Investigation of functional brain network reconfiguration during exposure to naturalistic stimuli using graph-theoretical analysis

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Keywords: naturalistic stimuli, inter-subject functional correlation, time-varying functional connectivity, modularity, emotions

Abstract

Objective. One of the most significant features of the human brain is that it can dynamically reconfigure itself to adapt to a changing environment. However, dynamic interaction characteristics of the brain networks in naturalistic scenes remain unclear. Approach. We used open-source functional magnetic resonance imaging (fMRI) data from 15 participants who underwent fMRI scans while watching an audio–visual movie 'Forrest Gump'. The community detection algorithm based on inter-subject functional correlation was used to study the time-varying functional networks only induced by the movie stimuli. The whole brain reconfiguration patterns were quantified by the temporal co-occurrence matrix that describes the probability of two brain regions engage in the same community (or putative functional module) across time and the time-varying brain modularity. Four graph metrics of integration, recruitment, spatio-temporal diversity and within-community normalised centrality were further calculated to summarise the brain network dynamic roles and hub features in their spatio-temporal topology. Main results. Our results suggest that the networks that were involved in attention and audio–visual information processing, such as the visual network, auditory network, and dorsal attention network, were considered to play a role of ‘stable loners’. By contrast, ‘unstable loner’ networks such as the default mode network (DMN) and fronto-parietal network tended to interact more flexibly with the other networks. In addition, global brain network showed significant fluctuations in modularity. The ‘stable loner’ networks always maintained high functional connectivity (FC) strength while ‘unstable loner’ networks, especially the DMN, exhibited high intra- and inter-network FC only during a low modularity period. Finally, changes in brain modularity were significantly associated with variations in emotions induced by the movie. Significance. Our findings provide new insight for understanding the dynamic interaction characteristics of functional brain networks during naturalistic stimuli.

1. Introduction

The most significant characteristic of the human brain network is that it can dynamically reconfigure itself to adapt to the complex external environment (Gu et al 2021). However, the neural mechanism by which the brain adapts to changes in the environment is unknown. Generally, cognitive processes are supported by the transient coupling and uncoupling of activity between distant brain regions (Bressler and Menon 2010). Therefore, the interactions between brain regions can be modelled as functional network, with nodes and edges representing the brain regions and functional connectivity (FC) between brain regions, respectively (Park and Friston 2013). We can then study the features of brain network using methodology from network science (Bullmore and Sporns 2009, Medaglia et al 2015).

Previously, most network science-based brain functional analyses have focused on resting state FC. Many important topological properties of brain networks have been identified (Rubinov and Sporns 2010).
such as node-level metrics and module-level properties. One of the most evident features of resting state FC is its modular organization (Sporns and Betzel 2016). The module is defined as a sub-network of densely connected nodes that are sparsely connected to other sub-networks. Many modules that are thought to be engaged in specialised brain functions have been identified as cognitive networks, such as the default mode network (DMN) and dorsal attention network (DAN). These modular structures also appear in response to task stimuli and can be adjusted by cognitive behaviour. For example, performing high cognition-demanding tasks requires more interactions between cognitive networks than at rest (Wig 2017). On a finer timescale, FC in the brain has been reported to fluctuate on a time scale of seconds (Allen et al 2014, Preti et al 2017, Cheng et al 2021). This has given rise to the hypothesis that the brain alternates between segregated and integrated states, reflecting periods of local, specialized information processing and inter-modular information transfer, respectively (Shine et al 2016). Previous studies have attempted to decode the correlation between such network topology and ongoing cognitive processes. For example, Bassett et al investigated each cognitive system’s dynamic role in response to successive stimuli of different tasks (Mattar et al 2015). However, the ecological validity of these laboratory-style experiments is debatable, as they do not resemble the complexity and dynamics of stimuli and behaviours in real life (Schmuckler 2001).

Recently, using movies as naturalistic stimuli in human neuroimaging studies has yielded significant advances in understanding of cognitive and emotional functions (Jaaskelainena et al 2021). Studies also attempted to investigate the characteristics of the brain’s topological structure under naturalistic stimuli such as movie. Li et al reported that stability in the primary visual cortex was decreased, while that in the higher order regions of the ventral and dorsal visual systems increased during watching movie (Li et al 2020). Di et al found that the DMN dynamically interacted with posterior visual regions during visual movie watching; this may be associated with understanding of the movie (Di and Biswal 2020). Another study compared the FC during rest and movie-watching conditions and found that low inter-subject similarity was associated with increased system segregation and more rest-like architectures (Betzel et al 2020). Moreover, FC representations with movie-induced empathy (Jimenez et al 2020) and basic emotions (Ghahari et al 2020) have been reported previously. These studies of brain functional networks upon exposure to movie stimuli have advanced our understanding of how brain networks adapt to environmental changes. However, most of these studies focus on analyses of specific and local cognitive networks from the viewpoint of static network reconfiguration, and thus the dynamic roles of cognitive networks during this procedure is still unclear. Quantitative analysis of roles played by classical cognitive networks in a global and dynamic way and further exploration of the potential associations between dynamic evolution of whole-brain functional patterns and continuous cognitive behaviours will enrich our understanding of brain mechanisms underlying naturalistic stimuli processing.

For naturalistic stimulus data analysis, it is worth noting that stimulus-induced FC signals may be covered by the subject’s inherent FC (Hasson et al 2004). To this end, Simony et al proposed a novel method called inter-subject functional correlation (ISFC) to capture meaningful signals related to the stimulus (Simony et al 2016). This method can effectively isolate the FC induced by the task by calculating the correlation between different brain regions of different subjects performing the same task. Kim et al further confirmed the effectiveness of the ISFC method in eliminating intrinsic neural signals on the whole-brain scale (Kim et al 2018). Moreover, research by Bolton et al on depression confirmed that the dynamic ISFC method has the potential to capture the dynamic FC of a stimulus lock shared between subjects (Bolton et al 2018, 2019). The application of ISFC allows us to focus on the topological properties of dynamic FC networks induced only by naturalistic stimuli.

In this study, we performed the dynamic brain network topological analyses on an open functional magnetic resonance imaging (fMRI) dataset (Hanke et al 2016) in which the participants watched an 2 h audio–visual movie with strong emotional experience. We first used the dynamic ISFC approach to extract the subject-shared time-varying brain graph of FC networks when watching a movie. Then, dynamic graphical metrics based on community detection algorithms, such as integration, recruitment, spatio-temporal diversity, and within-community normalised centrality, were applied to quantitatively evaluate the dynamic spatial-topology features of each cognitive network upon exposure to realistic and continuous stimuli. We also analysed the dynamic temporal topology features of cognitive networks by tracking the time-varying modularity of brain networks, which reflect the fluctuation of brain network segregation and integration. Finally, considering that movies can induce obvious emotional changes, we studied the correlation of large-scale network modularity fluctuation with ongoing emotional variations. We hypothesized that the whole brain networks may be dynamically reorganized to adapt to the complex movie stimuli and these dynamic interaction characteristics among brain networks may be related to the continuous emotional changes.
2. Method

2.1. Data description
A high-quality public dataset was used in this study (Hanke et al. 2016). This dataset is extracted from the studyforrest project (www.studyforrest.org) in which 15 native German speakers (mean age 29.4 years, range 21–39, 6 females) watched an German dubbed movie ‘Forrest Gump’ visual–audio movie during fMRI acquisition. All participants had normal hearing and normal or corrected-to-normal vision, and no known history of neurological disorders. The studyforrest dataset provides the required ethics and consent needed for study and dissemination, such that no further institutional review board approval is required.

The data were collected using a Philips 3.0T MRI scanner equipped with a 32-channel head coil. A gradient echo plane imaging sequence was used to obtain blood oxygenation level-dependent (BOLD) images with the following parameters: echo time (TE) = 30 ms, repetition time (TR) = 2000 ms, flip angle (FA) = 90°, field of view (FOV) = 240 mm × 240 mm, matrix = 80 × 80, slice thickness = 3.0 mm, slice gap = 0.3 mm, and number of slices = 35. The movie was divided into eight segments. All participants underwent two 1h fMRI sessions. Each session consisted of four runs. They were instructed to not perform any actions and to enjoy the movie. Some questions such as story depth, fatigue, feeling and rating were asked after the scanning to test whether subjects paid enough attention to the movie stimuli during the whole experiment. For details, please refer to the reference about the dataset (Hanke et al. 2016).

2.2. Data preprocessing
fMRI data were preprocessed using SPM12 and GRETNA (Wang et al. 2015). Functional data were adjusted for acquisition time, corrected for head motion, and normalised to the Montreal Neurological Institute space with a resample size of $3 \times 3 \times 3$ mm$^3$. Subsequently, spatial smoothing with 5 mm full-width at half-maximum Gaussian kernel was applied to the normalised data to improve the signal-to-noise ratio. Then, linear trends were removed from the smoothed data. Nuisance factors, including 24 motion parameters (three translation and three rotation motion parameters and their expansion) and average signals from white matter and cerebrospinal fluid masks, were regressed out from each BOLD time series. The low-frequency signals were removed using a high-pass filter with a threshold of 0.01 Hz. The data of two participants were excluded from further analysis owing to substantial motion (Hanke et al. 2016). The remaining preprocessed BOLD time series were used for the functional network analyses. The entire procedure is shown in figure 1.

2.3. Definition of brain nodes
Large-scale brain networks were identified based on an atlas of 264 brain nodes of interest (Power et al. 2011) (see figure 1(a)). This atlas was derived from both resting and task FC meta-analyses and has been widely used in brain network analyses (Vatansever et al. 2015, Schultz and Cole 2016). The 264 brain nodes were assigned to 14 sub-networks: sensory somatomotor hand network, sensory somatomotor mouth network, cingulo-opercular Task control network (CON), auditory network (Aud), DMN, memory retrieval network (Mem), visual network (Vis), fronto-parietal Task control network (FPN), salience network (SN), subcortical network (Sub), ventral attention network (VAN), DAN, cerebellar network (CBN), and a network of uncertain function (Uncertain). We combined two sensory somatomotor sub-networks as a single sensory somatomotor network (SMN) for convenience of analysis. For the assignment of nodes in each network, please see figure S1 (available online at stacks.iop.org/JNE/18/056027/mmedia) in the supplementary information. For each subject, the nodal signals were extracted by averaging the time series over all voxels in each of the 264 nodes and then by normalising to a zero mean and unit variance. The resulting time-series was used to construct the ISFC network.

2.4. Time-varying ISFC
Previous studies pointed that movie stimuli evoked highly synchronized signals across subjects (Hasson et al. 2004, Mantini et al. 2012). Therefore, averaging BOLD time series across subjects before computing FC (also called ISFC) helps to suppress correlations due to intrinsic activity and subject-specific movie-evoked activity, and could enhance the movie-related activity shared across subjects. In this study, time-varying ISFC was computed using the sliding window method, as shown in figures 1(b) and (c). Window size is a parameter that can affect the results. In the context of video stimuli, it has been suggested that the 30-TR window seems to be balanced (Di and Biswal 2020). We repeated the time-varying ISFC analysis using window sizes from 30 to 40 TRs, and the results showed that they were very similar in the brain graph (see figures S2 and S3 in the supplementary information). Therefore, we selected a window width of 35-TRs and a step of 1-TR between windows. In each window, all subjects were evenly and randomly divided into two groups. The group-level ROI time series was obtained by averaging the corresponding ROI time series of all subjects within that group, and the ISFC matrix was constructed by calculating the Pearson correlation between two groups of ROIs. This procedure was repeated 50 times by randomly assigning the subjects to each group. The $r$-values of these matrices were converted to $z$-values using Fisher’s $z$-transformation and then averaged to obtain the mean ISFC matrix. Subsequently, this ISFC matrix
Figure 1. Schematic overview of the method. (a) Functional MRI BOLD signals were extracted from spherical regions of interest (ROIs) based on the Power’s atlas. (b) The ISFC matrix was computed by Pearson correlation of the subject-averaged ROIs time series from one group with that from the other group. This procedure was repeated 50 times with different random groupings of subjects, and the resulting ISFC matrices were averaged to produce the group ISFC matrix. (c) The dynamic-ISFC was constructed by the sliding-window way, with a window width of 35-TR and a between-window step of 1-TR, and the ISFC matrix in each window were calculated according to (b). (d) The time-varying community structure of ISFC networks were obtained by a community detection algorithm, which calculates the optimal community division and modularity in each window. (e) The temporal co-occurrence matrix was constructed after community division and four dynamic spatial topological metrics were extracted based on this matrix. (f) The time-varying modularity was extracted to describe the temporal changes in brain community structure, and they were grouped into high, medium, and low periods by calculating whether the modularity at each moment is greater than or within or less than one standard deviation around the mean value.

was converted back to the $r$-value by inverse Fisher $z$-transformation. We took the $(\text{ISFC} + \text{ISFC}^T)/2$ as the result to ensure symmetry (Kim et al 2018). Finally, we obtained the time-varying ISFC network induced by movie stimuli.

2.5. Dynamic community detection analysis
The community detection algorithm divides nodes into non-overlapping communities. It generally detects the community structure in a functional network by maximising the module quality metric $Q$.
(Newman and Girvan 2004), which is also called modularity. A higher value of modularity represents a more evident community structure. Therefore, this algorithm provides not only the community partition but also an index to evaluate whether the network community structure is evident. Recent studies have proposed that the negative correlation in the FC matrix also possesses some physiological significance, and the correlated and anti-correlated brain activity may signify cooperative and competitive interactions between brain areas that subserve adaptive behaviors (Khambhati et al 2018). Therefore, we used the original ISFC matrix with no threshold to perform community division. An optimised community detection algorithm in the Brain Connectivity Toolbox was used to detect the community structure of the ISFC matrix in each time window. It considers both positive and negative correlations in a network (Blondel et al 2008). We ran this algorithm 100 times and chose the maximum Q and its corresponding community partition as the result. The default resolution parameter of \( \gamma = 1 \) was selected, yielding the modularity scores \( Q \) and time-resolved partitions \( D_t \) for \( t = 1 \ldots T \), where \( T \) is the number of windows, as shown in figure 1(d).

2.6. Calculation of temporal co-occurrence matrix

We first calculated the temporal co-occurrence matrix of the dynamic brain networks, which summarise the profile of node-to-node ISFC stability across time, as shown in figure 1(e). The community structure \( D_t \) within each window was used to construct an adjacency matrix \( A_{ijt} \), and \( A_{ijt} = 1 \) if nodes \( i \) and \( j \) are in the same community at time window \( t \); otherwise, \( A_{ijt} = 0 \). The temporal co-occurrence matrix was calculated as \( P_{ij} = \frac{\sum_{t=1}^{T} A_{ijt}}{N-1} \) (Bassett et al 2015, Braun et al 2015). Each element in this matrix measures the proportion of times that the two brain nodes are part of the same community. A higher value indicates that the two nodes participate more frequently in the same community.

2.6.1. Node-level topological metrics

Based on the temporal co-occurrence matrix, we characterised each node’s dynamic topological properties using four metrics: integration, recruitment, spatio-temporal diversity, and within-community normalised centrality as shown in figure 1(e).

The integration of node \( i \) was computed as:

\[
I_i = \frac{1}{N-n_i} \sum_{j \in S} P_{ij}
\]

where \( P_{ij} \) is the probability of node \( i \) and \( j \) within the same community, \( S \) is the cognitive network to which node \( i \) belongs, and \( n_i \) is the number of nodes in \( S \). \( N \) is the total number of brain nodes. \( I_i \) corresponds to the average probability that brain node \( i \) is in the same community as that of nodes from networks other than \( S \). A node with a high integration coefficient tends to interact with nodes within other cognitive networks (Mattar et al 2015).

The recruitment of node \( i \) was computed as:

\[
R_i = \frac{1}{n_i} \sum_{j \in S} P_{ij}
\]

where the meaning of each symbol is the same as above. The recruitment of node \( i \) measures the tendency of its interaction with other nodes within the same cognitive network (Mattar et al 2015).

The spatio-temporal diversity of node \( i \) was computed as:

\[
H_i = -\frac{1}{\log(m)} \sum_{u \in M} p_i(u) \log p_i(u)
\]

where \( p_i(u) = \frac{s_i(u)}{N(n-1)} \), \( s_i \) is the temporal co-occurrence strength of node \( i \) with nodes in all networks, \( s_i(u) \) is the strength of node \( i \) with nodes in network \( u \), \( m \) is the total number of networks, and \( M \) is the set of networks. Nodes with high spatio-temporal diversity scores are those that have relatively spatially varied distribution of time-varying interactions with all communities and are putative loci for integrating information between communities (Fornito et al 2012). However, in this study, we have adapted this formula slightly to focus more on the interactions between nodes of different networks than on the interactions between nodes of different communities.

The within-community normalised centrality of node \( i \) was computed as:

\[
Z_i = \frac{S_i(m_i) - S(m_i)}{\sigma_S(m_i)}
\]

where \( m_i \) is the reference community that contains node \( i \), \( S(m_i) \) is the temporal co-occurrence strength of node \( i \) within the reference community \( m_i \), \( S(m_i) \) is the mean strength of all nodes within the reference community \( m_i \), and \( \sigma_S(m_i) \) is the standard deviation of the node strength within the reference community \( m_i \). This reference community was calculated using the static ISFC network, which was constructed using the entire movie dataset. We ran the community detection algorithm on this static network 100 times and chose the maximum Q and its corresponding partition as the reference community. The within-community normalised centrality quantifies the centrality of a node within its own community. Nodes with high centrality tend to be local information-processing hubs (Chen et al 2016).

The integration and spatio-temporal diversity simultaneously assess the tendency of a node to interact with other nodes in other networks from different perspectives. We regarded the nodes with the top 50% highest coefficients in both the integration and spatio-temporal diversity of all nodes as flexible nodes in brain network reconfiguration. The distributions
of these nodes were studied. In addition, because the physiological significance of the uncertain network is unknown, the nodes in this network were excluded when we calculated the flexible nodes.

2.6.2. Network-level topological metrics
Understanding the role of specific cognitive networks could provide new insights into how brain interactions occur during continuous naturalistic stimuli. We defined network-level graph metrics by averaging the corresponding metric coefficients of nodes within a network. The uncertain network was also excluded from our analysis for the same reason as that before.

To verify the significance of these dynamic metrics of each cognitive network, we compared the dynamic metrics of each cognitive network with the expectations of the null model. The null models were constructed by random permutations of node-to-network assignments in the real data. This procedure ensured that the number of sizes of cognitive networks in the null model was identical to that observed in the real data. We ran this procedure 1000 times to construct corresponding null distributions, and permutation tests were performed to confirm whether the dynamic metrics under real data significantly deviated from the null model.

2.6.3. The dynamic 'role' of each network
The dynamic 'role' of each cognitive network in the evolution of the brain community structure was specified by calculating whether the network-level integration and recruitment extent of each cognitive network were less than, similar to, or more than the corresponding value range of the null model. Along the dimension of dynamic network integration, we assigned a role title to each cognitive network as either (a) loner (less than null), (b) connector (similar to null), or (c) integrator (greater than null); in the context of dynamic network recruitment, networks could be classified as either (a) ephemeral (less than null), (b) unstable (similar to null), or (c) stable (greater than null) (Mattar et al 2015).

2.7. Time-varying modularity of the brain
The community detection algorithm divides functional brain networks into an assumed community structure or module. Meanwhile, the time-varying modularity is obtained by calculating the modular index Q, within each time window (see figure 1(f)), which describes the functional separation or integration of the whole brain across time. We divided the time-varying modularity into high, medium, and low periods by calculating whether the brain network's modularity at each moment is greater than or within or less than one standard deviation of the modularity sequence (Hilger et al 2020). The average of all FC in each period was regarded as the centroid matrix of each period.

2.8. Brain-emotion correlation analysis
Because the Forrest Gump movie can evoke fruitful variations in emotions, we further investigated whether changes in brain modularity were associated with emotional fluctuation. Lettieri et al previously rated the emotions at each moment in Forrest Gump (2019). In this section, we briefly describe the experimental paradigm. This experiment enrolled 12 healthy native Italian speakers (mean age 26.6 years, range 24–34, 5 females). None of the participants reported having watched the movie in the 1 year period before the experiment. The participants were instructed to continuously score the subjectively perceived intensity of the six basic emotions throughout the entire movie that was with the same edit but in Italian. The scores for each basic emotion were significantly consistent among the subjects. The emotion ratings of all subjects were averaged to obtain group-level basic emotions time series, and principal component analysis of the group-level series identified six orthogonal principal components (PCs). The first component reflected a measure of polarity (PC1: 45% explained variance) as positive (happiness) and negative (sadness) emotions demonstrated opposite loadings. The second component was interpreted as a measure of complexity (PC2: 24% explained variance) of the perceived affective state, ranging from a positive pole where happiness and sadness together denoted inner conflict and ambivalence, to a negative pole mainly representing fearful events. The third component was a measure of intensity (PC3: 16% explained variance), which is unipolar and mimics arousal level. Considering that the first three components explained ~85% of the total variance, so only the first three components are named (Lettieri et al 2019). Two multiple linear regression analyses were performed to measure the association of brain modularity with the six basic emotions and the six PCs, respectively. Next, we tested the significance of the regression coefficients corresponding to each basic emotion and PC and the results were corrected for multiple comparisons by Bonferroni corrections (individual p < 0.05/6 = 0.0083).

3. Results

3.1. Profile of brain network community structure across time
Figure 2(a) shows the temporal co-occurrence matrix that provides a summary description of node-to-node ISFC stability over time while watching the movie. We converted the node-level temporal co-occurrence matrix of 264 × 264 into a network-level temporal co-occurrence matrix of 12 × 12 to further analyse the community allocation consistency among classical cognitive networks (figure 2(b)). SN, FPN, and Mem were found to form a closely connected module; Vis, DAN, and CBN formed another more closely connected module. Figure 2(c) shows
the corresponding temporal co-occurrence matrix in the null model. Compared with the real data result in figure 2(b), a significant difference was found in the null model (two-sample ks-test, $k = 0.580$, $p$-value < 0.001). These results indicate that the dynamic interaction of different cognitive networks under naturalistic stimuli has a significant modular structure.

3.2. Dynamic properties and roles of cognitive networks

Figures 3(a) and (b) show the network-level dynamic metrics of integration and recruitment based on the temporal co-occurrence matrix. The null model’s expectations are shown in yellow in both figures. As shown in figure 3(a), the integration of all cognitive networks, except Mem, was less than that under the null model. The permutation test showed that the integration of all cognitive networks significantly deviated from the null model’s range ($p < 0.001$). Further, as shown in figure 3(b), the recruitment of SMN, CON, DMN, FPN, and Sub was not significantly more than the expectation of the null model.

Figure 3(c) displays the dynamic ‘role’ of each cognitive network after mapping the network-level metrics of integration and recruitment into a two-dimensional space. The results showed that Mem was regarded as a ‘stable integrator’ because it has both high coefficients of integration and recruitment. The recruitment coefficients of SMN, CON, DMN, FPN, and Sub fell into the null model’s range; thus, they are regarded as ‘unstable loners’. Moreover, Vis, DAN, VAN, Aud, SN, and CBN are regarded as ‘stable loners’ because they have low integration and high recruitment coefficients.

Although most cognitive networks were considered to be ‘loners’ (see figure 3(c)), we still wanted to explore which network play an important role in dynamic information interaction. Nodes with both high coefficients of integration and spatio-temporal diversity were defined as flexible nodes, which means that they tend to interact not only with nodes in other networks but also with nodes in multiple networks. Therefore, they may act as a hub node for information interactions among networks. Figure 4(a) shows that all flexible nodes in the brain were mainly distributed in the networks of DAN, SMN, FPN, DMN, and Sub. The details about each flexible node in each network were reported in table S1 in the supplementary information. Except for DAN, most flexible nodes were located in an ‘unstable loner’ network (see figure 3(c)). This means that these networks have a tendency to facilitate information interaction in the brain. Figure 4(b) further shows that DMN and FPN have positive within-community normalised centrality among these ‘unstable loner’ networks. Because DMN and FPN show hub features in both figures 4(a) and (b), they may play a more important role in ongoing information exchanges with other networks under naturalistic stimuli.

3.3. Time-varying modularity of brain networks

Figure 5(a) summaries the time-varying modularity of whole-brain networks. It is clear that the modularity changes significantly on a short time scale, suggesting that functional segregation and integration of the brain alternate continuously under naturalistic stimuli. We divided the time-varying modularity into three periods of high, median, and low by one standard variation around the mean value and then averaged all FC patterns in each period (figure 5(b)). We found that when brain networks transitioned from the high to low modularity period, the strength of within- and between-network FC generally improved. For the within-network FC, most ‘stable loner’ networks, such as Vis, Aud, VAN, DAN

Figure 2. The temporal co-occurrence matrix that describes the FC stability across time. (a) The node-level temporal co-occurrence matrix summarizes the probability that two brain nodes are part of the same community during watching movie. Each node was ordered according to which cognitive networks they belong to. The colour bar shows the range of probability that two brain nodes are part of the same community (b) the network-level temporal co-occurrence matrix was constructed by averaging the values of node-level temporal co-occurrence matrix in each network. The colour bar shows the range of average probability that two networks are part of the same community (c) the comparative network-level result in the null model is displayed. This colour bar is same as (b). SMN: sensory somatomotor network, CON: cingulo-opercular network, Aud: auditory network, DMN: default mode network, Sub: subcortical network, VAN: ventral attention network, SN: salience network, FPN: fronto-parietal Task control network, Mem: memory retrieval network, Vis: visual network, DAN: dorsal attention network, CBN: cerebellum network.
Figure 3. The dynamic metrics and roles of cognitive networks. (a) The integration coefficients of cognitive networks are shown in colour bars, and the expectation of null model is shown in the yellow area. (b) The recruitment coefficients of each cognitive network are shown in colour bars. (c) The dynamic role of each cognitive network is estimated by the parameter space consisting of integration and recruitment metrics, and the yellow areas are consistent with (a) and (b).

Figure 4. The cognitive networks with hub features. (a) The proportion of flexible brain nodes in each cognitive network. The flexible node has both high integration and spatio-temporal diversity. (b) The within-community normalized centrality of 'unstable loner' networks. and CBN, maintained the top strength in each period. This result is highlighted when converting the node-level FC matrix into the network-level FC matrix (see figure S4 in the supplementary information). Contrastingly, most 'unstable loner' cognitive networks showed only obvious intra- and inter-network interactions during the low modularity period. These results suggested that the dynamic brain networks’ reconfiguration was affected by the roles of cognitive networks. The change in the functional interaction strength between the ‘stable loner’ networks and the ‘unstable loner’ networks may promote the segregation and integration of the large-scale brain functional networks.

3.4. Correlation of brain modularity with emotion variations
Results of the multiple linear regression analysis of the time-varying modularity with the six basic emotions and the six PCs are listed in Table 1. For the basic emotions, modularity was positively correlated with happiness ($r = 0.00029, p = 0.0040$) and was negatively correlated with anger ($r = -0.00057, p = 0.0050$). Further, modularity was negatively correlated with emotional polarity (PC1, $r = -0.00024, p = 0.0002$) and positively correlated with emotional complexity (PC2, $r = 0.00034, p = 0.0002$). These results suggest that the evolution of the brain network topology reflects emotion variations during movie stimuli.

4. Discussion
The human brain is composed of various brain nodes with specific functions, and they cooperate to adapt to the complex external environment. However, the underlying neural mechanisms of the brain remain unclear. In this study, we used the ISFC approach to extract the shared and meaningful time-varying brain FC across individual subjects.
induced by movie-watching; furthermore, dynamic graph metrics obtained by community detection were used to study the spatio-temporal topological characteristics of the brain functional network during naturalistic stimuli. Based on integration and recruitment metrics, we found that different dynamic roles are played by classical cognitive networks. We also identified the hub features of the cognitive networks using spatio-temporal diversity and within-community normalised centrality. In addition, we found significant changes in brain modularity, which were represented by the changes in functional coupling among ‘stable loner’ and ‘unstable loner’ networks across time. Moreover, dynamic changes in brain modularity were associated with emotional features induced by the movie. Altogether, our findings provide new insights regarding the understanding of dynamic brain network reorganisation under continuous and complex stimuli.

In accordance with previous studies, ISFC was used as the first step to effectively extract shared FC patterns between subjects, which are believed to be related only to external stimuli (Wen et al 2019). We further extended the analysis in a dynamic manner and tracked the evolution of the whole brain network community structure. The temporal co-occurrence matrix (figure 2(a)), obtained by dynamic ISFC analysis, summarises the consistency of the community affiliation of brain nodes across time under naturalistic stimuli. Intuitively, the network-level temporal co-occurrence matrix with real data (figure 2(b)) displayed a significant modular structure composed of Vis, DAN, and CBN compared with the null model (figure 2(c)), while other network connectivity showed significant dynamic changes over time. It is well known that DAN is related to attention allocation (Ptak and Schnider 2010, Vossel et al 2014) and that Vis is responsible for visual information processing.

![Figure 5. Modularity changes in brain networks. (a) The time-varying modularity of dynamic-ISFC networks shows significant fluctuation of segregation and integration during entire process of watching movie. The area of yellow, green and cyan correspond to periods of high, median and low modularity, respectively. (b) Centroids of time-resolved FC are displayed in the high, the median and the low modularity periods. The nodes were ordered to be consistent with the node-level temporal co-occurrence matrix mentioned earlier. The colour bar shows the range of FC strength.]

| Basic emotion | $\beta$ | p-value | Emotional PC | $\beta$ | p-value |
|---------------|--------|---------|--------------|--------|---------|
| Happiness     | 0.000 29 | 0.0040  | PC1          | −0.000 24 | 0.0002  |
| Surprise      | 0.000 18 | 0.2820  | PC2          | 0.000 34 | 0.0002  |
| Fear          | −0.000 17 | 0.1160  | PC3          | 0.000 01 | 0.9256  |
| Sadness       | 0.000 09 | 0.2730  | PC4          | 0.000 36 | 0.0221  |
| Anger         | −0.000 57 | 0.0050  | PC5          | 0.000 16 | 0.3671  |
| Disgust       | 0.000 25 | 0.4530  | PC6          | 0.000 46 | 0.2021  |

Note: PC1, PC2 and PC3 are emotions’ polarity, complexity, and intensity (Lettieri et al 2019). *p < 0.05 after the Bonferroni correction for multiple comparisons.
(Li et al 2011). Previous study found that connections between DAN and Vis were strengthened during the movie, allowing the subjects to focus on visual information (Kim et al 2018). Therefore, these findings indicate that visual attention allocation is continuous while watching a movie, which is in line with the instructions of the experimenter and our hypothesis.

Further analyses of dynamic metrics quantitatively described the characteristics of each cognitive network. From the integration and recruitment results (figure 3(c)), it can be seen that Mem has high coefficients in both metrics and is thus regarded as a ‘stable integrator’. The same role was reported in a previous study on 64 discrete and simple tasks (Mattar et al 2015). Whether during a discrete task or continuous movie-watching, people are likely to understand what is happening at present by reflecting on recent events. In addition, Mem contains the precuneus and portions of the posterior cingulate and lateral parietal cortex, which are all highly integrated regions of the brain both structurally and functionally (van den Heuvel and Sporns 2013). Except for Mem, the dynamic roles of the remaining cognitive networks in the current study on continuous stimuli are largely different from the findings of previous studies on simple and discrete tasks. This may be due to the modulation effects of different tasks and the time-varying brain network analysis in this study. In the current study, the ‘stable loner’ networks included Vis, Aud, DAN, VAN, CB, and SN, and they tended to interact with nodes in the same network. These networks are thought to be involved in the processing of attention and audio-visual information. Some studies on movie-watching have found that these networks, such as Vis, VAN, and DAN, have high inter-subject FC strength (Lynch et al 2018). In addition, these networks also tend to form stable modules such as Vis, DAN, and CBN, as well as Aud and VAN (figure 2(b)). All these lines of evidence indicate that these ‘stable loner’ networks form a stable module during movie-watching and that they may be related to the consistent attention demanding and audio-visual information processing when subjects are immersed in movies.

On the contrary, ‘unstable loner’ networks may be responsible for information integration. This feature of the DMN and FPN is more obvious. Although the network-level average integration of DMN and FPN is not high, this is not true for all nodes within these networks. From figure 4(a), we can see that the flexible nodes in brain networks are distributed in the DMN and FPN. This indicates that some nodes in these networks may show a high integration value with other networks, but the network-level integration is reduced after averaging. Meanwhile, the results of intra-community connections (figure 4(b)) indicate that these two networks also show positive community centrality, indicating good local integration ability. Moreover, DMN and FPN are associated with working memory (Sala-Llonch et al 2012), creativity (Zhu et al 2017), attention (Ptak and Schnider 2010), executive control, and top-down modulation for information processing (Wen et al 2013). All these results show that while watching a movie, the ‘unstable loner’ networks participate not only in local connections but also in global connections with other networks to process high-level cognitive function. Previous studies based on movie stimuli mainly stressed that within-network connections in the DMN play an important role in complex scene processing (Brandman et al 2021). Our results highlight that nodes within the DMN also tend to flexibly interact with nodes in multiple other networks, which may be more beneficial for processing complex movie stimuli.

The above discussions emphasise the characteristics of the dynamic evolution of community structure from the perspective of spatial topology. We now discuss the temporal characteristics of dynamic brain network patterns using time-varying modularity. Time-varying modularity has recently been reported in resting-state brain intrinsic functional networks (Fukushima et al 2018). Our findings show that the naturalistic stimulus can also evoke obvious temporal fluctuations in brain modularity (figure 5(a)), suggesting the modulation of ongoing movie stimuli on brain functional patterns. In addition, our result confirmed that Vis, DAN, VAN and other ‘stable loner’ networks have higher inter-subject functional correlativity from the perspective of dynamic analysis. We also found that some moments, especially those in the low modularity period, induced high inter-subject functional correlativity in the ‘unstable loner’ networks, which is consistent with the findings of previous studies showing that the number of ISFC-excursions was related to specific movie clips (Bolton et al 2018), and that similarities in the community structure between subjects fluctuated over time (Betzel et al 2020). It also suggests that the fluctuation of interaction patterns between cognitive networks may promote people to adapt to the different cognitive needs in processing the outer stimuli. Among these results, the characteristics of the DMN have attracted our attention. The DMN is considered to be a task-dependent network, and the resting-state DMN shows positive within-network correlations and negative between-network correlations with other task-positive networks (Fox and Raichle 2007). Our results show that the DMN and the task-positive network (such as Vis and DAN) significantly decoupled in the high modularity period, while they coupled in the low modularity period during movie-watching. Therefore, we infer that decoupling and coupling between ‘unstable loner’ networks (especially the DMN) and ‘stable loner’ networks (Vis, DAN) at the large-scale brain network level
may be the neural mechanism underlying continuous stimulus processing.

Movies are considered to contain rich emotional information. Existing studies have pointed out that changes in brain network topological characteristics are related to emotional valence and arousal (Lin et al 2019). We further explored the correlation between dynamic decoupling and coupling of large-scale brain networks and ongoing emotional activities. The results showed that modularity was negatively correlated with emotions’ polarity and positively correlated with emotional complexity (table 1). Although the definition of the dimension of emotion is not the same as that of the traditional method, the polarity of emotion is positively correlated with positive emotions and negatively correlated with negative emotions. Hence, emotion polarity is similar to the valence, but the polarity is negatively correlated with happiness, as shown in the analysis conducted by Lettieri et al (2019). We verified the positive correlation between the modularity of large-scale brain networks and happiness from the perspective of the emotional dimension and basic emotion (table 1). Specifically, this analysis demonstrates that the emotion is likely represented not only by the local brain nodes but also by the whole-brain network, which extends the possibility of analysing emotion at the large-scale brain network level (Barrett and Bliss-Moreau 2009, Lindquist et al 2016). This also provides a new understanding of the correlation between brain network topology and emotion.

Finally, our study has two limitations. First, the number of communities detected by the algorithm was limited by the spatial resolution. We used the default spatial resolution parameters, as in most previous studies. However, the optimal parameters require further exploration. Second, the ISFC approach advances our understanding of brain network patterns in naturalistic environments. Using this approach, we identified shared time-varying FC patterns among the subjects. However, we also ignored the unique FC topological characteristics of each subject. In the future, we will consider exploring individual subject characteristics in realistic situations.

5. Conclusion

In this study, we first analysed the dynamic role of classical cognitive networks in the evolution of functional brain networks induced by naturalistic stimuli. We then analysed how cognitive networks that play different dynamic roles interact to support changes in the large-scale brain network topology. We found that the decoupling and coupling of this large-scale brain network were associated with the emotion evoked by the movie. In summary, decoding the dynamic properties of brain networks during naturalistic scenes is helpful for understanding the neural mechanisms of the brain in processing continuous and complex stimuli.

Data availability statement

The description about the dataset that supports the findings of this study is openly available at the URL: www.studyforest.org. The 3T audio–visual fMRI data can be downloaded at the following URL: https://gin.gnode.org/studyforest. The raw emotion ratings are open available at the following URL: https://osf.io/3g2zq.

Acknowledgments

The research leading to these results has received funding from the National Natural Science Foundation of China (No. 61876126), and Tianjin Municipal Science and Technology Program for New Generation of Artificial Intelligence (No. 19ZXZNGX00030).

Author contributions

Gaoyan Zhang inspired the research idea; Xin Liu performed the experiments, analyzed the data and prepared the manuscript; Gaoyan Zhang interpreted the results of the experiments and revised the manuscript. All authors approved the final version of the manuscript for submission.

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