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Functional connectivity profiles of the default mode and visual networks reflect temporal accumulative effects of sustained naturalistic emotional experience



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ABSTRACT

Determining and decoding emotional brain processes under ecologically valid conditions remains a key challenge in affective neuroscience. The current functional Magnetic Resonance Imaging (fMRI) based emotion decoding studies are mainly based on brief and isolated episodes of emotion induction, while sustained emotional experience in naturalistic environments that mirror daily life experiences are scarce. Here we used 12 different 10-minute movie clips as ecologically valid emotion-evoking procedures in n = 52 individuals to explore emotion-specific fMRI functional connectivity (FC) profiles on the whole-brain level at high spatial resolution (432 parcellations including cortical and subcortical structures). Employing machine-learning based decoding and cross validation procedures allowed to investigate FC profiles contributing to classification that can accurately distinguish sustained happiness and sadness and that generalize across subjects, movie clips, and parcellations. Both functional brain network-based and subnetwork-based emotion classification results suggested that emotion manifests as distributed representation of multiple networks, rather than a single functional network or subnetwork. Further, the results showed that the Visual Network (VN) and Default Mode Network (DMN) associated functional networks, especially VN-DMN, exhibited a strong contribution to emotion classification. To further estimate the temporal accumulative effect of naturalistic long-term movie-based video-evoking emotions, we divided the 10-min episode into three stages: early stimulation (1~200 s), middle stimulation (201~400 s), and late stimulation (401~600 s) and examined the emotion classification performance at different stimulation stages. We found that the late stimulation contributes most to the classification (accuracy=85.32%, F1-score=85.62%) compared to early and middle stimulation stages, implying that continuous exposure to emotional stimulation can lead to more intense emotions and further enhance emotion-specific distinguishable representations. The present work demonstrated that sustained happiness and sadness under naturalistic conditions are presented in emotion-specific network profiles and these expressions may play different roles in the generation and modulation of emotions. These findings elucidated the importance of network level adaptations for sustained emotional experiences during naturalistic contexts and open new venues for imaging network level contributions under naturalistic conditions.

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1. Introduction

Human emotion represents a dynamic process involving different levels of processing and integration (Cowen and Keltner, 2017; Horikawa et al., 2020). Determining the specific neurophysiological basis of emotions and their distinct neural representations can facilitate discriminating specific emotional states from other mental processes (Putkinen et al., 2021; Saarimäki et al., 2022; Vytal and Hamann, 2010; Zhou et al., 2020, 2021) and help evaluate emotion-specific dysregulations and corresponding treatment approaches (Reddan et al., 2018; Xu et al., 2022; Zhang et al., 2022). To capture the complex and dynamic nature of emotional processes, an increasing number of functional Magnetic Resonance Imaging (fMRI) studies examined cortical and subcortical responses during naturalistic contexts such as narratives or movies (Jääskeläinen et al., 2021; Putkinen et al., 2021; Saarimäki et al., 2022). The decodability of emotions using high-dimensional patterns of brain activity is supported by previous studies (Kragel et al., 2018; Kragel and LaBar, 2016). Recent neuroimaging studies have shown that distributed activity and functional connectivity (FC) patterns underly emotion perception and processing (Baucom et al., 2012; Kassam et al., 2013; Saarimäki et al., 2016; Zhou et al., 2020, 2021). However, the existing fMRI-based emotion studies seldom explore how emotions are represented under sustained and dynamic emotional engagement which better mirrors emotional processes in everyday life. To better understand emotion-related brain states under a naturalistic condition, we introduce a long-term naturalistic continuous emotion-evoking paradigm based on a number of movie clips. We chose comparably long-term movie clips to establish a naturalistic paradigm, which allows to neurofunctionally map the sustained emotional experience in real-world environments (Sonkusare et al., 2019). This naturalistic fMRI approach could offer a more powerful and reliable strategy to capture the complexity and variation of emotions across subjects and allow to generate ecologically valid brain signatures of emotional processes (Eickhoff et al., 2020).

Recent network level based perspectives on emotional brain processes suggest that dynamic interactions between brain regions play a significant role in emotional experience and regulation. To examine complex changes within integrative brain networks and interpret large-scale neuronal communication, FC has gained increasing interest. This approach provides a powerful tool to examine connectivity changes and complex integrative brain networks and to further determine the role of large-scale networks in emotional states, as has been demonstrated robust across individuals and task paradigms (Betti et al., 2013; Vanderwal et al., 2017; Wang et al., 2017b). FC reflects functional interaction between anatomically separated brain regions and is thought to reflect the temporal dependency of brain regions in terms of neural activation patterns. FC has been increasingly suggested to represent a robust biomarker for mental processes and their dysregulation, including emotion (Magalhães et al., 2021; Putkinen et al., 2021; Saarimäki et al., 2022; Zhuang et al., 2021), cognition (Cohen, 2018; Ptak et al., 2020; Zimmermann et al., 2018a), developmental changes (Ciarrusta et al., 2020; Liu et al., 2021; Teeuw et al., 2019), and brain disorders (Du et al., 2018; Xu et al., 2021; Zheng et al., 2018; Zhou et al., 2018; Zimmermann et al., 2018b). The feasibility of analyzing FC at the level of concordant patterns of temporal variations under both mental states of rest and task has been demonstrated (Cohen and D'Esposito, 2016). Recently, a number of FC-based emotionrelated brain network studies have been conducted (Pessoa, 2017, 2018; Putkinen et al., 2021; Saarimäki et al., 2022). For example, Putkinen et al. examined the emotion-related neurofunctional basis of four separate emotions evoked by music (happiness, sadness, fear, and tender) and observed that brain activity patterns in the auditory and primary motor cortices correlated with the respective emotional states (Putkinen et al., 2021). Saarimäki et al. introduced multivariate pattern analysis to develop a cross-subject emotion recognition approach that was based on whole-brain FC profiles. The study collected brain activity in 16 subjects during fMRI while the subjects were presented with 1-minute emotional audio narratives from six emotion categories (anger, fear, disgust, happiness, sadness, and surprise) (Saarimäki et al., 2022). The results showed that the most accurate emotion classification could be obtained from the Default Mode Network (DMN), indicating an important contribution of the DMN in emotional processing under naturalistic conditions. Collectively, these studies have demonstrated the feasibility to detect emotional changes via FC patterns in naturalistic environments. The high discriminative power of FCs has moreover been demonstrated in the classification of emotion-related diseases (Wang et al., 2020; Zeng et al., 2012, 2014). However, most previous emotion decoding studies relied on a few minutes of fMRI data, such as 45-second music (Putkinen et al., 2021) or 1-minute narratives (Saarimäki et al., 2022). Although these studies demonstrated the feasibility to decode specific emotions from FC patterns, the performance varied between emotional categories, in particular the specificity and accuracy for sadness remained limited. For instance, despite a high accuracy obtained for most emotions in Saarimäki et al.'s study (Saarimäki et al., 2022), it revealed a classification accuracy of sadness (18%) was close to chance level (16.67%). One possible reason might be the different time frames of emotional experiences and thus the difficulty in robustly evoking strong and engaging feelings of sadness with experimental stimuli as short as one minute. In contrast to emotions such as fear, surprise, or general negative affect which can be reliably induced by short and sparse stimuli (Čeko et al., 2022; Xin et al., 2020; Zhou et al., 2021), a strong subjective experience of sadness may require a longer time frame and more contextual information. To this end, longer immersive experimental stimuli may facilitate the induction of robust emotional experiences and allow more robust decoding (Waugh and Kuppens, 2021; Waugh et al., 2012).

On the other hand, recent studies using naturalistic paradigms with the presentation of movie clips (Demirtas et al., 2019; Gilson et al., 2018; Kim et al., 2018; Ren et al., 2018; Sonkusare et al., 2019) have shown that the estimated FC during movie-watching exhibits high testretest reliability and may allow to capture brain function under more naturalistic contexts thus better mimicking brain processes during reallife (Di and Biswal, 2020; Di et al., 2021; Wang et al., 2017b). In the context of emotion research, naturalistic movies in combination with fMRI could offer a more powerful and reliable tool for capturing the complexity and variation of emotions across subjects and under ecologically more valid emotion processing conditions (Eickhoff et al., 2020). To describe the dynamic functional integration of neural systems during induced sadness, Raz et al. (2012) employed films with respective lengths of 10 min and 8.27 min to induce sadness in more naturalistic contexts and employed a multi-layered dynamic approach to successfully track sadness based on predefined brain systems, including limbic, medial prefrontal and cognitive networks. This study underscored the potential of using continuous and complex stimulation to unravel the emotional experience of sadness. However, to our knowledge, a wholebrain network analysis under naturalistic long movie stimulation (e.g. 10 min) for distinguishing emotions and exploring the emotion-related temporal effects has not been conducted. In turn, the current evidence for emotion-related cortical and subcortical engagement in naturalistic contexts - especially for long and dynamic emotional experiences remains elusive (Kragel and LaBar, 2014; Lindquist and Barrett, 2012; Lindquist et al., 2012). To this end, the present study aimed to address the following open questions:

- 1. Which brain networks and connections exhibit emotion-specific contributions to the sustained emotional state on the whole-brain level?
- 2. To which extent do the network level profiles vary over time during the sustained emotion induction procedure?

To address these questions, we designed a naturalistic emotion induction paradigm including 12 different 10-minute movie clips (6 happy and 6 sad movie clips) and simultaneously recorded fMRI data in n = 52healthy subjects. We primarily focused on two distinct basic emotions, happiness, and sadness, which cover the positive and negative valence dimensions. To capture the hemodynamic brain changes during the movie clips on the whole-brain FC network level, a high spatial resolution parcellation with 400 cortical regions (Schaefer et al., 2018) and 32 subcortical regions (Tian et al., 2020) was adopted to examine emotionrelated network level changes. Next, a cross-subject cross-episode emotion classification model based on whole-brain-level FC analysis was developed and evaluated using a strict cross-subject leave-one-subject-out cross-validation. This data-driven analysis using the whole-brain FC patterns for the classification of two distinct basic emotions (happiness and sadness) allowed validation of the decoding models. The current study further allowed us to better examine the communications between different key brain regions during emotional processing under a naturalistic stimulation paradigm with movie clips. The decodability and generalizability of different functional networks on emotions across different subjects and movie clips were examined at different stimulation stages while the contributions of the brain areas during continuous emotion evoking under naturalistic movie clips could be determined and important discriminating whole-brain FC patterns could be evaluated.

2. Materials and methods

2.1. Participants

A total of 52 healthy right-handed subjects (male/female: 26/26; age: 19 to 28 years old, 23.52 ± 2.05 ; with normal or corrected-to-normal vision) from Shenzhen University were recruited to participate in the experiment. Exclusion criteria for subject recruitment included neurological or psychiatric diagnosis, heavy alcohol consumption within the past six months, cardiovascular disease, and severe visual impairment.

a Experimental design (naturalistic condition)

All the subjects signed the informed consent before starting the experiment, and the experiment was approved by the Ethics Committee of the Health Science Center, Shenzhen University. The experiment was in line with the latest version of the Declaration of Helsinki. After quality control, data from one subject (female; age: 19 years old) was excluded due to excessive head motion (refer to the given exclusion criteria for data preprocessing presented below).

2.2. Stimuli

Twelve 10-minute complex and naturalistic movie clips with strong and reliable emotion eliciting effects were selected from 12 different natural-colored movies. The 12 different 10-minute movie clip candidates included 6 happy stimuli (positive emotion) and 6 sad stimuli (negative emotion). There was no content overlap between the selected movie clips. The 6 happy stimuli were from the movies of "Mr. Popper's Penguins", "Ted", "The Onion Movie", "Liar", "A Thousand Words", and "Absolutely Anything", and the 6 sad stimuli were from "Miracle In Cell No.7", "Prayers For Bobby", "The Classic", "Grave Of The Fireflies", "Only The Brave", and "The Last Train". More details about the selected stimuli are reported in Appendix I of the Supplementary Materials.

2.3. Experimental paradigm

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The experimental paradigm is shown in Fig. 1(a). For each subject, the fMRI experiment under naturalistic stimulation included a total of 6 episodes (corresponding to 6 movie clips). The 6 movie clips were randomly chosen from the selected 12 different 10-minute movie clips, including 3 happy stimuli and 3 sad stimuli. The average selection rate of each stimulus was $8.33 \pm 1.28\%$. The total stimulation duration in the

Functional systems of interest



Fig. 1. Schematic overview of the study. (a) The experimental paradigm. For each subject, the experiment included 6 movie clips (episodes) presented in a randomized order. For each subject, 6 movie clips, including 3 happy movie clips and 3 sad movie clips, were randomly selected from a total of 12 different 10-minute movie clips. (b) The functional neural system and pathways of interest were defined based on the Schaefer 400 parcellations fMRI atlas (Schaefer et al., 2018). The left panel shows the coarse-level 7 network organization; the right panel shows the more fine-grained 17 subnetwork organization. (c) Next emotion classification models were established based on the calculated whole-brain functional connectivity (FC) matrices. The leave-one-subject-out cross-validation method was adopted to demonstrate the model robustness and generalizability. (d) Episode-based emotion classification models were employed to determine changes over the timecourse. To this end, FC profiles were extracted for different stimulation stages, i.e. early stimulation, middle stimulation, and late stimulation. The brain heatmaps visualize the regional contribution to the emotion classification, with cold(er) colors indicating lower contribution and hot(ter) colors reflecting a higher contribution.

fMRI experiment was 60 min for each subject, and the stimuli presentation order was randomized to counterbalance the order effect. Considering the difficulty in matching the sound quality and in warranting the understanding of the audio in the MRI environment the movie clips were presented without audio (similar approach see also (Horikawa et al., 2020; Mandelkow et al., 2016; Saarimäki et al., 2016)). To facilitate an understanding of the content, subtitles were incorporated into the movies. For a single episode, it comprised a 30-second baseline (subjects looked at the white cross shown in the center of a black screen to clear their mind), 10-minute movie playing (subjects passively viewed the movie clips with full engagement), and subjective feedback (subjects rated their emotional experience evoked by the presented movie clips using a 5-point happy-sad scale; more details are reported in Appendix I of the Supplementary Materials). At the end of one episode, the subjects could take a self-paced break. Throughout the whole procedure, the subjects were requested to remain still.

Brain images were recorded using a Siemens Prisma 3 Tesla MRI scanner with a 64-channel head coil. High-resolution T1-weighted structural images covering the entire brain were acquired using a magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence with the parameters as: voxel resolution=1×1×1 mm³, repetition time (TR)=2300 ms, echo time (TE)=2.26 ms, field of view (FOV)=256×232 mm², flip angle (FA)=8° During the experimental task, the functional images were acquired using a single gradient echo-planar imaging (EPI) sequence, with the parameters as: voxel resolution=2×2×2 mm³, TR=1000 ms, TE=30 ms, FOV=192×192mm², FA=90° Each volume of EPI functional images consisted of 65 slices. During scanning, all subjects were instructed to remain awake, keep their eyes open, and be in full engagement with the presented movie clips. All subjects completed six functional scans according to the selected 6 different 10-minute movie clips presented via E-Prime version 3.0. Movie clips were counter-projected on a screen and viewed through a mirror mounted on a head coil.

2.4. fMRI preprocessing

The functional images were preprocessed using SPM (Friston, 2003) and DPARSF (Yan et al., 2016) in MATLAB. Given that the scanner included dummy scans to stabilize the magnetic field, the first five volumes of each time series were not discarded. The structural images were first stripped of the skull and segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF) based on the results of the stripped skull. Then, all the functional images of each episode were aligned with the first volume of functional images using six head-motion parametric linear transformations, and the functional images of each subject were coregistered with the structural images. To remove the linear drift and reduce the interference of head movements and other physiological signals, nuisance covariate regression was conducted using the Friston 24-parameter model. The functional images were then normalized to Montreal Neurological Institute (MNI) space. A Gaussian kernel of 6 mm (FWHM) was adopted for spatial smoothing and a bandpass filter of 0.008-0.15 Hz was conducted for eliminating the low-frequency drift and high-frequency noise and improving the signal-to-noise ratio of the blood-oxygen-level-dependent (BOLD) signal (Wang et al., 2017b). Data with excessive head motion were discarded according to the following exclusion criteria: (1) an episode with a maximum translation of more than 2 mm or rotation of more than 2°; (2) for one subject, if more than 2 episodes (total 6 episodes) were discarded, data from this subject would be fully excluded. Following these quality assessment criteria, data from n = 51 subjects (total 293 samples, subjects × episodes) were retained for the following whole-brain FC analysis.

2.5. Definition of regions of interest

To ensure whole-brain coverage, the FC estimation was conducted using a brain parcellation atlas with 400 regions of interest (ROI) from the Schaefer 400 fMRI atlas that covers large-scale functional networks (Schaefer et al., 2018). Schaefer 400 ROIs parcellation integrated both local gradient and global similarity from rest-state and task-state FC. According to the clearly defined coordinates of the location of structural subdivisions in the whole-brain cortex, the parceled ROIs could be further categorized into 7 networks or 17 subnetworks at the coarse or fine level, respectively. As shown in Fig. 1(b), the coarse-level 7 networks included Visual Network (VN), SomatoMotor Network (SMN), Dorsal Attention Network (DAN), Ventral Attention Network (VAN), Limbic Network (LN), FrontoParietal Network (FPN), and Default Mode Network (DMN). The fine-level 17 subnetworks included VN-a, VN-b, SMNa, SMN-b, DAN-a, DAN-b, VAN-a, VAN-b, LN-a, LN-b, FPN-a, FPN-b, FPN-c, DMN-a, DMN-b, DMN-c, and Temporal Parietal Network (TPN). Besides, consistent with previous studies (Luppi et al., 2022; Luppi and Stamatakis, 2021), 32 subcortical ROIs were also considered based on the recently developed Melbourne subcortical functional parcellation atlas (Tian et al., 2020), which was obtained based on resting-state and task-state functionally connectivity and was consistent with the parcellation methodology in Schaefer 400. The 32 subcortical ROIs covered 7 subcortical regions, including the hippocampus, thalamus, amygdala, caudate nucleus, putamen, and globus pallidus. All the 32 ROIs were grouped into the Subcortex Network (SN). In total, 8 networks (7 cortical networks and 1 subcortical network) and 18 subnetworks (17 cortical subnetworks and 1 subcortical network) were included reflecting a broad and more fine-grained level of organization, respectively. Then, for each episode, the corresponding fMRI data could be represented as a $r \times t$ matrix, where r and t referred to the number of ROIs and time length (r = 432 and t = 600).

2.6. Functional connectivity estimation

In this study, we investigated whether the alternations of FC at different functional networks are associated with emotional states based on 432 ROIs (400 cortical regions and 32 subcortical regions). The functional signal time series of each ROI was extracted by averaging the BOLD signals of all voxels within the ROI according to the template, resulting in a BOLD time series of the size of $r \times t$ (r was the number of ROIs and t was the BOLD time series length) for each subject per episode. Here, an r-by-r FC matrix was obtained by Pearson's correlation between the averaged BOLD time series of each pair of ROIs. Further, Fisher's z-transform was applied to improve the normality of these correlation coefficients. Upper triangle elements of the FC matrix will be used as features to classify emotions in a cross-subject cross-episode manner.

2.7. Emotion classification modeling

A cross-subject cross-episode Support Vector Machine (SVM) with a linear kernel was trained to identify two distinct basic emotions (happiness and sadness), as shown in Fig. 1(c). In the previous literature (Du et al., 2018), SVM is among the most commonly used classification methods for cognitive and emotional brain states and achieves a stable and reliable classification performance. Here, a total of 293 samples (the retained data after fMRI preprocessing) were used for modeling based on the given video-based emotional labels, where the number of samples corresponding to happiness and sadness was 147 and 146, respectively. In the present study, three types of episode-based emotion classification models were built (Fig. 1(d)). (1) Whole-brain-based emotion classification modeling. We converted the upper triangular data of the FC matrix into a $(r \times (r-1))/2$ by 1 feature vector to perform modeling. (2) Network-based emotion classification modeling. We used the functional connection values within a network (e.g., the connection strength of ROIs within the VN) or between two networks (e.g., the connection strength of ROIs between the VN and DMN) as features for modeling. Since the connection matrices within networks were symmetric, only upper triangular data of the connection matrix within a network was

adopted. (3) Subnetwork-based emotion classification modeling. Similar to network-based modeling, we used the functional connection values within a subnetwork (e.g., the connection strength of ROIs in the VNa) or between two subnetworks (e.g., the connection strength of ROIs within the VN-a and VN-b) as features for modeling. To verify the model effectivity and stability on cross-subject cross-episode application, the classification performance was evaluated under a leave-one-subject-out cross-validation method which helps to verify the model generalizability on unknown subjects and episodes.

On the other hand, to further investigate whether the distributed FC patterns could reflect the accumulative (temporal) effect of sustained emotional experience, we separately estimated the classification performance of FC patterns at different stimulation stages. Here, we divided each episode into three stimulation stages: early stimulation stage $(1\sim200 \text{ s})$, middle stimulation stage ($201\sim400 \text{ s}$), and late stimulation stage ($401\sim600 \text{ s}$). Each stimulation stage was a 200 s duration. For each stage, a separate linear SVM classifier with a linear kernel was trained based on the same leave-one-subject-out cross-validation protocol.

Here, a strict leave-one-subject-out cross-validation was conducted as below. For each validation round, one subject's all episodes were used as the test data, and the remaining subjects' episodes were treated as the training data. The training data was used to train the classification model, and the trained model will be then utilized on the unused test data to measure the model performance. We repeated the training validation process until each subject's all episodes were used as the test data for once. The final model performance was an average of the obtained classification results across all the validation rounds.

2.8. Model performance evaluation

Five different evaluation metrics, classification accuracy P_{acc} , precision P_{pre} , sensitivity P_{sen} , F1-Score P_f , and specificity P_{spe} , were adopted to evaluate the model performance. Suppose the correctly predicted positive and negative samples are n_{TP} and n_{TN} and the incorrectly predicted positive and negative samples are n_{FP} and n_{FN} . The classification accuracy (P_{acc}) measures an overall classification performance, given as

$$P_{acc} = \frac{n_{TP} + n_{TN}}{n_{TP} + n_{FP} + n_{TN} + n_{FN}}.$$
 (1)

The precision (P_{pre}) and sensitivity (P_{sen}) are the measurement of the classification performance on positive samples, given as

$$P_{pre} = \frac{n_{TP}}{n_{TP} + n_{FP}},\tag{2}$$

$$P_{sen} = \frac{n_{TP}}{n_{TP} + n_{FN}}.$$
(3)

To be less susceptible to biased classification problems, we also estimated the corresponding F1-Score (P_f), which is defined as

$$P_f = \frac{2 \times P_{pre} \times P_{sen}}{P_{pre} + P_{sen}}.$$
(2)

The specificity (P_{spe}) is defined as

$$P_{spe} = \frac{n_{TN}}{n_{FP} + n_{TN}}.$$
(5)

The statistical significance of all the cross-validation results was further assessed using a permutation test (Combrisson and Jerbi, 2015). To obtain a zero distribution (with a chance level of 50%: 1 divided by the number of emotion categories) for assessing classification performance, we repeated the following procedure 1000 times to simulate the classification probability distribution as below: (1) randomly shuffled the video-based emotional labels of the samples; (2) conducted leave-one-subject-out cross-validation and measured the corresponding performance by averaging the classification accuracies in all the crossvalidation rounds; (3) compared the permutation results with the truly obtained results. The p-value was calculated as the ratio of the number of accuracies in permutation results greater than the true accuracy to the total number of accuracies in permutation results. Further, to eliminate the influence of type I errors in the emotion classification modeling, all the obtained p-values were corrected using the false discovery rate (FDR) (Genovese et al., 2002) for multiple comparisons.

3. Results

3.1. Whole-brain-based emotion classification

To estimate whether different sustained emotions would be represented in distinct FC patterns, we trained a cross-subject classifier using a brain-wide FC matrix to identify the two distinct basic emotions of happiness and sadness. The average FC matrices of happiness and sadness across subjects and episodes are shown in Fig. 2(a) and (b), and the statistical difference between happiness and sadness in terms of the FC patterns is shown in Fig. 2(c). The corresponding FC matrices of individual movie clips are presented in Appendix II of Supplementary Materials. The whole-brain-based emotion classification corresponded to an accuracy of 80.55%. All the results were significantly higher than the random accuracy level in the permutation test (chance level=50%; permutation test p < 0.0001). The distribution of the obtained random accuracies in the permutation test (repeated 1000 times) is shown in Fig. 2(d). The corresponding confusion matrix is shown in Fig. 2(e), where the average classification accuracy for happiness and sadness was 80.27% (p<0.0001) and 80.82% (p<0.0001), respectively. The results revealed that a high cross-subject cross-trial emotion classification performance could be achieved using whole-brain FC patterns suggesting that it is feasible to differentiate happiness and sadness based on wholebrain connectivity signatures. Next, based on the classification performance, we determined whether different large-scale networks in terms of 8 networks and 18 subnetworks show a specific contribution to emotion classification.

3.2. Network-based emotion classification

We next investigated which intra- and inter-brain functional networks are most contributing to the classification of the two distinct basic emotions (happiness and sadness). Based on the defined 8 networks (7 cortical networks and 1 subcortical network), we extracted the FC patterns within/between each network and built the emotion classification model separately. The average classification accuracy of each intra- and inter-network is reported in Fig. 3(a). The classification results were assessed using the permutation test, and only the classification results of both happiness and sadness were statistically greater than the random results were considered as significant (p < 0.0001, FDR corrected). The obtained significance of the classification results relative to the random level is reported in Appendix III of Supplementary Materials. The results showed that the FC profiles contributing the most to the classification of happiness and sadness were mainly located in within and between network connections involving the VN and DMN, as shown in Fig. 3 (b). This may reflect the visual and naturalistic nature of our paradigm, which will rely on the communication between the visual system with other brain systems such as the DMN. The statistical analysis allowed us to test the significant classification networks with detailed results (see Table 1). The best classification performance was obtained when the FC between the VN and DMN was adopted. The interactions between VN and DMN were in line with the economic account of large-scale brain network organization (Chen et al., 2013; Raichle, 2015; Vatansever et al., 2017; Vessel et al., 2019), which indicates the information transmissions between lower-level sensory brain areas and high-level functional brain areas. For all the reported results, the permutation test verified that the probability of achieving such high classification performance by chance was less than 0.0001 (p<0.0001, FDR corrected). The results showed the functional network connections contributing to emotion classification predominated involved VN and



Fig. 2. Whole-brain-based emotion classification results. The averaged FC matrices of (a) happiness and (b) sadness. The color indicates the obtained z values after Fisher's z transformation. (c) The statistical difference between (a) and (b). All the presented results were FDR corrected, with p<0.05. (d) The histogram distribution of the classification accuracies was obtained in the permutation test (repeated 1000 times). The red dot line indicates the obtained whole-brain-based emotion classification accuracy (P_{acc} =80.55%), where the corresponding P_f , P_{pre} , P_{sen} , P_{spe} are 80.55%, 80.82%, 80.27%, and 80.82%, respectively. (e) The obtained confusion matrix.



Fig. 3. The network-based emotion classification performance. (a) The classification accuracy when each network was separately used for modeling. Here, *** indicates the networks with statistically significant classification ability (p<0.0001, FDR corrected). (b) The VN and DMN related network-based functional connections with a statistically significant classification ability (p<0.0001, FDR corrected). (b) The VN and DMN related network-based functional connections with a statistically significant classification ability (p<0.0001, FDR corrected). Thicker and redder connection lines indicate higher classification accuracy and vice versa.

Table 1

The network-based emotion classification performance with detailed results. All the reported results were statistically significant (p<0.0001, FDR corrected).

Networks	Overall Perfo	Happiness	Sadness				
	Accuracy	F1-score	Precision	Sensitivity	Specificity	Accuracy	Accuracy
VN	72.01%	72.11%	72.11%	72.11%	71.92%	72.11%	71.92%
VN-DMN	77.82%	77.03%	80.15%	74.15%	81.51%	74.15%	81.51%
VN-VAN	75.77%	76.09%	75.33%	76.87%	74.66%	76.87%	74.66%
VN-DAN	75.09%	74.74%	76.06%	73.47%	76.71%	73.47%	76.71%
VN-SMN	72.01%	72.11%	72.11%	72.11%	71.92%	72.11%	71.92%
VN-LN	69.28%	68.53%	70.50%	66.67%	71.92%	66.67%	71.92%
VN-SN	69.62%	69.42%	70.14%	68.71%	70.55%	68.71%	70.55%
DMN-VAN	70.31%	70.51%	70.27%	70.75%	69.86%	70.75%	69.86%
DMN-FPN	74.40%	75.08%	73.38%	76.87%	71.92%	76.87%	71.92%
DMN-SMN	68.60%	69.74%	67.52%	72.11%	65.07%	72.11%	65.07%
DMN-LN	70.65%	71.14%	70.20%	72.11%	69.18%	72.11%	69.18%

DMN. Those network systems could be considered to involve the most informative features for emotion classification, where a high classification ability could be more prevalently observed.

3.3. Subnetwork-based emotion classification

The above network-based classification results suggested that the differences between happiness and sadness were primarily located in the functional connections within and between the VN and DMN. Next, we further investigated the details in the corresponding networks and analyzed the classification performance of the involved subnetworks. Examination of functional networks in terms of subnetworks was expected to offer a deeper understanding of the classification ability in the distinction of the two distinct basic emotions. Based on the subnetwork connections of the defined 18 large-scale subnetworks (17 cortical subnetworks and 1 subcortical network), we estimated the corresponding classification performance on the distinction of emotions (Fig. 4(a)). After the permutation test, the functional connections with significant classification accuracies (p<0.0001, FDR corrected) were mainly located within DMN, between DMN and other subnetworks, and between VN-a and other subnetworks, as shown in Fig. 4 (b). All the obtained significance of the classification results relative to the random level is reported in Appendix IV of Supplementary Materials. After the statistical analysis, the performance of the subnetworks contributing to the classification is reported in Table 2. The best classification performance was achieved when the FC between DMN-a and FPN-c was utilized. It was found that the classification performance using the functional connections related to the VN-a was better than that using the functional connections related



Fig. 4. The subnetwork-based emotion classification performance. (a) The VN and DMN related subnetwork-based classification results. (b) The VN and DMN related subnetwork-based functional connections with a statistically significant classification ability (*p*<0.0001, FDR corrected). Thicker and redder connection lines indicate higher classification accuracy and vice versa.

Table 2

The subnetwork-based emotion classification performance with detailed results. All the reported classification results were statistically significant (p<0.0001, FDR corrected).

	Overall Perfe	Happiness	Sadness				
Networks	Accuracy	F1-score	Precision	Sensitivity	Specificity	Accuracy	Accuracy
VN-a - VN-b	73.72%	73.36%	74.65%	72.11%	75.34%	72.11%	75.34%
VN-a - DMN-a	73.38%	72.54%	75.18%	70.07%	76.71%	70.07%	76.71%
VN-a - DMN-c	73.38%	72.14%	75.94%	68.71%	78.08%	68.71%	78.08%
VN-a - VAN-b	72.35%	72.16%	72.92%	71.43%	73.29%	71.43%	73.29%
VN-a - DAN-a	71.33%	70.63%	72.66%	68.71%	73.97%	68.71%	73.97%
VN-a - DAN-b	73.38%	72.34%	75.56%	69.39%	77.40%	69.39%	77.40%
VN-a - FPN-a	68.94%	69.36%	68.67%	70.07%	67.81%	70.07%	67.81%
VN-a - LN-a	70.99%	70.79%	71.53%	70.07%	71.92%	70.07%	71.92%
VN-b - FPN-a	68.60%	68.71%	68.71%	68.71%	68.49%	68.71%	68.49%
DMN-a - DMN-c	69.97%	69.44%	70.92%	68.03%	71.92%	68.03%	71.92%
DMN-a - VAN-a	67.92%	68.67%	67.32%	70.07%	65.75%	70.07%	65.75%
DMN-a - FPN-c	74.40%	75.08%	73.38%	76.87%	71.92%	76.87%	71.92%
DMN-b - DMN-c	69.97%	71.05%	68.79%	73.47%	66.44%	73.47%	66.44%
DMN-b - DAN-a	70.65%	70.55%	71.03%	70.07%	71.23%	70.07%	71.23%

Table 3

The stimulation-stage-based emotion classification performance using all the VN and DMN related FCs. All the results were statistically significant with p<0.0001 (FDR corrected).

Stimulation	Overall Perfor	mance	Happiness	Sadness			
	Accuracy	F1-score	Precision	Sensitivity	Specificity	Accuracy	Accuracy
Entire	80.55%	80.55%	80.82%	80.27%	80.82%	80.27%	80.82%
Early	78.50%	77.89%	80.43%	75.51%	81.51%	75.51%	81.51%
Middle	81.23%	81.36%	81.08%	81.63%	80.82%	81.63%	80.82%
Late	85.32%	85.62%	84.21%	87.07%	83.56%	87.07%	83.56%

to the VN-b. This indicated that the FC patterns in the VN contributing to classification mainly existed in the central visual area, instead of the surrounding visual area. For the functional connection between DMN and FPN, the FC patterns contributing the most to the classification were mainly distributed between DMN-a and FPN-c.

3.4. Stimulation-stage-based emotion classification

We further examined whether the FC profiles change over the period of sustained emotional experiences. To this end, we divided each episode into three stages: early stimulation (1~200 s), middle stimulation (201~400 s), and late stimulation (401~600 s), and performed the calculation of FC matrices at each stage separately. For each stimulation stage, the emotion classification models were separately built based on the FC of VN and DMN, and the efficient emotion-evoking stage(s) were investigated in terms of emotion classification ability. As shown in Table 3, the average classification accuracies based on the entire stimulation period, early stimulation stage, middle stimulation stage, and late stimulation stage were 80.55%, 78.50%, 81.23%, and 85.32%, respectively. The classification results between entire and late and between early and late were statistically different (p<0.05, FDR corrected). The corresponding confusion matrices are shown in Fig. 5. The results revealed that the classification performance of the entire stimulation period could be considered as an average performance of the early, middle, and late stimulation stages. Among the three stimulation stages, it was found that the classification performance based on the late stimulation period was superior to the other stimulation periods, which may additionally reflect that emotions evolve cumulatively over sustained exposure and long-term emotion stimulation could be beneficial to intense emotion elicitation.

Further, we estimated the subnetwork-based classification abilities at each stimulation stage and examined whether there exists an FC pattern shifting of emotion-related contributions of the brain areas during the long-term emotional processing. All the obtained significance of the classification results relative to the random level is reported in Appendix V of Supplementary Materials. As shown in Fig. 6, it was found the predominantly distributed emotion-related FC patterns were slightly different at different stimulation stages. A brain visualization of the results was presented in Fig. 1(e). On the other hand, all the classification results using one subnetwork or different subnetwork pairs were



Fig. 5. The obtained confusion matrices using all the VN and DMN related FCs at (a) the whole stimulation period, (b) the early stimulation stage, (c) the middle stimulation stage, and (d) the late stimulation stage.







(b)





Fig. 6. The classification results of FC patterns at different stimulation stages: (a) early, (b) middle, and (c) late. The corresponding subnetwork-based functional connections with statistically significant classification ability (p<0.0001, FDR corrected) are shown in (d), (e), and (f). Thicker and redder connection lines indicate higher classification accuracy and vice versa.

much lower than those using FC related to all subnetworks of the VN and DMN. The results demonstrated that emotion-related brain functions are dominated by distributed network systems, instead of a single network/area.

4. Discussion

The present study capitalized on sustained and ecologically valid induction of happiness and sadness via long movie clips and applied classification modeling to determine whether these emotions are represented in distinct whole-brain network level signatures. We therefore explored high-resolution network level profiles and developed neuroimaging-based cross-subject cross-episode emotion classification signatures via functional networks. The main objectives of the present study include: (1) applying the machine learning method to analyze fMRI FC information and providing a proof-of-concept emotion classification model under a naturalistic experimental design employing sustained emotional induction, and (2) exploring distinct network patterns associated with two distinct basic emotions through a more natural experimental paradigm. According to the results, we observed a significant difference in the whole-brain FC patterns when different emotions were evoked, where the results were fully evidenced by better emotion classification performance statistically significant than the random level (p < 0.0001, FDR corrected). The results suggested that distinct basic emotions, happiness and sadness, have distinguishable and distributed neural representations on the whole-brain connectivity level, with the VN and DMN associated networks (intra- and inter-FC patterns of VN and DMN) making the major contribution to the identification of the specific emotional states. Our key findings can be summarized as follows: (1) Happiness and sadness elicited by long-term movie clips have discrete neural representations, reflected in FC profiles. (2) The distinctive FC patterns for happiness and sadness are mainly represented in VN and DMN associated networks. (3) Examining changes over the stimulation period (early, middle, and late presentation periods of the movie) revealed that naturalistic emotional experience is an accumulative process such that the emotion-specific signatures became more distinct over the course of the sustained stimulation. (4) The estimated distinguishable ability of FC profiles on sustained happiness and sadness are consistent across subjects, movie clips, and parcellations. Together, these results underscore that interactions between brain regions contribute to emotional experiences under naturalistic conditions and that different emotions are represented in distinct network level profiles.

4.1. Functional connectivity profiles associated with emotions

The present study showed that different patterns of whole-brain FC characterize specific emotional experiences. The emotion classification results suggested that the whole-brain FC patterns can accurately distinguish happy and sad emotional processing and that the corresponding emotion-specific changes are not restricted to a single region/network, but distributed across multiple networks that primarily involve the VN and DMN. The VN and DMN may thus represent key network systems that encode specific emotional experiences and vary their interaction with other systems according to the external environment and the subjective emotional state. These findings converge with previous neuroimaging emotion studies which demonstrate the important roles of the VN and DMN networks during processes involving emotional experiences and emotion regulation (Jaworska et al., 2015; Nguyen et al., 2019; Phan et al., 2002; Satpute and Lindquist, 2019; Vytal and Hamann, 2010).

A previous fMRI study of emotion-related processing with visual stimuli revealed that the modulated brain regions in emotional processing critically relied on the stimulus type (Keightley et al., 2003). The superior classification performance between the VN and other networks in the present study further supports the idea and suggests an important role in visual processing regions as early processing nodes for emotional information. Recent visual-related fMRI studies suggest that the role of visual processing areas extends beyond the simple perception of visual information (Cai et al., 2017; Guo et al., 2012; Katzner and Weigelt, 2013). A number of studies have shown that emotional content is also encoded and recovered in brain areas of VN (ventral visual stream). For example, Mickley and Kensinger (2008) found that, in the emotion encoding process, the involvement of visual areas made it possible for negatively related emotional memories to be recalled vividly. A previous study reported that visual processing regions were closely related to the evoked complex emotions and that distributed representations in the human visual system reliably classify distinct emotions (Kragel et al., 2019). In addition, it has been found that different visual cortical areas are modulated by different categories of emotions (Thakral et al., 2022). Mourao-Miranda et al. (2003) found that the pictures with negative emotions produced stronger activity in V1, compared to the pictures with positive emotions. In our subnetwork-based emotion classification results, we observed that the emotion-related FC patterns in the visual areas are predominantly distributed in the central visual area (VN-a), instead of the peripheral visual area (VN-b). The central visual area includes the striate cortex (V1) and extrastriate cortex, while the peripheral visual area covers the extrastriate superior and inferior. One possible reason for the predominant distribution of the VN-a might be that emotions such as sadness involve stronger responses in sensory processing in the V1 cortex. One study has elucidated this phenomenon by suggesting that negative information elicits selective attentional priorities and attentional resources relative to positive information (Yiend, 2010).

The strong classification ability of DMN in the distinction of emotions aligns with previous studies. The DMN, including the posterior cingulate cortex (PCC), precuneus, medial prefrontal cortex (MPFC), inferior parietal lobule (IPL), and bilateral temporal cortex regions, encompasses important and unique mental capacities (Raichle, 2015; Raichle et al., 2001; Satpute and Lindquist, 2019). DMN has been widely found to be involved in internal attention, such as autobiographical memory (Buckner et al., 2008; Schacter and Addis, 2007), rumination (Hamilton et al., 2015; Whitfield-Gabrieli and Ford, 2012), social cognition (Spreng et al., 2009; Van Overwalle, 2009), social evaluation (Gusnard et al., 2001; Hamilton et al., 2015), and internal mentation (Andrews-Hanna et al., 2014). The neural substrates related to internal attention processing also contribute to emotional processing (Craig, 2009; Critchley et al., 2005; Pollatos et al., 2007). Previous studies also reported that the DMN plays a crucial role in the representation of individual emotions (Satpute and Lindquist, 2019), especially the ventral and anterior medial prefrontal cortices (vmPFC and amPFC). As the central areas in DMN, vmPFC, and amPFC are associated with emotion generation, integration, processing, and regulation (Gusnard et al., 2001; Raichle et al., 2001; Veer et al., 2011). Satpute and Lindquist also suggested that DMN may participate in emotion by supporting conceptual progress, which facilitates the ability to experience specific physiological sensations and contribute to the composition of emotion categories (Satpute and Lindquist, 2019). The present study confirms that DMN supports the integration of both visual and semantic information (Lim et al., 2013) and the involvement in emotion regulation and emotion-related decision-making (Rolls et al., 2022).

4.2. Emotion-related coordinated function of distributed network systems

Using the whole-brain FC profiles for emotion classification achieved a significantly better performance than using single network information. This suggests that emotion-specific FC patterns are not present in a single network or region, but require a distributed representation within and between multiple networks. In the investigation of the emotionassociated brain circuits, it was observed that emotion relies on largescale functional network interaction (Pessoa, 2017). Studying the wholebrain FC using multivariate and machine learning analysis benefits distinguishing emotions (Pessoa, 2018). The powerful classification ability of VN and DMN associated network systems supports that the neural representation of different emotional experiences is a widely distributed representation with VN and DMN as the core and multiple networks operating in concert. The involvement of large-scale brain interaction provides evidence that the connections between brain regions play a significant role in emotion.

These observations align with previous fMRI studies of emotions, reporting that a number of fundamental emotional states depend on large-scale cortical and subcortical interactions, rather than engaging isolated networks/regions (Damasio and Carvalho, 2013; Kober et al., 2008; Lindquist et al., 2012; Nummenmaa et al., 2014; Saarimäki et al., 2016; Vytal and Hamann, 2010). Together with the present findings, this reflects that emotions are represented in distributed networks spanning multiple brain systems (Kragel and LaBar, 2015; Wager et al., 2015; Zhou et al., 2021). It was found that the specific brain regions contributing to emotion decoding showed a similar tendency to distribute across the canonical networks while the VN and DMN networks accounted for about half of the total and the remaining DAN, VAN, LN, FPN, and SMN networks accounted for about the other half. Wager et al. (2015) used a hierarchical Bayesian model to analyze the patterns of human brain activity under five emotion categories (fear, anger, disgust, sadness, and happiness), showing that emotion categories were not contained in any one region or system but were represented as synergistic across multiple brain networks cooperation. Saarimäki et al. (2016) work also verified the neural representations of discrete emotional experiences are distributed across multiple brain regions (Gao et al., 2020; Horikawa et al., 2020; Saarimäki et al., 2018). Different emotions are associated with activation changes across multiple functional systems, and the underlying spatial distribution configuration ultimately defines specific emotions at the psychological and behavioral levels (Saarimäki et al., 2018). Furthermore, the theory of constructed emotion suggests that all emotions consist of a shared set of basic functional systems that are not specific to emotion processing per se (Kober et al., 2008; Lindquist et al., 2012). We consider that the shared basic emotional systems consisting of discrete emotional experiences induced by the long-term naturalistic continuous emotion-evoking paradigm exhibit a similar engagement of networks at the whole-brain level, yet that the VN and DMN may play an integrative role within these networks.

4.3. Engagement of brain networks during sustained naturalistic emotional experience

Naturalistic stimulation, such as audio narratives or short movies, has been increasingly demonstrated to allow a more ecologically valid and comprehensive experimental assessment of brain processes than sparse experimental stimuli (e.g. emotional words) with high reproducibility (Matusz et al., 2019; Zhang et al., 2021). Compared with the traditional experimental paradigms of blocked design or event-related design, naturalistic stimulation shows some compelling advantages (Bottenhorn et al., 2018; Meer et al., 2020; Simony and Chang, 2020) including the engagement of complex and interacting brain states while closely simulating brain processes in real-life (DuPre et al., 2020; Jääskeläinen et al., 2021). Emerging evidence and conceptual work suggest that ecologically valid scenarios offer some benefits over traditional parametric task designs, including a test of experimental brain models under ecologically valid conditions (Puckett et al., 2020; Sonkusare et al., 2019; Vanderwal et al., 2022). With respect to emotionrelated studies, the naturalistic paradigms enable a more ecologically valid approach to the dynamic neurophysiological processes that underly the different emotional states in everyday life (Lettieri et al., 2019).

However, most of the previous emotion-related studies were conducted using naturalistic stimuli with a short duration, such as pictures (Bush et al., 2018), music (Putkinen et al., 2021), short movie clips (Wang et al., 2017a), and movie trailers (Chan et al., 2020), to elicit subjects' specific emotional experience in a highly controlled laboratory environment. In real life, several emotional states evolve over longer time periods and emotions such as vivid sadness may require a high level of contextualization to fully evolve. The emotion elicitation with short stimuli may fail to effectively evoke the specific emotional experience, which would further affect the following brain analysis and lead to poor emotion estimation results. For example, in Saarimäki et al.'s work (Saarimäki et al., 2022), the mean classification accuracy on sadness was the lowest (18%), which was close to the chance level (16.67%). A similar situation occurred in another fMRI-based emotion recognition work (Saarimäki et al., 2016), where the emotion classification result on sadness was still the lowest. One possible reason for leading the classification performance of sadness being much worse than the other emotions could be that the stimulus ((Saarimäki et al., 2022): 1minute narrative; (Saarimäki et al., 2016): 10-second movie clips) is too short to elicit a strong and deep sad emotion and further fail to bring a significant change in the brain activities. On the other hand, it was found that prolonged and complex movie clips are more suitable to induce dynamic changes of sustained emotional experience of some emotions, i.e. sadness (Raz et al., 2012). The initial results suggest that an efficient induction of sadness may require longer periods of immersive emotional engagement. The present study extended the initial findings from Raz et al. (2012), with respect to employing a wholebrain connectivity approach to a broader emotional spectrum including both happiness and sadness, while capitalizing on a larger sample (52 individuals) and more movie clips (12 different 10-minute movie clips), thus providing a more holistic and comprehensive perspective on the dynamic interactions within and between functional networks during the prolonged experience of emotional states in naturalistic environments. Besides, Betzel et al. (2020) found the temporal fluctuation in network integration and segregation during movie-watching, sharing consistent patterns across individuals. In the present study, we divided the whole stimulation period into early, middle, and late stages to explore whether the network level representations change over time during sustained naturalistic emotion processing. We found that the corresponding classification performance at the late stimulation stage (85.32%) was considerably better as compared to the early (78.50%) and middle (81.23%) stimulation stages, while the decoding performance for both, happy and sad emotional experiences was generally high. As evidenced by the stimulation-stage-based emotion classification results, the emotional experience is sustainable accumulation, reflected in the corresponding brain activities with evidence of the growth classification ability. This resonates with previous findings suggesting that the time of emotional exposure may affect emotional experiences and neural expressions (Résibois et al., 2017; Waugh and Kuppens, 2021; Waugh et al., 2012). For instance, emotional stimuli tend to be better remembered in long-lasting contextual memory and those long-term emotional stimuli can enhance the effectiveness of emotional elicitation by enhancing contextual memory (Dolcos et al., 2013).

4.4. Classification ability is consistent across subjects, movie clips, and brain parcellations

A comprehensive network level description of whole-brain FC patterns may allow a powerful classification determination of specific emotional states such as happiness and sadness. Further, we examined the consistency of the classification ability on different subjects, movie clips, and brain parcellations, respectively.

To further explore the individual differences in classification performance, we separately examined each subject's decoding performance to clarify whether the brain networks exhibit a consistent contribution to classification. The corresponding results are presented in Appendix VI of the Supplementary Materials. A high classification accuracy of the VN and DMN associated networks was consistently observed across subjects, with an average performance enhancement of 5.87%, suggesting a consistent contribution of these networks to emotion classification on the individual level. On the other hand, variance in the classification performance among different individuals was observed, possibly reflecting individual differences in the emotional experience and emotional perception, or the corresponding neurofunctional representation across subjects. For instance, the emotion classification on subject 32 achieved good performance, with an average classification performance using all networks and VN and DMN associated networks were 80.56% and 85.33%, respectively. In contrast, both classification performance based on all networks and VN and DMN associated networks were close to the chance level in subject 24. These observations underscore individual differences and may reflect different levels of emotional engagement between the subjects or individual variations in the "typical" contextspecific functional brain organization. The difference in emotion perception may also be related to individual differences in emotional traits or past experiences (Kragel et al., 2016; Li et al., 2019; Maier et al., 2020) or by the nature of cognitive processes engaged in the interpretation of the movie or the interoceptive emotional experiences (Dolcos et al., 2013; Petro et al., 2018), rather than the properties of the stimuli themselves.

In addition, to verify the emotion stimulation effect of the selected movie clips, we also investigated the cross-subject classification performance of each movie clip separately based on different intra- and internetworks. The corresponding results are presented in Appendix VII of the Supplementary Materials. Comparing the classification performance using all networks and VN and DMN associated networks, a consistently better classification performance across all movie clips with an average enhancement of 5.01%, for the VN and DMN associated networks was observed. These results reflect that the classification contribution of the VN and DMN is highly consistent across different movie clips.

Moreover, we evaluated the consistency of the classification ability at different levels of granularity, i.e. different brain parcellations. In the main analysis, we adopted a higher spatial resolution parcellation (Schaefer 400) for the whole-brain network analysis of the sustained emotional experience. To explore whether the level of parcellation influences the results, we repeated the data analysis based on different parcellations (Schaefer et al., 2018): Schaefer 200, Schaefer 300, and Schaefer 400 each including the identical subcortical network parcellation (Tian et al., 2020). To this end, we conducted the emotion classification and comparison of the performance using all networks and VN and DMN associated networks. The corresponding results are reported in Appendix VII of the Supplementary Materials, and show that consistently better classification results could be obtained at different parcellations with an average enhancement of 4.09%, when VN and DMN associated networks were utilized. These results confirm that the classification ability of VN and DMN associated networks is highly consistent across different parcellations.

4.5. Limitations and future work

One limitation of the present study is that the movie clips were presented without sound. Although this approach is in line with previous studies and across these studies the emotion-related neural representation could be successfully established (Horikawa et al., 2020; Mandelkow et al., 2016; Saarimäki et al., 2016), future studies should consider to incorporate audiovisua presentations to further increase similarity to sustained emotional experiences in naturalistic environments. Another limitation of the present study refers to the emotional labels that were used for modeling. The evaluation of one movie clip was based on a summary emotional ratings across the entire movie. While our decoding model was capable of establishing the difference in FC profiles between two distinct basic emotions, the adopted emotional labels cannot reflect the emotional changes through a long-term movie clip with a duration of 10 min. Hence, to the extent that the emotion changes over time and the climax in emotion intensity across different movie clips could be different, future studies might annotate dynamic emotional labels for each movie clip and further study the dynamic relationship among neural representations, dynamic emotional labels, and video content. Finally, the temporal accumulative effect on different genres of movie clips (e.g. a stereotypical narrative in the movie clip with an intended climax in emotion intensity) was not explored in the present work. In a previous study from Kragel et al. (2019), it was reported that emotion classification during watching romantic comedies was more accurate than that during watching a horror or action movie. Future experiments are needed to examine the temporal accumulative effect of sustained emotional experience evoked by different genres of long movie clips at a more precise level.

5. Conclusion

The present study investigated the classification ability of wholebrain FC patterns to determine distinct neurofunctional representations of two distinct basic emotions during naturalistic movie watching. This approach allowed us to explore a higher-order neural process under ecologically valid experimental conditions of sustained emotional experiences. Our work provided preliminary evidence that the VN and DMN associated networks exhibit a strong contribution to the classification and thus may represent integrative networks that orchestrate the whole-brain network level expressions of specific emotional states. The results further emphasized the role of network level changes as the basis of different sustained emotional experiences under ecologically valid conditions and revealed the temporal accumulative effect in emotions could be reflected by neural representations. Our findings suggested that the naturalistic long-term movie-watching paradigm evoked emotions manifest as distributed representations of multiple networks operating in concert with the VN and DMN as the core. This paper provides compelling evidence and unique insights into the emotion-related FC patterns that support emotion perceiving and processing and reveal the importance of the VN and DMN coordination to emotions.

Data and code availability statement

The data and code used in the present study are made available on the website "https://sites.google.com/site/janezhenliang/fmriemo".

To gain access to the data and code materials, a license agreement should be printed, signed, scanned, and returned to us via email to "janezliang@szu.edu.cn", with the subject line "fMRI Happy/Sad account request". Please send the request using your institutional email.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Credit authorship contribution statement

Shuyue Xu: Investigation, Data curation. Zhiguo Zhang: Methodology, Funding acquisition. Linling Li: Methodology, Validation. Yongjie Zhou: Conceptualization. Danyi Lin: Validation. Min Zhang: Methodology. Li Zhang: Visualization. Gan Huang: Software. Xiqin Liu: Writing – review & editing. Benjamin Becker: Conceptualization, Writing – review & editing. Zhen Liang: Conceptualization, Resources, Writing – original draft, Project administration.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119941.

References

- Andrews-Hanna, J.R., Saxe, R., Yarkoni, T., 2014. Contributions of episodic retrieval and mentalizing to autobiographical thought: evidence from functional neuroimaging, resting-state connectivity, and fMRI meta-analyses. Neuroimage 91, 324–335.
- Baucom, L.B., Wedell, D.H., Wang, J., Blitzer, D.N., Shinkareva, S.V., 2012. Decoding the neural representation of affective states. Neuroimage 59, 718–727.
- Betti, V., Della Penna, S., De Pasquale, F., Mantini, D., Marzetti, L., Romani, G.L., Corbetta, M., 2013. Natural scenes viewing alters the dynamics of functional connectivity in the human brain. Neuron 79, 782–797.
- Betzel, R.F., Byrge, L., Esfahlani, F.Z., Kennedy, D.P., 2020. Temporal fluctuations in the brain's modular architecture during movie-watching. Neuroimage 213, 116687.
- Bottenhorn, K.L., Flannery, J.S., Boeving, E.R., Riedel, M.C., Eickhoff, S.B., Sutherland, M.T., Laird, A.R., 2018. Cooperating yet distinct brain networks engaged during naturalistic paradigms: a meta-analysis of functional MRI results. Netw. Neurosci. 3, 27–48.
- Buckner, R.L., Andrews-Hanna, J.R., Schacter, D.L., 2008. The brain's default network: anatomy, function, and relevance to disease. Ann. N. Y. Acad. Sci. 1124, 1–38.
- Bush, K.A., Privratsky, A., Gardner, J., Zielinski, M.J., Kilts, C.D., 2018. Common functional brain states encode both perceived emotion and the psychophysiological response to affective stimuli. Sci. Rep. 8, 1–10.
- Cai, S., Chong, T., Peng, Y., Shen, W., Li, J., von Deneen, K.M., Huang, L., 2017. Altered functional brain networks in amnestic mild cognitive impairment: a resting-state fMRI study. Brain Imaging Behav. 11, 619–631.
- Čeko, M., Kragel, P.A., Woo, C.W., López-Solà, M., Wager, T.D., 2022. Common and stimulus-type-specific brain representations of negative affect. Nat. Neurosci. 1–11.
- Chan, H.Y., Smidts, A., Schoots, V.C., Sanfey, A.G., Boksem, M.A., 2020. Decoding dynamic affective responses to naturalistic videos with shared neural patterns. Neuroimage 216, 116618.
- Chen, A.C., Oathes, D.J., Chang, C., Bradley, T., Zhou, Z.W., Williams, L.M., Glover, G.H., Deisseroth, K., Etkin, A., 2013. Causal interactions between fronto-parietal central executive and default-mode networks in humans. In: Proceedings of the National Academy of Sciences, 110, pp. 19944–19949.
- Ciarrusta, J., Dimitrova, R., Batalle, D., O'Muircheartaigh, J., Cordero-Grande, L., Price, A., Hughes, E., Kangas, J., Perry, E., Javed, A., 2020. Emerging functional connectivity differences in newborn infants vulnerable to autism spectrum disorders. Transl. Psychiatry 10, 1–10.
- Cohen, J.R., 2018. The behavioral and cognitive relevance of time-varying, dynamic changes in functional connectivity. Neuroimage 180, 515–525.
- Cohen, J.R., D'Esposito, M., 2016. The segregation and integration of distinct brain networks and their relationship to cognition. J. Neurosci. 36, 12083–12094.
- Combrisson, E., Jerbi, K., 2015. Exceeding chance level by chance: the caveat of theoretical chance levels in brain signal classification and statistical assessment of decoding accuracy. J. Neurosci. Methods 250, 126–136.
- Cowen, A.S., Keltner, D., 2017. Self-report captures 27 distinct categories of emotion bridged by continuous gradients. In: Proceedings of the National Academy of Sciences, 114, pp. E7900–E7909.
- Craig, A.D., 2009. How do you feel—Now? The anterior insula and human awareness. Nat. Rev. Neurosci. 10, 59–70.
- Critchley, H.D., Rotshtein, P., Nagai, Y., O'Doherty, J., Mathias, C.J., Dolan, R.J., 2005. Activity in the human brain predicting differential heart rate responses to emotional facial expressions. Neuroimage 24, 751–762.
- Damasio, A., Carvalho, G.B., 2013. The nature of feelings: evolutionary and neurobiological origins. Nat. Rev. Neurosci. 14, 143–152.
- Demirtaş, M., Ponce-Alvarez, A., Gilson, M., Hagmann, P., Mantini, D., Betti, V., Romani, G.L., Friston, K., Corbetta, M., Deco, G., 2019. Distinct modes of functional connectivity induced by movie-watching. Neuroimage 184, 335–348.
- Di, X., Biswal, B.B., 2020. Intersubject consistent dynamic connectivity during natural vision revealed by functional MRI. Neuroimage 216, 116698.
- Di, X., Zhang, Z., Xu, T., Biswal, B.B., 2021. Dynamic and stable brain connectivity during movie watching as revealed by functional MRI. Biorxiv.
- Dolcos, F., Iordan, A.D., Kragel, J., Stokes, J., Campbell, R., McCarthy, G., Cabeza, R., 2013. Neural correlates of opposing effects of emotional distraction on working memory and episodic memory: an event-related FMRI investigation. Front. Psychol. 4, 293.
- Du, Y., Fu, Z., Calhoun, V.D., 2018. Classification and prediction of brain disorders using functional connectivity: promising but challenging. Front. Neurosci. 12, 525.
- DuPre, E., Hanke, M., Poline, J.B., 2020. Nature abhors a paywall: how open science can realize the potential of naturalistic stimuli. Neuroimage 216, 116330.
- Eickhoff, S.B., Milham, M., Vanderwal, T., 2020. Towards clinical applications of movie fMRI. Neuroimage 217, 116860.
- Friston, K.J., 2003. Statistical Parametric Mapping. Neuroscience Databases. Springer, pp. 237–250.
- Gao, C., Weber, C.E., Wedell, D.H., Shinkareva, S.V., 2020. An fMRI study of affective congruence across visual and auditory modalities. J. Cogn. Neurosci. 32, 1251– 1262.
- Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. Neuroimage 15, 870–878.
- Gilson, M., Deco, G., Friston, K.J., Hagmann, P., Mantini, D., Betti, V., Romani, G.L., Corbetta, M., 2018. Effective connectivity inferred from fMRI transition dynamics during

movie viewing points to a balanced reconfiguration of cortical interactions. Neuroimage 180, 534–546.

- Guo, W.B., Liu, F., Xue, Z.M., Xu, X.J., Wu, R.R., Ma, C.Q., Wooderson, S.C., Tan, C.L., Sun, X.L., Chen, J.D., 2012. Alterations of the amplitude of low-frequency fluctuations in treatment-resistant and treatment-response depression: a resting-state fMRI study. Prog. Neuropsychopharmacol. Biol. Psychiatry 37, 153–160.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proc. Natl Acad. Sci. 98, 4259–4264.
- Hamilton, J.P., Farmer, M., Fogelman, P., Gotlib, I.H., 2015. Depressive rumination, the default-mode network, and the dark matter of clinical neuroscience. Biol. Psychiatry 78, 224–230.
- Horikawa, T., Cowen, A.S., Keltner, D., Kamitani, Y., 2020. The neural representation of visually evoked emotion is high-dimensional, categorical, and distributed across transmodal brain regions. Iscience 23, 101060.
- Jääskeläinen, I.P., Sams, M., Glerean, E., Ahveninen, J., 2021. Movies and narratives as naturalistic stimuli in neuroimaging. Neuroimage 224, 117445.
- Jaworska, N., Yang, X.R., Knott, V., MacQueen, G., 2015. A review of fMRI studies during visual emotive processing in major depressive disorder. World J. Biol. Psychiatry 16, 448–471.
- Kassam, K.S., Markey, A.R., Cherkassky, V.L., Loewenstein, G., Just, M.A., 2013. Identifying emotions on the basis of neural activation. PLoS One 8, e66032.
- Katzner, S., Weigelt, S., 2013. Visual cortical networks: of mice and men. Curr. Opin. Neurobiol. 23, 202–206.
- Keightley, M.L., Winocur, G., Graham, S.J., Mayberg, H.S., Hevenor, S.J., Grady, C.L., 2003. An fMRI study investigating cognitive modulation of brain regions associated with emotional processing of visual stimuli. Neuropsychologia 41, 585–596.
- Kim, D., Kay, K., Shulman, G.L., Corbetta, M., 2018. A new modular brain organization of the BOLD signal during natural vision. Cereb. Cortex 28, 3065–3081.
- Kober, H., Barrett, L.F., Joseph, J., Bliss-Moreau, E., Lindquist, K., Wager, T.D., 2008. Functional grouping and cortical–subcortical interactions in emotion: a meta-analysis of neuroimaging studies. Neuroimage 42, 998–1031.
- Kragel, P.A., Kano, M., Van Oudenhove, L., Ly, H.G., Dupont, P., Rubio, A., Delon-Martin, C., Bonaz, B.L., Manuck, S.B., Gianaros, P.J., 2018. Generalizable representations of pain, cognitive control, and negative emotion in medial frontal cortex. Nat. Neurosci. 21, 283–289.
- Kragel, P.A., Knodt, A.R., Hariri, A.R., LaBar, K.S., 2016. Decoding spontaneous emotional states in the human brain. PLoS Biol. 14, e2000106.
- Kragel, P.A., LaBar, K.S., 2014. Advancing emotion theory with multivariate pattern classification. Emot. Rev. 6, 160–174.
- Kragel, P.A., LaBar, K.S., 2015. Multivariate neural biomarkers of emotional states are categorically distinct. Soc. Cogn. Affect. Neurosci. 10, 1437–1448.
- Kragel, P.A., LaBar, K.S., 2016. Decoding the nature of emotion in the brain. Trends Cogn. Sci. (Regul. Ed.) 20, 444–455.
- Kragel, P.A., Reddan, M.C., LaBar, K.S., Wager, T.D., 2019. Emotion schemas are embedded in the human visual system. Sci. Adv. 5, eaaw4358.
- Lettieri, G., Handjaras, G., Ricciardi, E., Leo, A., Papale, P., Betta, M., Pietrini, P., Cecchetti, L., 2019. Emotionotopy in the human right temporo-parietal cortex. Nat. Commun. 10, 1–13.
- Li, J., Xu, L., Zheng, X., Fu, M., Zhou, F., Xu, X., Ma, X., Li, K., Kendrick, K.M., Becker, B., 2019. Common and dissociable contributions of alexithymia and autism to domain-specific interoceptive dysregulations. Psychother. Psychosom. 88, 187–189.
- Lim, S.L., O'Doherty, J.P., Rangel, A., 2013. Stimulus value signals in ventromedial PFC reflect the integration of attribute value signals computed in fusiform gyrus and posterior superior temporal gyrus. J. Neurosci. 33, 8729–8741.
- Lindquist, K.A., Barrett, L.F., 2012. A functional architecture of the human brain: emerging insights from the science of emotion. Trends Cogn. Sci. (Regul. Ed.) 16, 533–540.
- Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Barrett, L.F., 2012. The brain basis of emotion: a meta-analytic review. Behav. Brain Sci. 35, 121.
- Liu, J., Chen, Y., Stephens, R., Cornea, E., Goldman, B., Gilmore, J.H., Gao, W., 2021. Hippocampal functional connectivity development during the first two years indexes 4-year working memory performance. Cortex 138, 165–177.
- Luppi, A.I., Mediano, P.A., Rosas, F.E., Holland, N., Fryer, T.D., O'Brien, J.T., Rowe, J.B., Menon, D.K., Bor, D., Stamatakis, E.A., 2022. A synergistic core for human brain evolution and cognition. Nat. Neurosci. 25, 771–782.
- Luppi, A.I., Stamatakis, E.A., 2021. Combining network topology and information theory to construct representative brain networks. Netw. Neurosci. 5, 96–124.
- Magalhães, R., Picó-Pérez, M., Esteves, M., Vieira, R., Castanho, T.C., Amorim, L., Sousa, M., Coelho, A., Fernandes, H.M., Cabral, J., 2021. Habitual coffee drinkers display a distinct pattern of brain functional connectivity. Mol. Psychiatry 1–10.
- Maier, A., Gieling, C., Heinen-Ludwig, L., Stefan, V., Schultz, J., Güntürkün, O., Becker, B., Hurlemann, R., Scheele, D., 2020. Association of childhood maltreatment with interpersonal distance and social touch preferences in adulthood. Am. J. Psychiatry 177, 37–46.
- Mandelkow, H., De Zwart, J.A., Duyn, J.H., 2016. Linear discriminant analysis achieves high classification accuracy for the BOLD fMRI response to naturalistic movie stimuli. Front. Hum. Neurosci. 10, 128.
- Matusz, P.J., Dikker, S., Huth, A.G., Perrodin, C., 2019. Are we ready for real-world neuroscience? J. Cogn. Neurosci. 31 (3), 327–338.
- Meer, J.N., Breakspear, M., Chang, L.J., Sonkusare, S., Cocchi, L., 2020. Movie viewing elicits rich and reliable brain state dynamics. Nat. Commun. 11, 1–14.
- Mickley, K.R., Kensinger, E.A., 2008. Emotional valence influences the neural correlates associated with remembering and knowing. Cogn. Affect. Behav. Neurosci. 8, 143–152.
- Mourao-Miranda, J., Volchan, E., Moll, J., de Oliveira-Souza, R., Oliveira, L., Bramati, I.,

Gattass, R., Pessoa, L., 2003. Contributions of stimulus valence and arousal to visual activation during emotional perception. Neuroimage 20, 1955–1963.

- Nguyen, T., Zhou, T., Potter, T., Zou, L., Zhang, Y., 2019. The cortical network of emotion regulation: insights from advanced EEG-fMRI integration analysis. IEEE Trans. Med. Imaging 38, 2423–2433.
- Nummenmaa, L., Saarimki, H., Glerean, E., Gotsopoulos, A., Sams, M., 2014. Emotional speech synchronizes brains across listeners and engages large-scale dynamic brain networks. Neuroimage 102.
- Pessoa, L., 2017. A network model of the emotional brain. Trends Cogn. Sci. (Regul. Ed.) 21, 357–371.
- Pessoa, L., 2018. Understanding emotion with brain networks. Curr. Opin. Behav. Sci. 19, 19–25.
- Petro, N.M., Tong, T.T., Henley, D.J., Neta, M., 2018. Individual differences in valence bias: fMRI evidence of the initial negativity hypothesis. Soc. Cogn. Affect. Neurosci. 13, 687–698.
- Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage 16, 331–348.
- Pollatos, O., Gramann, K., Schandry, R., 2007. Neural systems connecting interoceptive awareness and feelings. Hum. Brain Mapp. 28, 9–18.
- Ptak, R., Bourgeois, A., Cavelti, S., Doganci, N., Schnider, A., Iannotti, G.R., 2020. Discrete patterns of cross-hemispheric functional connectivity underlie impairments of spatial cognition after stroke. J. Neurosci. 40, 6638–6648.
- Puckett, A.M., Schira, M.M., Isherwood, Z.J., Victor, J.D., Roberts, J.A., Breakspear, M., 2020. Manipulating the structure of natural scenes using wavelets to study the functional architecture of perceptual hierarchies in the brain. Neuroimage 221, 117173.
- Putkinen, V., Nazari-Farsani, S., Seppälä, K., Karjalainen, T., Sun, L., Karlsson, H.K., Hudson, M., Heikkilä, T.T., Hirvonen, J., Nummenmaa, L., 2021. Decoding music-evoked emotions in the auditory and motor cortex. Cereb. Cortex 31, 2549–2560.
- Raichle, M.E., 2015. The brain's default mode network. Annu. Rev. Neurosci. 38, 433– 447.
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl Acad. Sci. 98, 676–682.
- Raz, G., Winetraub, Y., Jacob, Y., Kinreich, S., Maron-Katz, A., Shaham, G., Podlipsky, I., Gilam, G., Soreq, E., Hendler, T., 2012. Portraying emotions at their unfolding: a multilayered approach for probing dynamics of neural networks. Neuroimage 60, 1448–1461.
- Reddan, M.C., Wager, T.D., Schiller, D., 2018. Attenuating neural threat expression with imagination. Neuron 100, 994–1005 e1004.
- Ren, Y., Nguyen, V.T., Sonkusare, S., Lv, J., Pang, T., Guo, L., Eickhoff, S.B., Breakspear, M., Guo, C.C., 2018. Effective connectivity of the anterior hippocampus predicts recollection confidence during natural memory retrieval. Nat. Commun. 9, 1–10.
- Résibois, M., Verduyn, P., Delaveau, P., Rotgé, J.Y., Kuppens, P., Van Mechelen, I., Fossati, P., 2017. The neural basis of emotions varies over time: different regions go with onset-and offset-bound processes underlying emotion intensity. Soc. Cogn. Affect. Neurosci. 12, 1261–1271.
- Rolls, E.T., Deco, G., Huang, C.C., Feng, J., 2022. The human orbitofrontal cortex, vmPFC, and anterior cingulate cortex effective connectome: emotion, memory, and action. Cereb. Cortex 33 (2), 330–356.
- Saarimäki, H., Ejtehadian, L.F., Glerean, E., Jääskeläinen, I.P., Vuilleumier, P., Sams, M., Nummenmaa, L., 2018. Distributed affective space represents multiple emotion categories across the human brain. Soc. Cogn. Affect. Neurosci. 13, 471–482.
- Saarimäki, H., Glerean, E., Smirnov, D., Mynttinen, H., Jääskeläinen, I.P., Sams, M., Nummenmaa, L., 2022. Classification of emotion categories based on functional connectivity patterns of the human brain. Neuroimage 247, 118800.
- Saarimäki, H., Gotsopoulos, A., Jääskeläinen, I.P., Lampinen, J., Vuilleumier, P., Hari, R., Sams, M., Nummenmaa, L., 2016. Discrete neural signatures of basic emotions. Cereb. Cortex 26, 2563–2573.
- Satpute, A.B., Lindquist, K.A., 2019. The default mode network's role in discrete emotion. Trends Cogn. Sci. (Regul. Ed.) 23, 851–864.
- Schacter, D.L., Addis, D.R., 2007. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. Philos. Trans. R. Soc. B Prog. Nucl. Energy 6 Biol. Sci. 362, 773–786.
- Schaefer, A., Kong, R., Gordon, E.M., Laumann, T.O., Zuo, X.N., Holmes, A.J., Eickhoff, S.B., Yeo, B.T., 2018. Local-global parcellation of the human cerebral cortex from intrinsic functional connectivity MRI. Cereb. Cortex 28, 3095–3114.
- Simony, E., Chang, C., 2020. Analysis of stimulus-induced brain dynamics during naturalistic paradigms. Neuroimage 216, 116461.
- Sonkusare, S., Breakspear, M., Guo, C., 2019. Naturalistic stimuli in neuroscience: critically acclaimed. Trends Cogn. Sci. (Regul. Ed.) 23, 699–714.
- Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21, 489–510.
- Teeuw, J., Brouwer, R.M., Guimarães, J.P., Brandner, P., Koenis, M.M., Swagerman, S.C., Verwoert, M., Boomsma, D.I., Pol, H.E.H., 2019. Genetic and environmental influences on functional connectivity within and between canonical cortical resting-state networks throughout adolescent development in boys and girls. Neuroimage 202, 116073.
- Thakral, P.P., Bottary, R., Kensinger, E.A., 2022. Representing the Good and Bad: fMRI signatures during the encoding of multisensory positive, negative, and neutral events. Cortex 151, 240–258.
- Tian, Y., Margulies, D.S., Breakspear, M., Zalesky, A., 2020. Topographic organization of the human subcortex unveiled with functional connectivity gradients. Nat. Neurosci. 23, 1421–1432.
- Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30, 829–858.

- Vanderwal, T., Eilbott, J., Finn, E.S., Craddock, R.C., Turnbull, A., Castellanos, F.X., 2017. Individual differences in functional connectivity during naturalistic viewing conditions. Neuroimage 157, 521–530.
- Vanderwal, T., Finn, E.S., Glerean, E., Hasson, U., 2022. Naturalistic Imaging: the use of ecologically valid conditions to study brain function. Neuroimage 247.
- Vatansever, D., Menon, D.K., Stamatakis, E.A., 2017. Default mode contributions to automated information processing. In: Proceedings of the National Academy of Sciences, 114, pp. 12821–12826.
- Veer, I.M., Oei, N.Y., Spinhoven, P., van Buchem, M.A., Elzinga, B.M., Rombouts, S.A., 2011. Beyond acute social stress: increased functional connectivity between amygdala and cortical midline structures. Neuroimage 57, 1534–1541.
- Vessel, E.A., Isik, A.I., Belfi, A.M., Stahl, J.L., Starr, G.G., 2019. The default-mode network represents aesthetic appeal that generalizes across visual domains. Proc. Natl Acad. Sci. 116, 19155–19164.
- Vytal, K., Hamann, S., 2010. Neuroimaging support for discrete neural correlates of basic emotions: a voxel-based meta-analysis. J. Cogn. Neurosci. 22, 2864–2885.
- Wager, T.D., Kang, J., Johnson, T.D., Nichols, T.E., Satpute, A.B., Barrett, L.F., 2015. A Bayesian model of category-specific emotional brain responses. PLoS Comput. Biol. 11, e1004066.
- Wang, F., Li, Y., Gu, Z., 2017a. An MVPA method based on sparse representation for pattern localization in fMRI data analysis. Neurocomputing 269, 206–211.
- Wang, J., Ren, Y., Hu, X., Nguyen, V.T., Guo, L., Han, J., Guo, C.C., 2017b. Test-retest reliability of functional connectivity networks during naturalistic fMRI paradigms. Hum. Brain Mapp. 38, 2226–2241.
- Wang, Y., Sun, K., Liu, Z., Chen, G., Jia, Y., Zhong, S., Pan, J., Huang, L., Tian, J., 2020. Classification of unmedicated bipolar disorder using whole-brain functional activity and connectivity: a radiomics analysis. Cereb. Cortex 30, 1117–1128.
- Waugh, C.E., Kuppens, P., 2021. Affect Dynamics. Springer.
- Waugh, C.E., Schirillo, J.A., Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Barrett, L.F., 2012. Timing: a missing key ingredient in typical fMRI studies of emotion. Behav. Brain Sci. 35, 170.
- Whitfield-Gabrieli, S., Ford, J.M., 2012. Default mode network activity and connectivity in psychopathology. Annu. Rev. Clin. Psychol. 8.
- Xin, F., Zhou, X., Dong, D., Zhao, Z., Yang, X., Wang, Q., Gu, Y., Kendrick, K.M., Chen, A., Becker, B., 2020. Oxytocin differentially modulates amygdala responses during topdown and bottom-up aversive anticipation. Adv. Sci. 7, 2001077.
- Xu, T., Zhou, X., Kanen, J.W., Wang, L., Chen, Z., Zhang, R., Jiao, G., Feng, Z., Zhao, W., Yao, S., 2022. Angiotensin blockade enhances motivational reward learning via enhancing ventral striatal prediction error and frontostriatal communication. Biorxiv.
- Xu, X., Dai, J., Chen, Y., Liu, C., Xin, F., Zhou, X., Zhou, F., Stamatakis, E.A., Yao, S., Luo, L., 2021. Intrinsic connectivity of the prefrontal cortex and striato-limbic system respectively differentiate major depressive from generalized anxiety disorder. Neuropsychopharmacology 46, 791–798.
- Yan, C.G., Wang, X.D., Zuo, X.N., Zang, Y.F., 2016. DPABI: data processing & analysis for (resting-state) brain imaging. Neuroinformatics 14, 339–351.
- Yiend, J., 2010. The effects of emotion on attention: a review of attentional processing of emotional information. Cogn. Emot. 24 (1), 3–47.
- Zeng, L.L., Shen, H., Liu, L., Wang, L., Li, B., Fang, P., Zhou, Z., Li, Y., Hu, D., 2012. Identifying major depression using whole-brain functional connectivity: a multivariate pattern analysis. Brain 135, 1498–1507.
- Zeng, L.L., Shen, H., Liu, L., Hu, D., 2014. Unsupervised classification of major depression using functional connectivity MRI. Hum. Brain Mapp. 35, 1630–1641.
- Zhang, R., Zhao, W., Qi, Z., Xu, T., Zhou, F., Becker, B., 2022. Angiotensin II regulates the neural expression of subjective fear in humans-precision pharmaco-neuroimaging approach. Biol. Psychiatry Cogn. Neurosci. Neuroimaging doi:10.1016/j.bpsc.2022.09.008, Online Ahead of Print.
- Zhang, Y., Kim, J.H., Brang, D., Liu, Z., 2021. Naturalistic stimuli: a paradigm for multiscale functional characterization of the human brain. Curr. Opin. Biomed. Eng. 19, 100298.
- Zheng, W., Su, Z., Liu, X., Zhang, H., Han, Y., Song, H., Lu, J., Li, K., Wang, Z., 2018. Modulation of functional activity and connectivity by acupuncture in patients with Alzheimer disease as measured by resting-state fMRI. PLoS One 13, e0196933.
- Zhou, F., Li, J., Zhao, W., Xu, L., Zheng, X., Fu, M., Yao, S., Kendrick, K.M., Wager, T.D., Becker, B., 2020. Empathic pain evoked by sensory and emotional-communicative cues share common and process-specific neural representations. Elife 9, e56929.
- Zhou, F., Zhao, W., Qi, Z., Geng, Y., Yao, S., Kendrick, K.M., Wager, T.D., Becker, B., 2021. A distributed fMRI-based signature for the subjective experience of fear. Nat. Commun. 12, 1–16.
- Zhou, F., Zimmermann, K., Xin, F., Scheele, D., Dau, W., Banger, M., Weber, B., Hurlemann, R., Kendrick, K.M., Becker, B., 2018. Shifted balance of dorsal versus ventral striatal communication with frontal reward and regulatory regions in cannabis-dependent males. Hum. Brain Mapp. 39, 5062–5073.
- Zhuang, Q., Xu, L., Zhou, F., Yao, S., Zheng, X., Zhou, X., Li, J., Xu, X., Fu, M., Li, K., 2021. Segregating domain-general from emotional context-specific inhibitory control systems-ventral striatum and orbitofrontal cortex serve as emotion-cognition integration hubs. Neuroimage 238, 118269.
- Zimmermann, J., Griffiths, J.D., McIntosh, A.R., 2018a. Unique mapping of structural and functional connectivity on cognition. J. Neurosci. 38, 9658–9667.
- Zimmermann, K., Yao, S., Heinz, M., Zhou, F., Dau, W., Banger, M., Weber, B., Hurlemann, R., Becker, B., 2018b. Altered orbitofrontal activity and dorsal striatal connectivity during emotion processing in dependent marijuana users after 28 days of abstinence. Psychopharmacology 235, 849–859 (Berl.).