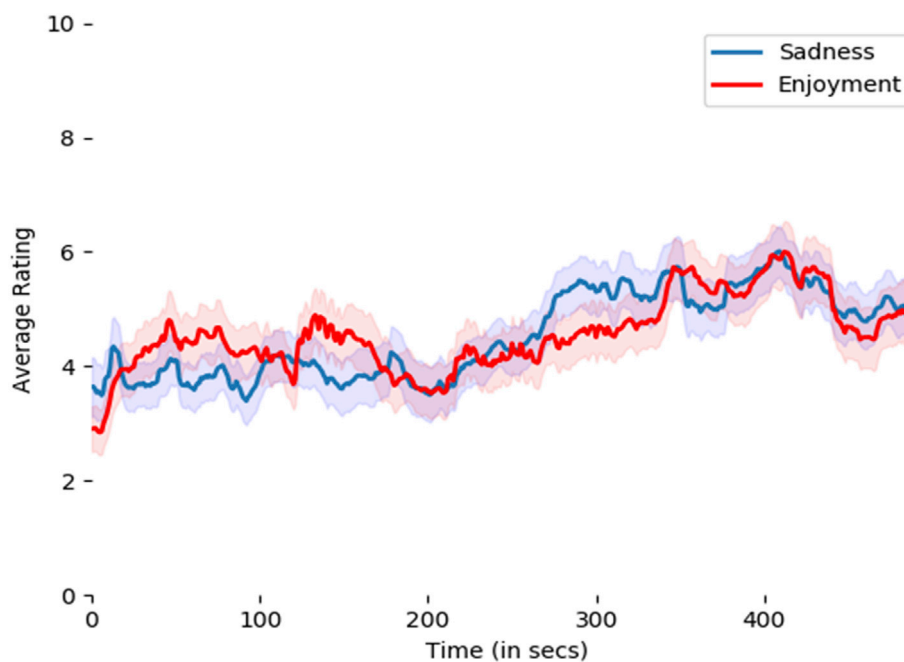


Fig. 1. Mean ratings of intensity of sadness and intensity of enjoyment. The first 20 s of the piece have been removed. 10 = high sadness/enjoyment and 0 = no feelings of sadness/enjoyment. Lighter-colored bounded lines represent +1 standard deviation from the mean.

Table 2
Regions and networks of interest used for intersubject synchronization.

Region	Right Hemisphere			Left Hemisphere			Network
	x	y	z	x	y	z	
Heschl's gyrus	-42	-19	10	46	-17	10	Auditory
Middle temporal gyrus	-56	-34	-2	57	-37	-1	Auditory
Middle temporal pole	-36	15	-34	44	15	-32	Auditory
Superior temporal gyrus	-53	-21	7	58	-22	7	Auditory
Superior temporal pole	-40	15	-20	48	15	-17	Auditory
Inferior temporal gyrus	-50	-28	-23	54	-31	-22	Auditory
Caudate	-11	11	9	15	12	9	Striatal
Pallidum	-18	0	0	21	0	0	Striatal
Putamen	-24	4	2	28	5	2	Striatal
Medial prefrontal	-5	54	-7	8	52	-7	DMN
Angular gyrus	-44	-61	36	46	-60	39	DMN
Inferior parietal lobule	-43	-46	47	46	-46	50	DMN
Posterior cingulate	-5	-43	25	7	-42	22	DMN
Precuneus	-7	-56	48	10	-56	44	DMN
Anterior orbitofrontal	-17	47	-13	18	48	-14	Orbitofrontal
Lateral orbitofrontal	-31	50	-10	33	53	-11	Orbitofrontal
Gyrus rectus	-5	37	-18	8	36	-18	Orbitofrontal
Amygdala	-23	-1	-17	27	1	-18	Limbic
Hippocampus	-25	-21	-10	29	-20	-10	Limbic
Thalamus	-11	-18	8	13	-18	8	Limbic
Insula	-35	7	3	39	6	2	Limbic
Anterior cingulate	-4	35	14	8	37	16	Limbic
Mid cingulate	-5	-15	42	8	-9	40	Limbic
Parahippocampal gyrus	-21	-16	-21	25	-15	-20	Limbic

Note: stereotactic coordinates (x,y,z) in MNI from the AAL atlas.

with average rating of felt sadness during the piece of music ($r = 0.34$, $p = 0.03$) and marginally correlated with average rating of felt enjoyment during the piece of music ($r = 0.28$, $p = 0.09$). Importantly, Fantasy was not significantly correlated with the general music sophistication ($r = 0.19$, $p = 0.27$) nor with music training ($r = -0.01$, $p = 0.95$).

3.2. Whole-brain intersubject correlation

Across the entire piece of sad music, significant intersubject correlation was found in large bilateral clusters in the auditory cortex, including Heschl's gyrus, superior temporal gyrus and sulcus. This cluster extends medially into the posterior insula as well as posteriorly into the supramarginal gyrus in both hemispheres. Additional significant clusters were found in the left inferior frontal gyrus, left anterior insula, left anterior cingulate cortex, left precentral gyrus, and left cerebellum (see

Table 3
Peak voxels and correlation values for significant ISC clusters.

Region	Hemisphere	Corr value	x	y	z
Superior temporal gyrus	right	0.15	-64	-18	6
Superior temporal gyrus	left	0.08	58	-34	10
Heschl's gyrus	right	0.11	50	-20	6
Heschl's gyrus	left	0.12	-55	-20	6
Cerebellum	left	0.04	-16	-78	-36
Supramarginal gyrus	right	0.04	63	-40	23
Supramarginal gyrus	left	0.03	-56	-42	24
Inferior frontal gyrus, pars opercularis	right	0.04	49	21	24
Inferior frontal gyrus, pars triangularis	right	0.02	49	26	7
Precentral gyrus	right	0.03	54	2	46
Posterior insula	left	0.02	-40	-16	1
Anterior insula	right	0.02	36	24	4
Anterior cingulate cortex	right	0.02	6	32	28
Anterior insula	right	0.02	32	28	-3
Lateral occipital	right	0.02	50	-76	8
Lateral occipital	left	0.02	-19	-74	47

N = 36.

FDR adjusted p-value calculated using Benjamin-Hochberg procedure ($q < 0.01$).

Table 3, Fig. 2).

3.3. ISC differences between high and low empathy participants

When comparing participants who score high on the Fantasy subcomponent of empathy to participants who score low on the Fantasy subcomponent of empathy, significantly greater ISC values were found in the left auditory cortex, including the superior temporal gyrus, the middle temporal gyrus, extending into the supramarginal gyrus. ISC values in the left superior frontal gyrus, extending into the middle frontal gyrus, the right precuneus, as well as parts of the right visual cortex, including the intracalcarine cortex (calcarine sulcus and lingual gyrus) were additionally higher in the high-Fantasy group. For the reverse contrast (low-Fantasy group > high-Fantasy group), greater ISC was found in the left angular gyrus, extending into the supramarginal gyrus, the left insula, as well as the right putamen, superior frontal gyrus to paracingulate, and superior parietal lobule (see Table 4, Fig. 4).

3.4. Intra-network phase synchronization predicted by affective ratings

When correcting for multiple comparisons across two models and all five networks, continuous ratings of enjoyment positively predicted changes in phase synchronization in several networks of interest (see Table 5). These included the auditory ($\beta = 0.016$, $p = 0.01$, $p_{adj} = 0.03$), striatal ($\beta = 0.006$, $p = 0.01$, $p_{adj} = 0.03$), default mode networks ($\beta = 0.008$, $p < 0.01$, $p_{adj} = 0.02$), as well as the orbitofrontal cortex ($\beta = 0.003$, $p = 0.01$, $p_{adj} = 0.03$). Sadness, on the other hand, significantly predicted phase synchronization in the striatal ($\beta = 0.006$, $p = 0.02$, $p_{adj} = 0.03$) and limbic network ($\beta = 0.002$, $p = 0.03$, $p_{adj} = 0.05$).

3.5. Inter-network phase synchronization predicted by affective ratings

Next we evaluated whether changes in phase synchronization between networks was associated with changes in affective ratings. Neither ratings of sadness nor enjoyment significantly predicted seed-based phase synchronization between networks when correcting for multiple comparisons (see Table 6).

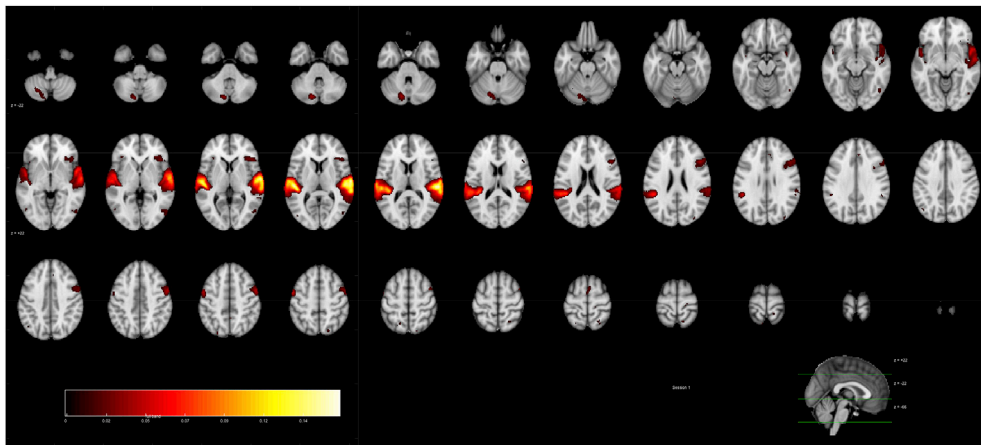


Fig. 2. Significant voxelwise intersubject correlation across the entire length of the sad piece of music. Statistical significance voxels based on nonparametric voxelwise permutation testing with FDR-correction ($q < 0.001$).

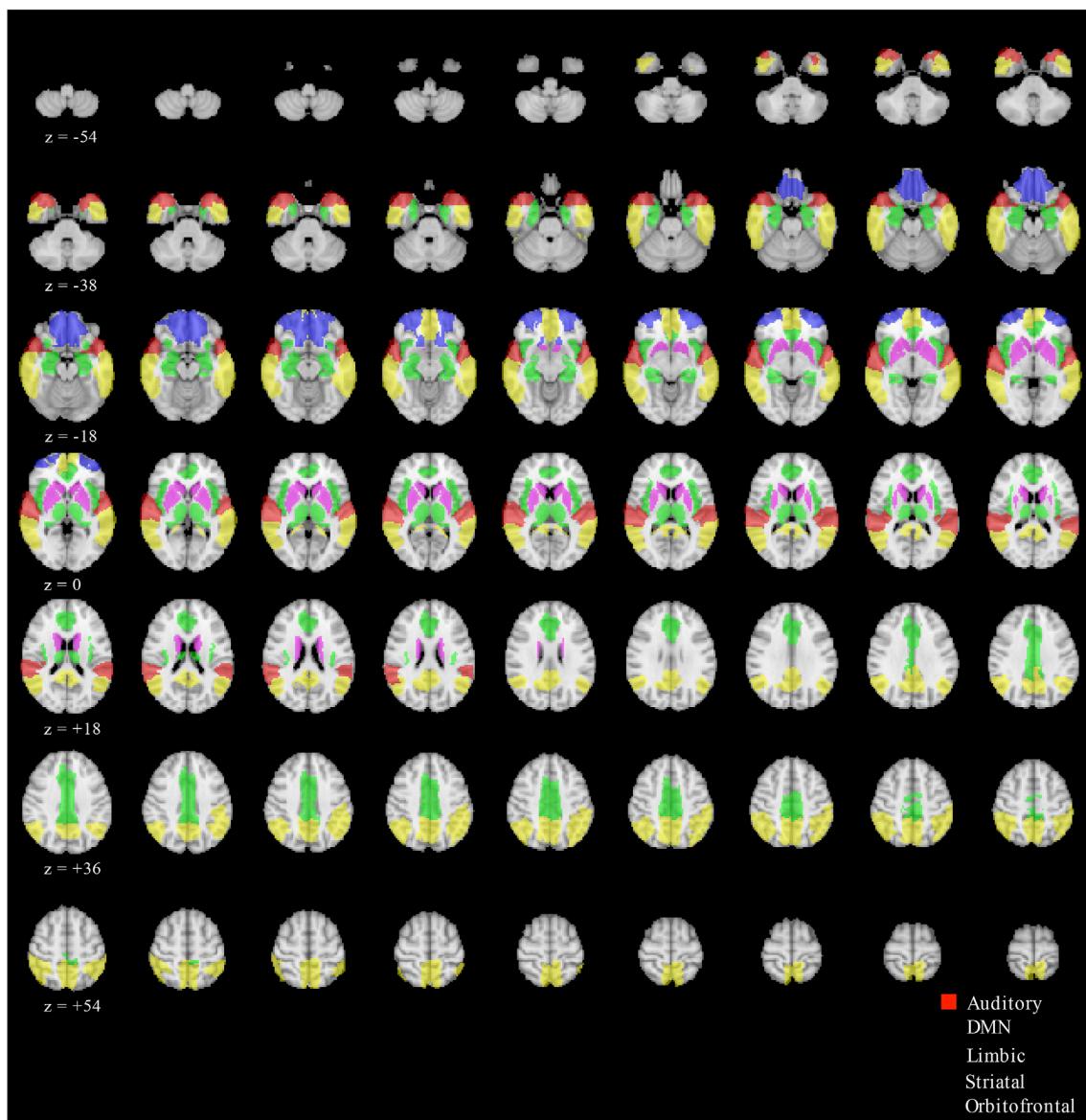


Fig. 3. Visual representation of the five functional networks used for dynamic intersubject synchronization analyses.

Table 4
Peak voxels and correlation values for significant ISC clusters modulated by Fantasy.

Region	Hemisphere	Corr value	x	y	z
<i>ISC{high,high} > ISC{low, low}</i>					
Superior temporal gyrus/ Heschl's gyrus	left	0.04	-62	-22	4
Superior frontal gyrus/Middle frontal gyrus	left	0.08	-24	30	50
Intracalcarine cortex	right	0.05	24	-60	4
Precuneus	right	0.05	4	-58	46
<i>ISC{low, low} > ISC{high,high}</i>					
Angular gyrus/Supramarginal gyrus	left	0.05	-42	-60	56
Superior frontal gyrus/ paracingulate	right	0.04	4	30	58
Superior parietal lobule	right	0.04	32	-52	56
Anterior Insula	left	0.03	-30	18	-8
Putamen	right	0.02	26	14	-4

N = 36.

FDR adjusted p-value calculated using Benjamin-Hochberg procedure.

3.6. Additional information provided by continuous changes in acoustic information

When running the GLM with a continuous measure of RMS and brightness (orthogonalized to emotion ratings), the positive associations between enjoyment ratings and phase synchronization in the auditory, striatal, orbitofrontal, and default mode networks remained significant. The association between sadness ratings and limbic and striatal network phase synchronization was no longer significant when including RMS into the model and the association between sadness and limbic network phase synchronization was no longer significant when including brightness in the model (see [Supplementary Tables 2 and 3](#)).

4. Discussion

Using several measures of intersubject neural synchronization combined with continuous ratings of subjective affective experience, we uncovered brain regions and networks involved in the representation of enjoyment and sadness as they unfold over time in response to a sad piece of music. The findings contribute to our current understanding of affective processing in the brain and enrich it by illuminating the time-varying patterns of neural synchronization and communication that map onto two distinct aspects of emotional experience.

While participants were listening to a full-length piece of music, we found significant intersubject correlations in voxels within the primary and secondary auditory cortex, as well as within the insula (posterior and anterior), anterior cingulate, and inferior frontal gyrus. While it is likely that synchronization of voxels in the primary auditory cortex reflects changes in acoustic aspects of the music, the secondary auditory cortex, i.e., the superior temporal gyrus and sulcus, has been shown to be involved in representing emotions conveyed through a variety of sounds with different acoustical properties ([Escoffier et al., 2013](#); [Sachs et al., 2018](#)), as well as across a variety of non-auditory stimuli, such as body movements and faces ([Peelen et al., 2010](#)).

The insular cortex is widely considered to be involved in subjective experiences of emotion ([Damasio et al., 2013](#); [Immordino-Yang et al., 2014](#)). More specifically, recent evidence suggests that the posterior insula is involved in processing interoceptive changes in the body and the anterior portion is involved in integrating the interoceptive information with external sensory information to generate a subjective representation of the feeling state ([Nguyen et al., 2016](#)). Relatedly, the insula may play a role in the immediate and automatic responses to emotions observed in others, given that it responds to stimuli depicting others in pain regardless of conscious attention or cognitive demand.

Significant ISC was additionally found in the inferior frontal gyrus and anterior cingulate, regions that are activated both when mentally simulating the emotions of others and when personally experiencing those same emotions ([Lawrence et al., 2006](#); [Singer and Lamm, 2009](#)). The fact that these regions were significantly synchronized across participants during presentation of a sad piece of music mirrors the results of previous findings with other types of emotional naturalistic stimuli ([Jääskeläinen et al., 2008](#)) and provides evidence that (a) participants were feeling emotions in response to the piece of music at similar times and (b) these music-evoked emotional responses likely engaged empathic processing.

To further test this notion, whole-brain ISC differences were calculated between groups of participants with high and low measures of trait empathy. The Fantasy subscale of the IRI, which reflects a tendency to become mentally transported into a story or narrative, has been shown to predict the intensity of emotional responses to and enjoyment of sad music ([Kawamichi et al., 2016](#); [Taruffi and Koelsch, 2014](#); [Sachs et al., under review](#)). In particular, in [Sachs et al. \(under review\)](#), we found that Fantasy was correlated with feeling intense, positive emotions in response to sad music, such as tenderness and wonder, rather than negative emotions, such as sadness and unease. Our results suggest a possible neural explanation for these behavioral differences and highlight the advantages of using inter-group ISC as a method of identifying psychologically -relevant variations in how individuals process the natural world ([Hasson et al., 2010](#)). In our study, participants who scored higher on a self-report measure of Fantasy showed increased within-group synchronization in the left superior temporal gyrus and sulcus, the left dorsal medial prefrontal cortex (DMPFC), including the superior frontal and middle frontal gyri, the precuneus, and parts of the visual cortex. The DMPFC, superior temporal sulcus, and the precuneus have all previously been shown to be involved in recognizing and inferring the emotion states of others as well as reflecting upon one's own emotional state ([Schnell et al., 2011](#)). Across studies, they appear to be associated with both affective and social cues in situations requiring empathy ([Krämer et al., 2010](#)). Because of this, this network of regions is often thought of as being involved both in inferring external emotional information and reflecting on one's own emotional experiences ([Lamm et al., 2011](#)). Increased ISC in these regions for high-Fantasy participants may therefore reflect the mental processes involved in identifying the emotions being conveyed and becoming cognitively engaged with the music as it unfolds.

In the reverse contrast, low fantasy was correlated with higher ISC in the insula and caudate, two regions thought to be involved in representing core affective states ([Lindquist et al., 2012](#)). The anterior insula in particular is repeatedly found to be associated with empathy for the pain of others ([Lamm et al., 2011](#)). With music in particular, negative valence ratings have previously been shown to correlate with caudate activity ([Trost et al., 2015](#)) and insular-based network activity is associated with increases in affective experiences ([Raz, Touroutoglou, Wilson-mendenhall et al., 2016](#); [Touroutoglou et al., 2012](#)). One potential interpretation of these results is that low Fantasy participants are more likely to engage processes related to emotional responding, rather than emotional understanding and reflection, while listening to sad music. Taken together, the differences between the two groups in terms of the brain networks that show high synchronization may explain the link between Fantasy and feeling positively in response to sad music.

The additional finding of increased synchronization of the visual cortex in the high-empathy group may indicate that such participants were engaging in visual imagery while listening to music, picturing scenes and/or characters that might accompany the music. The left occipital lobe, cuneus and lingual gyrus have been shown to be activated during visual mental imagery of objects as well as visual perception of those same objects ([Ganis et al., 2004](#)). Previous research has argued that the enhancement of visual mental imagery in response to music mediates the relationship between Fantasy and emotional responses to sad music ([Schubert et al., 2018](#)). Although we cannot say for certain that the high

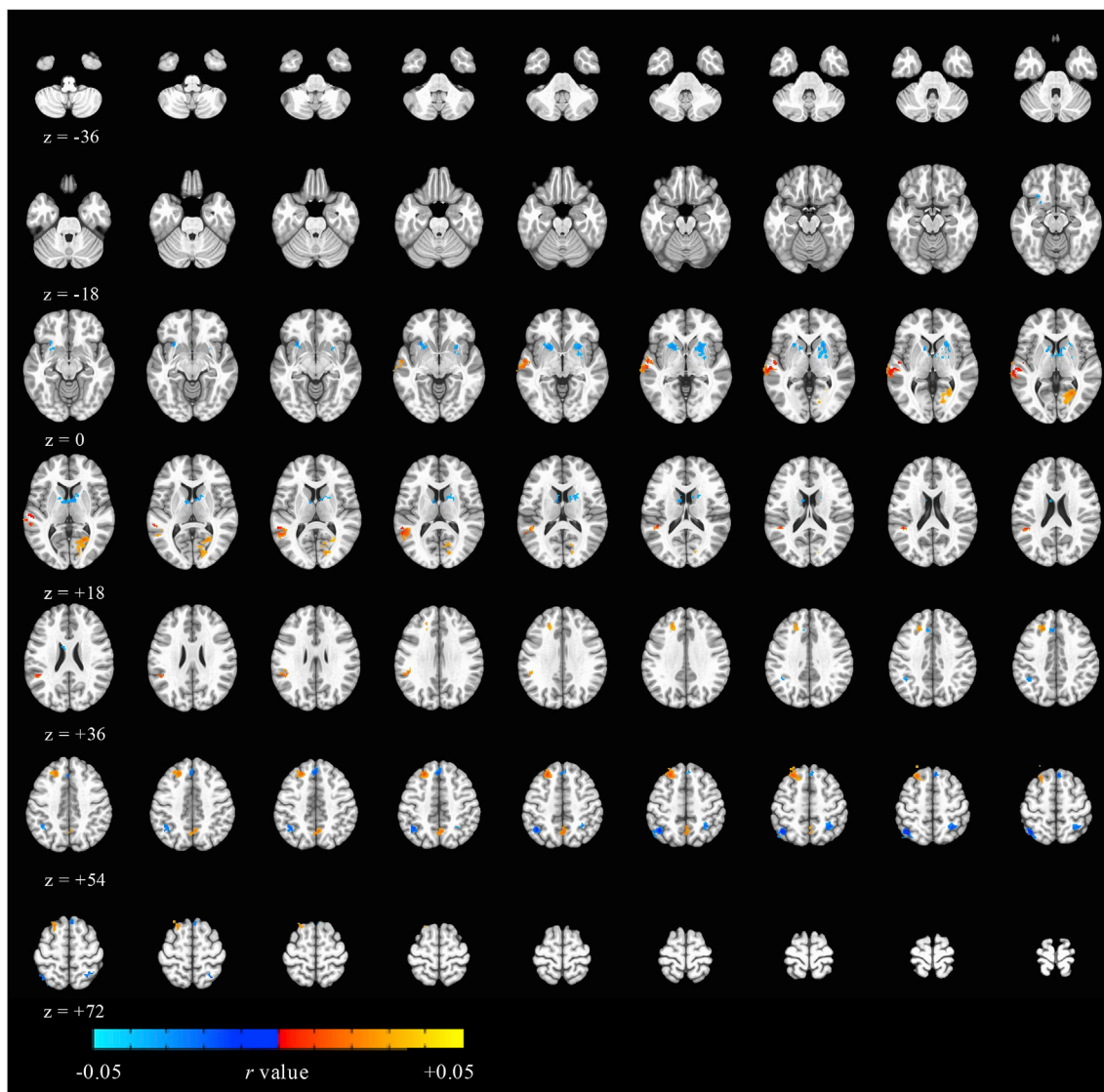


Fig. 4. Trait empathy modulates ISC in response to sad music. Whole-brain, voxelwise contrast revealing clusters that are significantly more synchronized between pairs of high-Fantasy participants than pairs of low-Fantasy participants are shown in red. The reverse contrast, brain regions that are more synchronized within the high-Fantasy group than across the Fantasy groups are shown in blue. For both contrasts, results are shown at an initial threshold of $p < 0.001$ with cluster correction corresponding to $p < 0.05$.

Table 5
Regression of network-based intersubject synchronization with ratings.

Network	β	P-value	Adjusted P-value
<i>Enjoyment</i>			
Auditory	0.016	0.013	0.032
Striatal	0.006	0.008	0.027
Limbic	0.002	0.045	>0.05
Prefrontal	0.003	0.006	0.027
DMN	0.008	0.002	0.016
<i>Sadness</i>			
Auditory	0.009	0.080	>0.05
Striatal	0.006	0.017	0.033
Limbic	0.002	0.028	0.046
Prefrontal	0.002	0.069	>0.05
DMN	0.005	0.068	>0.05

N = 36.

FDR adjusted p-value calculated using Benjamin-Hochberg procedure.

empathy group engaged in more visual imagery during music listening, it is important to note that the piece of music used in this study was written for a television show and therefore, was likely composed in a way that complemented or enhanced certain aspects of the accompanying visual scene; it would therefore be unsurprising if images were conjured in response to this type of music.

To further probe the meaningfulness of ISC in terms of a collective emotional experience, we calculated a moment-to-moment measure of intersubject synchronization and used continuous ratings of enjoyment and sadness to predict changes in synchronization over time. In this analysis, enjoyment ratings were positively associated with intersubject phase synchronization in auditory, orbitofrontal, and striatal regions, as well as the default mode network, whereas sadness ratings were positively associated with limbic and striatal network synchronization. Importantly, when continuous enjoyment ratings were used to predict BOLD activity using the more traditional GLM framework (see Supplementary Materials), only voxels within the right Heschl's gyrus were significantly correlated with continuous enjoyment ratings, highlighting the usefulness of this method for understanding time-varying patterns of neural activity.

Table 6
Regression of cross-network intersubject synchronization with ratings.

Network connection	β	Uncorrected P-value
<i>Enjoyment</i>		
Auditory - striatal	0.020	0.132
Auditory - limbic	0.012	0.505
Auditory - orbitofrontal	0.004	0.629
Auditory - DMN	-0.016	0.956
Striatal - limbic	0.011	0.062
Striatal - orbitofrontal	0.028	0.303
Striatal - DMN	-0.003	0.946
Limbic - orbitofrontal	0.015	0.133
Limbic - DMN	-0.010	0.919
Orbitofrontal - DMN	0.005	0.545
<i>Sadness</i>		
Auditory - striatal	0.026	0.170
Auditory - limbic	0.014	0.441
Auditory - orbitofrontal	0.021	0.387
Auditory - DMN	-0.007	0.750
Striatal - limbic	0.017	0.125
Striatal - orbitofrontal	0.031	0.170
Striatal - DMN	0.004	0.688
Limbic - orbitofrontal	0.013	0.111
Limbic - DMN	-0.008	0.758
Orbitofrontal - DMN	0.002	0.528

N = 36.

FDR adjusted p-value calculated using Benjamin-Hochberg procedure.

These results corroborate several previous studies using emotional naturalistic stimuli. In response to both evocative speeches and film clips, negative emotional valence was shown to predict dynamic intersubject synchronization in the striatum as well as areas of the limbic system and orbitofrontal cortex (Nummenmaa et al., 2012; Nummenmaa et al., 2014). Because participants only rated valence along a single axis (pleasantness to unpleasantness), the authors interpret these findings as evidence that these regions process both feeling states and reward. By separating enjoyment from valence ratings, our findings help clarify the specific functions of these regions in different aspects of emotion.

The orbitofrontal cortex is consistently found to be activated during tasks requiring aesthetic judgment and appreciation (Brown et al., 2011) as well as reward-processing and reward-prediction (Howard et al., 2015). Structurally, the region receives input from higher sensory areas, the hypothalamus and thalamus, and projects to striatal areas, the ACC, amygdala, and insula (Kringelbach and Rolls, 2004). Resting-state connectivity data has suggested that the orbitofrontal cortex can be subdivided into functional units. The medial portion of the OFC is functionally connected with the posterior cingulate, medial and lateral temporal cortex, and the ventral striatum, whereas the more anterior and lateral portions of the OFC appears to be functionally connected with the caudate, putamen, dorsal ACC, and anterior insula (Kahnt et al., 2012). These results imply that the medial cluster may be more involved in monitoring, learning, and prediction reward value, whereas the more anterior and lateral clusters may be more involved in behavioral responses to both reward and punishment (Kringelbach and Rolls, 2004). In this study, enjoyment ratings were positively associated with intersubject synchronization in the medial and lateral portions of the orbitofrontal cortex, suggesting that multiple, related functions are occurring in response to music, including monitoring one's current affective state and using this information to assess and predict the music's current and upcoming reward value and ultimately make decisions regarding its aesthetic quality and one's behavioral response.

Moments when the piece of music was found to be most enjoyable were additionally associated with across-participant synchronization of signal from the default mode network. This findings corroborates previous indications that the DMN is involved in aesthetic processing (Belfi et al., 2019; Cela-Conde et al., 2013; Vessel et al., 2012), though the exact role of the DMN in the enjoyment of art and music remains unclear. It is possible that the domain-general functions of the DMN, such as

processing emotionally-relevant stimuli for their reward value, engaging in self-referential thought (Li et al., 2014; Pearson et al., 2011) and detecting changes in the internal and external environment in order to modify cognitive and behavioral processes (Pearson et al., 2011), all contribute in some way to aesthetic experiences. There is some indication that sad music, as compared to happy music, is more likely to induce these types of cognitive processes and thought patterns, as evidenced by enhanced functional connectivity of the DMN in response to sad music (Taruffi et al., 2017). Based on the fact that in our study, moment-to-moment intersubject synchronization was associated with changes in subjective enjoyment, we hypothesize that the DMN is involved in monitoring the flow of internal information related to feelings, memory, mental simulation, and self-referential thought that likely occurs as the particular piece of sad music progresses.

Striatal network synchronization was additionally correlated with both sadness and enjoyment ratings. The striatum, which includes a group of structures that are part of the basal ganglia, i.e., the putamen, caudate and globus pallidus, is typically regarded as the center of the reward system in the brain. Across a variety of studies, this system triggers the pleasurable sensations that accompany the presentation of rewarding stimuli such as food, sex, drugs, and music (Berridge and Kringelbach, 2013). There is some evidence that the striatum is involved in reward learning of musical stimuli (Gold et al., 2019; Salimpoor et al., 2009; Salimpoor et al., 2013) and the basal ganglia in particular may be involved in the intensity of emotional responses to music (Brattico et al., 2011; Pereira et al., 2011; Trost et al., 2012). In light of its known functional role in movement (Albin et al., 1983), the basal ganglia may additionally process rhythmic and melodic aspects of musical stimuli (Bengtsson and Ullén, 2006), which are potential musical features known to evoke emotions (Juslin, 2013). The fact that synchronization in the striatum was correlated with both enjoyment and sadness ratings needs to be interpreted with caution given that the two ratings were highly related. Nonetheless, the results may indicate that the striatum is tracking changes in musical features that are strongly tied to both moments of evoked emotion and subjective enjoyment.

Despite recent findings that emotional responses to naturalistic stimuli may be best captured by changes in inter-network connectivity and synchronization (Nummenmaa and Saarimäki, 2019; Raz et al., 2016), when correcting for multiple comparisons across the two models in our analysis, we did not find that sadness nor enjoyment ratings significantly predicted inter-network phase synchronization. Using the same seed-based phase synchronization approach we used here, Nummenmaa et al. (2014) found that negative valence was associated with increased connectivity between the insular, inferior temporal, cingulate, and orbitofrontal cortices and similar results have been found with other methods of assessing dynamic functional connectivity (Raz et al., 2012). While there are a number of reasons why we did not find inter-network changes associated with emotion ratings in our data, one possibility is that our method of defining large-scale intrinsic networks does not allow us to observe more fine-grained changes in interregional communication that may be involved in affective tracking.

When including acoustic features (loudness and timbre) into the model, the link between sadness ratings and limbic network phase synchronization was no longer significant. Furthermore, loudness was significantly correlated with both auditory and striatal network synchronization. This result suggests that the time-varying patterns of phase synchronization are partially driven by acoustic properties of the music, not only by subjective feelings, particularly in subcortical and sensory processing regions. Loudness is an important feature of music that is tightly linked to its emotional character and the accompanying affective response (Coutinho and Cangelosi, 2011; Trost et al., 2015). Indeed, acoustic features in general are inextricably linked to the emotional textures they are designed to convey. Therefore, it is difficult to completely remove the influence of changing acoustical features from the felt emotional response. It is likely, based on our findings, that the time-varying pattern of phase synchronization in auditory, limbic, and

striatal networks is a reflection of both musical features and higher-level affective responses, whereas the influence of musical features is less pronounced in higher-level cortical networks, i.e., the DMN and orbito-frontal regions.

Importantly, our results mirror previous findings showing hemispheric asymmetries associated with processing emotions in music. Several EEG studies have shown asymmetric responses in the brain to music of different valence. For example, [Proverbio and De Benedetto \(2018\)](#) found that, when compared to silence and nature sounds, the cortical surface activity recorded in response to a sad piece of music was associated with the right medial and superior frontal gyrus, as well as the left precentral and superior temporal gyri. In particular, the right superior temporal gyrus has been shown to have a specialized role in the processing of dissonant sounds ([Altenmüller et al., 2002](#); [Foo et al., 2016](#)). Several fMRI studies have corroborated these lateralization findings. In particular, [Flores-Gutiérrez et al. \(2007\)](#) showed that pleasant musical excerpts, as compared to unpleasant, dissonant clips, were associated with activity in the left superior and middle temporal gyri, whereas the reverse contrast revealed bilateral engagement of these regions. While others have failed to find evidence for cortical lateralization in response to positive vs. negative valence in music ([Khalfa et al., 2005](#)), meta-analytical findings of music-evoked emotions collapsing across all emotional categories have found evidence for involvement of the left caudate and right ventral striatum. In this study, enjoyment ratings significantly predicted synchronization in mostly left-lateralized frontal regions, as well as temporal and subcortical regions in the right hemisphere.

There are several limitations with this study that merit discussion. One difficulty with analyzing continuous self-report measures of affect is determining how best to account for and model variability across participants and how best to ascertain the stability and reliability of the average affective ratings. While simply averaging across participants has been used in previous studies with continuous ratings ([Lehne et al., 2013](#)), that method may miss important informational content with regards to the emotional responses that are reflected in the variance across participants. Consequentially, the average ratings are characterized by an overall pattern of low-frequency, temporal drift upwards. This raises an important psychological and methodological question with regards to how we accurately model affective ratings, isolating the variation that is due to error or idiosyncrasies across participants from the variation that says something meaningful about the ways in which participants interpret the stimulus. More complex methods have recently been developed that aim to remove the irrelevant differences in timing across people, such as differences in response time and coordination between cognitive processes and motor actions, in order to capture moments of high inter-subject agreement in the time series ([Booth et al., 2018](#); [Upham and McAdams, 2018](#)). Applying such approaches to the continuous ratings collected here may uncover moments of high agreement across participants with regards to the moments of peak sadness and enjoyment, resulting in a more reliable model that we can use to predict dynamic brain synchronization.

It is also possible that the inconsistencies in the ratings are due to the task itself. Continuously monitoring the existence of complex feelings such as enjoyment, while simultaneously listening to a piece of music may be too cognitively demanding or too abstract for participants. Future endeavors could explore different ways of obtaining a more objective measure of collective emotional responses to the sad piece of music. Previous studies have suggested a number of alternative methods, such as having participants tap along to the beat of the music, which has been shown to be an indirect measure of being moved by music ([Singer et al., 2016](#)) or stopping the music intermittently and asking participants to rate the emotional quality of the last 30 s ([Chang et al., 2018](#)).

Furthermore, because sadness ratings were highly correlated with enjoyment ratings, it is difficult to statistically dissociate the variation in the dynamic intersubject synchronization measure that was driven by the experience of sadness versus the experience of enjoyment, even with

orthogonalization. This may account for the fact that striatal regions appear to be involved in both enjoyment and sadness tracking. Future studies could attempt to tease these related concepts apart by assessing how the neural synchronization is related to enjoyment in response to a piece of music that induces a contrasting emotion, such as happiness.

In summary, while previous studies have employed dynamic methods of neural communication to better understand the brain regions and systems involved in processing ecologically-valid emotional experiences, this study is the first to capture the time-varying patterns of neural synchronization involved in subjective enjoyment within a sad emotional context. Our findings show that enjoyment in response to a sad piece of music predicts intersubject synchronization in auditory cortex, cortico-basal ganglia regions, OFC, and posterior cingulate. This lends credence to the hypothesis that changes in neural communication can reflect and represent different components of our everyday emotional experience. Moreover, synchronization in visual cortex and regions involved in both experiencing and mentally simulating the emotions of others, was found to be greater in participants who were more empathic, providing further indication that assessing stimulus-driven brain activity across people may be a useful tool for illuminating the ways in which humans experience the natural world differently. Future explorations will focus on evaluating the generalizability of these findings by using other types of naturalistic, affective stimuli as well as determining how intensity of emotions reflects neural communications in other emotional contexts, such as with happy stimuli, and in clinical populations characterized by aberrations in socioemotional processing.

Funding

Funding for this work was provided by the private donations made to the Brain and Creativity Institute.

Author Contribution

Matthew Sachs: Conceptualization, Methodology, Investigation, Formal analysis, Writing- Original Draft, Writing - Reviewing and Editing. **Assal Habibi:** Conceptualization, Methodology, Supervision, Reviewing and Editing. **Antonio Damasio:** Conceptualization, Supervision, Funding acquisition. **Jonas Kaplan:** Conceptualization, Methodology, Supervision Reviewing and Editing.

Acknowledgements

The authors would like to thank Hanna Damasio for her assistance and input regarding neuroanatomical distinctions, Anthony Vaccaro for assisting with the data analysis, Alexandria Yap, Tyler Troeg, and Negeen Farida for help with collecting the data, and all private donors to the Brain and Creativity Institute.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.116512>.

References

- Albin, R.L., Young, A.B., Penney, J.B., 1983. Speculations on the functional anatomy of basal ganglia disorders. *Annu. Rev. Neurosci.* 6 (1), 73–94. <https://doi.org/10.1146/annurev.ne.06.030183.000445>.
- Altenmüller, E., Schürmann, K., Lim, V.K., Parlitz, D., 2002. Hits to the left, flops to the right: different emotions during listening to music are reflected in cortical lateralisation patterns. *Neuropsychologia* 40 (13), 2242–2256. [https://doi.org/10.1016/S0028-3932\(02\)00107-0](https://doi.org/10.1016/S0028-3932(02)00107-0).
- Balkwill, L., Thompson, W.F., 1999. A cross-cultural investigation of the perception of and cultural cues emotion in music: psychophysical and cultural cues. *Music Perception* 17 (1), 43–64. <https://doi.org/10.2307/40285811>.
- Belfi, A.M., Vessel, E.A., Briellmann, A., Isik, A.L., Chatterjee, A., Leder, H., et al., 2019. Dynamics of aesthetic experience are reflected in the default-mode network.

- (GAD-7) in the general population. *Med. Care* 46 (3), 266–274. <https://doi.org/10.1097/MLR.0b013e31816d0d093>.
- Ma, B., Greer, T., Sachs, M., Habibi, A., Kaplan, J., Narayanan, S., 2019. Predicting human-reported enjoyment in happy and sad music. In: *International Conference on Affective Computing and Intelligent Interaction*.
- Martin, A., Rief, W., Klaiberg, A., Braehler, E., 2006. Validity of the brief patient health questionnaire mood scale (PHQ-9) in the general population. *Gen. Hosp. Psychiatry* 28, 71–77. <https://doi.org/10.1016/j.genhosppsych.2005.07.003>.
- McPherson, M.J., Barrett, F.S., Lopez-Gonzalez, M., Jiradejvong, P., Limb, C.J., 2016. Emotional intent modulates the neural substrates of creativity: an fMRI study of emotionally targeted improvisation in jazz musicians. *Sci. Rep.* 6 (November 2015), 18460. <https://doi.org/10.1038/srep18460>.
- Mullensiefen, D., Gingas, B., Musil, J., Steward, L., 2014. The musicality of non-musicians : an index for assessing musical sophistication in the general population. *PLoS One* 9 (2). <https://doi.org/10.1371/journal.pone.0089642>.
- Nguyen, V.T., Breakpear, M., Hu, X., Guo, C.C., 2016. The integration of the internal and external milieu in the insula during dynamic emotional experiences. *Neuroimage* 124, 455–463. <https://doi.org/10.1016/j.neuroimage.2015.08.078>.
- Nummenmaa, L., Glerean, E., Viinikainen, M., Jaaskelainen, I.P., Hari, R., Sams, M., 2012. Emotions promote social interaction by synchronizing brain activity across individuals. *Proc. Natl. Acad. Sci.* 109 (24), 9599–9604. <https://doi.org/10.1073/pnas.1206095109>.
- Nummenmaa, Lauri, Lahnakoski, J.M., 2018. Sharing the Social World via Intersubject Neural Synchronization. <https://doi.org/10.1016/j.copsyc.2018.02.021>. March.
- Nummenmaa, Lauri, Saarikmäki, H., 2019. Emotions as discrete patterns of systemic activity. *Neurosci. Lett.* 693, 3–8. <https://doi.org/10.1016/j.neulet.2017.07.012>.
- Nummenmaa, Lauri, Saarikmäki, H., Glerean, E., Gotsopoulos, A., Jääskeläinen, I.P., Hari, R., Sams, M., 2014. Emotional speech synchronizes brains across listeners and engages large-scale dynamic brain networks. *Neuroimage* 102 (P2), 498–509. <https://doi.org/10.1016/j.neuroimage.2014.07.063>.
- Pajula, J., Kauppi, J.P., Tohka, J., 2012. Inter-subject correlation in fMRI: method validation against stimulus-model based analysis. *PLoS One* 7 (8). <https://doi.org/10.1371/journal.pone.0041196>.
- Pearson, J.M., Heilbronner, S.R., Barack, D.L., Hayden, B.Y., Platt, M.L., 2011. Posterior cingulate cortex: adapting behavior to a changing world. *Trends Cogn. Sci.* 15 (4), 143–151. <https://doi.org/10.1016/j.tics.2011.02.002>.
- Peelen, M.V., Atkinson, A.P., Vuilleumier, P., 2010. Supramodal representations of perceived emotions in the human brain. *J. Neurosci.: Off. J. Soc. Neurosci* 30 (30), 10127–10134. <https://doi.org/10.1523/JNEUROSCI.2161-10.2010>.
- Pereira, C.S., Teixeira, J., Figueiredo, P., Xavier, J., Castro, S.L., Brattico, E., 2011. Music and emotions in the brain: familiarity matters. *PLoS One* 6 (11). <https://doi.org/10.1371/journal.pone.0027241>.
- Power, J.D., Barnes, K.A., Snyder, A.Z., Schlaggar, B.L., Petersen, S.E., 2012. Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage* 59 (3), 2142–2154. <https://doi.org/10.1016/j.neuroimage.2011.10.018>.
- Proverbio, A.M., De Benedetto, F., 2018. Auditory enhancement of visual memory encoding is driven by emotional content of the auditory material and mediated by superior frontal cortex. *Biol. Psychol.* 132, 164–175. <https://doi.org/10.1016/j.biopsycho.2017.12.003>.
- Pruim, R.H.R., Mennes, M., Buitelaar, J.K., Beckmann, C.F., 2015. Evaluation of ICA-AROMA and alternative strategies for motion artifact removal in resting state fMRI. *Neuroimage* 112, 278–287. <https://doi.org/10.1016/j.neuroimage.2015.02.063>.
- Raz, G., Touroutoglou, A., Wilson-mendenhall, C., Gilam, G., Lin, T., Gonen, T., et al., 2016. Functional connectivity dynamics during film viewing reveal common networks for different emotional experiences. *Cognit. Affect. Behav. Neurosci.* 16 (4), 709–723. <https://doi.org/10.3758/s13415-016-0425-4>.
- Raz, G., Winetraub, Y., Jacob, Y., Kinreich, S., Maron-Katz, A., Shaham, G., et al., 2012. Portraying emotions at their unfolding: a multilayered approach for probing dynamics of neural networks. *Neuroimage* 60 (2), 1448–1461. <https://doi.org/10.1016/j.neuroimage.2011.12.084>.
- Sachs, M.E., Damasio, A., Habibi, A., 2015. The pleasures of sad music: a systematic review. *Front. Hum. Neurosci.* 9, 1–12. <https://doi.org/10.3389/fnhum.2015.00404>. July.
- Sachs, M.E., Ellis, R.J., Schlaug, G., Loui, P., 2016. Brain connectivity reflects human aesthetic responses to music. *Soc. Cogn. Affect. Neurosci.* 1–8. <https://doi.org/10.1093/scan/nsw009>. October 2015.
- Sachs, M.E., Habibi, A., Damasio, A., Kaplan, J.T., 2018. Decoding the neural signatures of emotions expressed through sound. *Neuroimage* 174, 1–10. <https://doi.org/10.1016/j.neuroimage.2018.02.058>. March.
- Salimpoor, V.N., Benovoy, M., Longo, G., Cooperstock, J.R., Zatorre, R.J., 2009. The rewarding aspects of music listening are related to degree of emotional arousal. *PLoS One* 4 (10). <https://doi.org/10.1371/journal.pone.0007487>.
- Salimpoor, V.N., van den Bosch, I., Kovacevic, N., McIntosh, A.R., Dagher, A., Zatorre, R.J., 2013. Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science* 340 (6129), 216–219. <https://doi.org/10.1126/science.1231059>.
- Schnell, K., Bluschke, S., Konradt, B., Walter, H., 2011. Functional relations of empathy and mentalizing: an fMRI study on the neural basis of cognitive empathy. *Neuroimage* 54 (2), 1743–1754. <https://doi.org/10.1016/j.neuroimage.2010.08.024>.
- Schubert, E., Halpern, A.R., Kreutz, G., Garrido, S., 2018. Attraction to sad music: the role of imagery, absorption, and rumination. *Psychology of Aesthetics, Creativity, and the Arts* 12 (3), 251–258. <https://doi.org/10.1037/aca0000160>.
- Shakil, S., Lee, C., Dawn, S., 2016. Evaluation of sliding window correlation performance for characterizing dynamic functional connectivity and brain states. *Neuroimage* 133, 111–128. <https://doi.org/10.1016/j.neuroimage.2016.02.074>.
- Shirer, W.R., Ryali, S., Rykhlevskaia, E., Menon, V., Greicius, M.D., 2012. Decoding subject-driven cognitive states with whole-brain connectivity patterns. *Cerebr. Cortex* 22 (1), 158–165. <https://doi.org/10.1093/cercor/bhr099>.
- Simony, E., Honey, C.J., Chen, J., Lositsky, O., Yeshurun, Y., Wiesel, A., Hasson, U., 2016. Dynamic reconfiguration of the default mode network during narrative comprehension. *Nat. Commun.* 7, 1–13. <https://doi.org/10.1038/ncomms12141>. May 2015.
- Singer, N., Jacoby, N., Lin, T., Raz, G., Shpigelman, L., Gilam, G., et al., 2016. Common modulation of limbic network activation underlies musical emotions as they unfold. *Neuroimage* 141, 517–529. <https://doi.org/10.1016/j.neuroimage.2016.07.002>.
- Singer, T., Lamm, C., 2009. The social neuroscience of empathy. *Ann. N. Y. Acad. Sci.* 96, 81–96. <https://doi.org/10.1111/j.1749-6632.2009.04418.x>.
- Taruffi, L., Koelsch, S., 2014. The paradox of music-evoked sadness: an online survey. *PLoS One* 9 (10), e110490. <https://doi.org/10.1371/journal.pone.0110490>.
- Taruffi, L., Pehrs, C., Skouras, S., Koelsch, S., 2017. Effects of sad and happy music on mind-wandering and the default mode network. *Sci. Rep.* 7 (1), 1–10. <https://doi.org/10.1038/s41598-017-14849-0>.
- Taylor, S.F., Phan, K.L., Decker, L.R., Liberzon, I., 2003. Subjective rating of emotionally salient stimuli modulates neural activity. *Neuroimage* 18 (3), 650–659. [https://doi.org/10.1016/S1053-8119\(02\)00051-4](https://doi.org/10.1016/S1053-8119(02)00051-4).
- Touroutoglou, A., Hollenbeck, M., Dickerson, B.C., Barrett, L.F., 2012. Dissociable large-scale networks anchored in the right anterior insula subserved affective experience and attention. *Neuroimage* 60 (4), 1947–1958. <https://doi.org/10.1016/j.neuroimage.2012.02.012>.
- Touroutoglou, A., Lindquist, K.A., Dickerson, B.C., Barrett, L.F., 2014. Intrinsic connectivity in the human brain does not reveal networks for “basic” emotions. *Soc. Cogn. Affect. Neurosci.* 10 (9), 1257–1265. <https://doi.org/10.1093/scan/nsv013>.
- Trost, W., Ethofer, T., Zentner, M., Vuilleumier, P., 2012. Mapping aesthetic musical emotions in the brain. *Cerebr. Cortex* 22 (12), 2769–2783. <https://doi.org/10.1093/cercor/bhr353>.
- Trost, W., Frühholz, S., Cochrane, T., Cojan, Y., Vuilleumier, P., 2015. Temporal dynamics of musical emotions examined through intersubject synchrony of brain activity. *Soc. Cogn. Affect. Neurosci.* 10 (12), 1705–1721. <https://doi.org/10.1093/scan/nsv060>.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15 (1), 273–289. <https://doi.org/10.1006/nimg.2001.0978>.
- Upham, F., McAdams, S., 2018. Activity analysis and coordination in continuous responses to music. *Music Percept. Interdiscip. J.* 35 (3), 253–294. <https://doi.org/10.1525/mp.2018.35.3.253>.
- Vessel, E.A., Starr, G.G., Rubin, N., 2012. The brain on art: intense aesthetic experience activates the default mode network. *Front. Hum. Neurosci.* 6, 66. <https://doi.org/10.3389/fnhum.2012.00066>. April.
- Vuoskoski, J.K., Eerola, T., 2012. Can sad music really make you sad? Indirect measures of affective states induced by music and autobiographical memories. *Psychology of Aesthetics, Creativity, and the Arts* 6 (3), 204–213. <https://doi.org/10.1037/a0026937>.
- Vuoskoski, J.K., Thompson, W.F., McIlwain, D., Eerola, T., 2012. Who enjoys listening to sad music and why? *Music Perception* 29 (3), 311–317. <https://doi.org/10.1525/mp.2012.29.3.311>.
- Watson, D., Clark, L. a. Tellegen, a., 1988. Development and validation of brief measures of positive and negative affect: the PANAS scales. *J. Personal. Soc. Psychol.* 54 (6), 1063–1070. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/3397865>.
- Wilson-mendenhall, C.D., Barrett, L.F., Barsalou, L.W., 2015. Variety in Emotional Life : Within-Category Typicality of Emotional Experiences Is Associated with Neural Activity in Large-Scale Brain Networks, pp. 62–71. <https://doi.org/10.1093/scan/nsu037>.
- Yeo, B.T.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., et al., 2011. The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* 106, 1125–1165. <https://doi.org/10.1152/jn.00338.2011>.
- Zentner, M., Grandjean, D., Scherer, K.R., 2008. Emotions evoked by the sound of music: characterization, classification, and measurement. *Emotion (Washington, D.C.)* 8 (4), 494–521. <https://doi.org/10.1037/1528-3542.8.4.494>.