

Research Article

Eyes-open and eyes-closed resting states differentially modulate intra-network organization of the default mode network

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ABSTRACT

This study aimed to investigate the effects of eyes-open (EO) and eyes-closed (EC) resting-state conditions on the functional organization of the default mode network (DMN). Resting-state functional MRI data acquired under EO and EC conditions were analyzed using seed-based functional connectivity and graph-theoretical approaches. Group-averaged DMN connectivity patterns were compared between conditions. Connection-level differences, global topological properties, hub distributions, and highly weighted edges were further examined. The overall DMN connectivity architecture was highly similar between EO and EC conditions, indicating a largely preserved intrinsic network structure. However, significant condition-related differences were observed. At the connection level, EO showed increased functional connectivity between the anterior medial prefrontal cortex and left superior frontal gyrus, and between the left cerebellar tonsil and left cuneus, whereas connectivity between the retrosplenial cortex and left cuneus was reduced compared with EC. At the network level, global efficiency and clustering coefficient differed significantly between conditions, with higher values during EC. Hub and edge analyses further revealed condition-dependent changes in network centrality and connection strength, including the emergence of the right precuneus as a hub in EO and more prominent superior frontal connections in EC. EO and EC resting-state conditions systematically modulate DMN functional organization within an otherwise stable intrinsic architecture. These findings highlight the importance of acquisition condition when interpreting and comparing DMN measures across studies.

1. Introduction

Resting-state brain activity has become a key focus in neuroscience, providing valuable insights into the brain's intrinsic functional organization (Cong et al., 2023, Biswal and Uddin, 2025, Uddin et al., 2025). Among commonly used resting-state paradigms, eyes-open (EO) and eyes-closed (EC) conditions are widely adopted as baseline states to probe spontaneous neural activity and to contextualize task-evoked brain dynamics (Zhang et al., 2015, Smallwood et al., 2021, Pan et al., 2022). Accumulating evidence suggests that these two conditions are not functionally equivalent: EO and EC differ systematically in sensory input, arousal level, and large-scale neural activity patterns, leading to

distinct configurations of functional brain networks (Han et al., 2023, Ingram et al., 2024). Despite this growing recognition, it remains unclear how such state-dependent differences are reflected within specific intrinsic networks, which is closely associated with internally oriented and self-generated cognitive processes.

One intrinsic network that is particularly well suited for addressing this question is the default mode network (DMN). The DMN is preferentially engaged during internally oriented and self-generated cognitive processes, including autobiographical memory retrieval, future-oriented simulation, and spontaneous mind-wandering (Menon, 2023, Satpute and Lee, 2026). Rather than supporting general mental activity or baseline brain function, the DMN facilitates cognition that is relatively

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decoupled from immediate external sensory input and explicit task demands, especially under resting or low-demand conditions (Yeshurun et al., 2021, Menon, 2023). As such, the DMN provides a critical window into how the brain balances internal mentation with changes in sensory context and arousal, even in the absence of overt behavioral requirements (Zhang et al., 2025c). Anatomically and functionally, the DMN comprises a distributed set of cortical regions, including the medial prefrontal cortex, posterior cingulate cortex/precuneus, and inferior parietal lobule, and can be further fractionated into interacting subsystems with partially distinct functional roles (Andrews-Hanna et al., 2010, Du et al., 2016, Bathelt and Geurts, 2021). These subsystems support different aspects of internally oriented cognition and exhibit flexible patterns of functional coupling that vary across cognitive states. Importantly, accumulating evidence suggests that DMN connectivity is sensitive to changes in sensory environment and attentional focus, indicating that its internal organization may be systematically modulated by commonly used resting-state conditions.

Previous studies comparing EO and EC conditions have primarily characterized differences in whole-brain activity, functional connectivity, and large-scale network organization, consistently indicating that the two resting-state conditions are not functionally interchangeable (Xu et al., 2014, Costumero et al., 2020, Ingram et al., 2024). Recent fMRI evidence further suggests that eye-state effects are not uniformly distributed across the brain (Agcaoglu et al., 2019, Feng et al., 2021, Zhang et al., 2025a, Zhong et al., 2025). For example, Zhang et al. (2025a) reported greater inter-individual variability in functional connectivity during EC, with prominent effects involving the DMN, dorsal attention, and visual networks. Convergent electrophysiological evidence likewise demonstrates marked eye-state sensitivity of spontaneous neural dynamics. Earlier EEG studies reported lower oscillatory power during EO than EC across several conventional frequency bands, particularly in the alpha range (Barry et al., 2007, Li et al., 2021), while a recent large-sample study of 608 healthy adults confirmed substantially lower occipital alpha expression during EO and emphasized that EO and EC should be considered distinct resting-state recording contexts (Park et al., 2026). Together, these electrophysiological and fMRI findings reinforce the view that eye condition represents a biologically meaningful state variable rather than a minor procedural feature of resting-state acquisition. However, despite accumulating evidence for EO/EC-related changes in large-scale brain activity and connectivity, it remains unclear whether and how these effects are expressed within the internal architecture of the DMN itself, particularly in terms of network integration, segregation, and hub organization.

Addressing this gap is critical for both theoretical and methodological reasons. Theoretically, examining EO/EC modulation within the DMN can provide insight into how internally oriented networks adapt to changes in sensory input and arousal, even in the absence of explicit task demands. Methodologically, because EO and EC are widely used as baseline conditions in resting-state fMRI studies, a clearer understanding of their impact on DMN topology is essential for interpreting network-level findings and for improving the comparability of results across studies. To this end, the present study focused specifically on the DMN and combined seed-based functional connectivity with graph-theoretical analysis to systematically compare its internal connectivity patterns and topological properties under EO and EC resting-state conditions. We hypothesized that while the overall functional architecture of the DMN would remain largely preserved across states, localized differences in connectivity strength and network topology would emerge, reflecting state-dependent modulation associated with differences in sensory input and arousal.

2. Materials and methods

2.1. Participants

The present study was a secondary analysis of de-identified, publicly

available resting-state fMRI data from the Beijing EO/EC dataset (https://fcon_1000_projects.nitrc.org/indi/retro/BeijingEOEC.html) and involved no new participant recruitment or data acquisition. The original dataset comprised 48 healthy college participants recruited at Beijing Normal University, China (age range, 19–31 years; 24 females; 45 right-handed), none of whom had a history of neurological or psychiatric disorders. According to the original dataset report, the original data collection was approved by the Institutional Review Board of Beijing Normal University Imaging Center for Brain Research, and written informed consent was obtained from all participants prior to data acquisition. The original publication and public dataset documentation do not report an ethics approval/reference number or approval date, nor do they provide a separate national-level ethics approval number (Liu et al., 2013).

For the present study, the imaging data were subjected to quality-control assessment before FC and graph-theoretical analyses. One participant was excluded because the imaging data did not satisfy the image-quality criterion. Head motion was additionally assessed using the realignment parameters, with exclusion defined as translation exceeding 1.5 mm or rotation exceeding 1.5° in any direction. None of the remaining participants exceeded these motion thresholds. Consequently, 47 participants with valid EO and EC scans were retained for all subsequent analyses.

2.2. Resting-state fMRI image acquisition

This open resting-state dataset included three resting-state sessions. The first session is EC resting-state, where the participants were asked to close their eyes but not fall asleep (this session design was for other purpose and not adopted in the current study). The second and third sessions were counter-balanced with EO and EC resting-state (Liu et al., 2013). Because the counterbalanced scans order across scanning sessions and subjects, it is ensured that the observed differences are due to differences in resting conditions rather than scan order (Schwab et al., 2018). Moreover, the dataset from this site was validated to ensure that the rs-fMRI measures were reliable and reproducible in these three resting-state scans (Glomb et al., 2017, Schwab et al., 2018). Thus, in this study, we used the second and third resting-state sessions data for further analysis.

During the resting-state scan, participants were asked to remain still and relaxed, stay awake, and avoid engaging in any deliberate or structured thoughts. Throughout the acquisition, a uniform black (blank) screen was displayed. Imaging data were acquired from a SIEMENS 3.0 T MRI scanner at the Beijing Normal University Imaging Center for Brain Research. All functional images were acquired by a gradient-recalled echo-planar imaging (EPI) sequence with TR = 2000 ms, TE = 30 ms, flip angle = 90°, matrix size = 64 × 64, field of view = 20 × 20 cm², slice thickness/gap = 3.5 mm/0.7 mm, and 33 slices-oriented AC-PC line. Each resting-state scan lasts 8 min, resulting in 240 functional volumes. High-resolution T1-weighted images were acquired by using a dimensional fast spoiled gradient echo (T1-3D FSPGR) sequence (TR = 2.53 ms, TE = 3.39 ms, flip angle = 7°, matrix size = 256 × 192, FOV = 25.6 × 25.6 cm², and slice thickness (no gap) = 1.33 mm).

2.3. Data preprocessing

Functional data were preprocessed and analyzed using the statistical parametric mapping software (SPM25; <https://www.fil.ion.ucl.ac.uk/spm>) (Tierney et al., 2025) and the toolbox of Data Processing and Analysis of Brain Imaging (DPABI; <https://rfmri.org/DPABI>) (Yan et al., 2016). First, the initial 10 volumes were discarded to allow the longitudinal magnetization to reach a steady state, leaving a total of 230 volumes for subsequent analyses. Second, a standard pipeline of slice scan-time and 3D motion correction was performed. Third, individual T1-weighted images were co-registered to the mean EPI image and segmented into

white matter (WM), gray matter (GM), and cerebrospinal fluid (CSF) by the “new segment + DARTEL” implemented in the toolbox DPABI. Fourth, nuisance regression was performed by removing the linear trend, Friston 24 head-motion parameters, and mean signals from white matter (WM) and cerebrospinal fluid (CSF). Global signal regression (GRS) was not performed. Given the ongoing methodological debate regarding GSR and its potential to alter the distribution of functional connectivity values and remove globally distributed signal components with possible neural or physiological relevance, the whole-brain global signal was retained in the present analyses (Murphy and Fox, 2017, Zhu et al., 2021, Feng et al., 2023). After nuisance regression, the functional volumes were then normalized to MNI152 space in $3 \times 3 \times 3 \text{ mm}^3$ voxel resolution by using transformation information acquired from the previous DARTEL step. Then a 6 mm full width at half maximum (FWHM) Gaussian kernel was used to spatially smooth the data. Finally, temporal band-pass filtering (0.01–0.08 Hz) was applied to reduce low-frequency drift and high-frequency physiological noise. For the included subjects, the maximum mean frame displacement (FD) is 0.25 mm and 0.19 mm in EC and EO resting-state conditions, respectively.

2.4. ROIs definition

The posterior cingulate cortex (PCC) is a canonical hub of the DMN and exhibits extensive functional coupling with distributed regions of the network (Menon, 2023, Huang et al., 2024). PCC-centered seed-based functional connectivity analysis has been widely used to delineate

and characterize DMN organization in resting-state fMRI studies (Sanz-Morales and Melero, 2024, Foster and Koslov, 2025). We therefore selected the PCC as the seed region in the present study. Based on a previously defined DMN node, a spherical PCC ROI (6-mm radius; MNI coordinates: $x = -6$, $y = -44$, $z = 34$) was constructed for seed-based FC analysis (Uddin et al., 2011, Zhang et al., 2015).

For each resting-state condition, voxel-wise FC between the PCC seed and the rest of the brain was calculated. The resulting individual correlation maps were transformed using Fisher's r -to- z transformation before group-level analysis. To define a common set of DMN-related regions without favoring either resting-state condition, the EO and EC PCC connectivity maps were first averaged within each participant, yielding one condition-averaged PCC connectivity map for each participant. A group-level one-sample t -test was then performed across these 47 participant-level maps ($df = 46$). Voxels showing significant positive FC with the PCC were identified using a voxel-level family-wise error (FWE)-corrected threshold of $p < 0.01$. Only significant positive PCC connectivity is displayed in Fig. 1, which is generated using BrainNet Viewer (Xia et al., 2013).

The final ROI set was determined from anatomically distinct PCC-positive regions with reference to prior DMN-related literature (Sanz-Morales and Melero, 2024, Foster and Koslov, 2025). The number of ROIs was therefore not predetermined. To reduce potential hemispheric imbalance, bilateral homologous regions were retained where applicable. The resulting network consisted of four midline regions (PCC, amPFC, vmPFC, and RSC) and seven bilateral regional pairs (angular

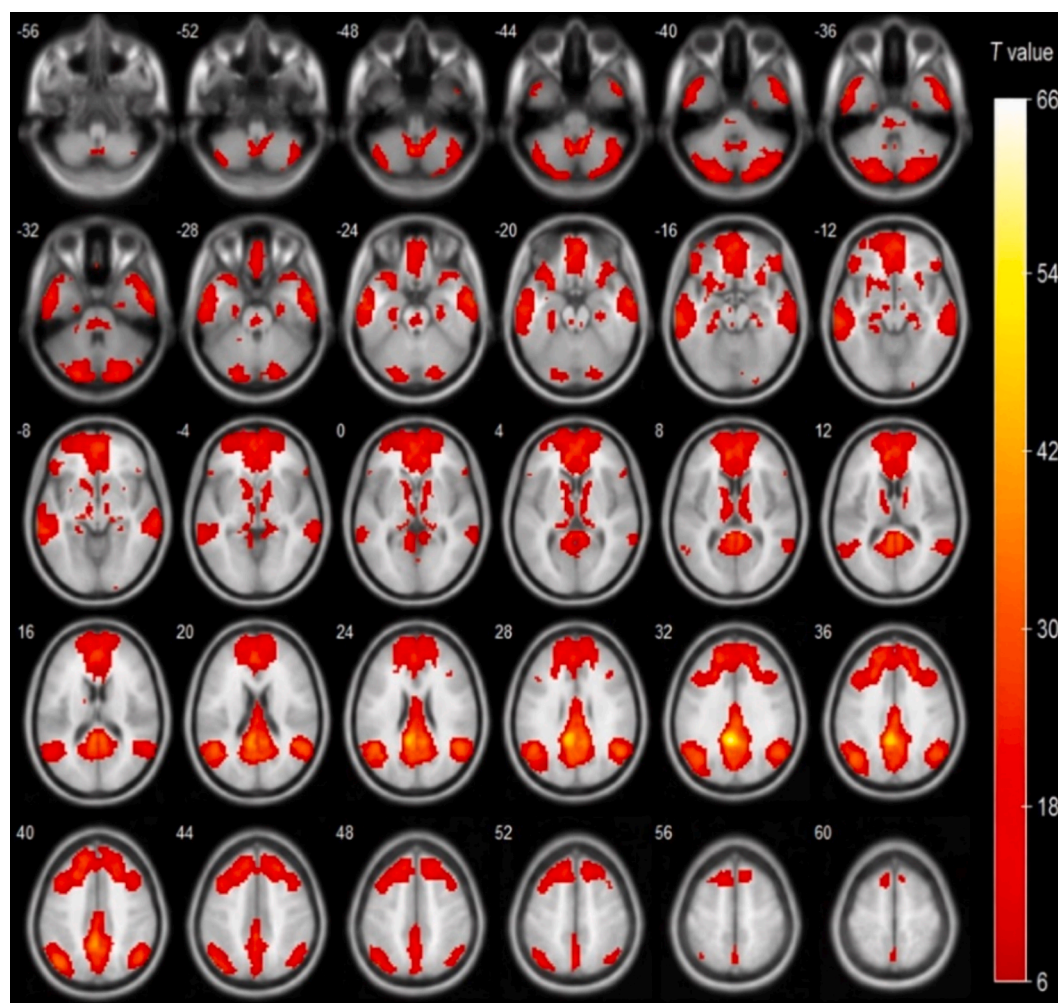


Fig. 1. Group-level PCC seed-based positive functional connectivity map used for ROI definition. The map was derived from within-participant averaged EO and EC PCC connectivity maps using a one-sample t -test ($n = 47$, $df = 46$; voxel-level FWE-corrected $p < 0.01$). The color bar indicates T values.

gyrus, superior frontal gyrus, middle temporal gyrus, precuneus, parahippocampal cortex, cerebellar tonsil, and cuneus), yielding 18 ROIs in total. The coordinates of the final ROIs are provided in Table 1.

2.5. FC of DMN

Six-mm radius spheres centered on each ROI coordinate were constructed to generate ROI masks for the FC analyses. For each participant, BOLD time series were extracted by averaging the signals across all voxels within each ROI, yielding a single representative time course per region. Pairwise functional connectivity among the ROIs was then estimated using Pearson's correlation, producing an 18×18 DMN connectivity matrix for each participant in each resting-state condition. We performed absolute value operation on the negative correlation coefficients in the matrix (Sporns, 2013, Markett et al., 2014). After that, these correlation matrices were transformed to Fisher's Z scores for further analyses.

2.6. Threshold value selection

Because there is no consensus on a single optimal threshold for constructing functional brain networks, graph-theoretical properties are commonly evaluated across a range of sparsity thresholds rather than at a single arbitrary cutoff (Garrison et al., 2015, Theis et al., 2023). Proportional thresholding ensures comparable network density across participants and conditions, facilitating comparison of network topology (van Wijk et al., 2010). Accordingly, undirected binary graphs were constructed across a predefined sparsity range. Small-world organization was evaluated using the normalized clustering coefficient (γ), normalized characteristic path length (λ), and small-worldness coefficient ($\sigma = \gamma/\lambda$), with small-world topology characterized by $\gamma > 1$, $\lambda \approx 1$, and $\sigma > 1$ (Humphries and Gurney, 2008). Recent resting-state fMRI graph-theoretical studies have similarly evaluated network topology across predefined sparsity ranges while requiring preservation of small-world organization (Tian et al., 2025, Zhu et al., 2026). In the present study, the sparsity range was set from 0.06 to 0.40 in increments of 0.01, consistent with previous DMN graph-theoretical analyses using the same sparsity range (Wang et al., 2013).

Table 1

DMN-related ROIs identified from the group-level functional connectivity map.

Region	Abb	MNI coordinate			Peak T-value
		x	y	z	
Posterior cingulate cortex	PCC	−6	−44	34	65.86
anterior medial prefrontal cortex	aMPFC	0	61	13	14.49
ventromedial medial prefrontal cortex	vMPFC	−4	43	−11	18.78
Retrosplenial cortex	RSC	9	−54	24	18.2
Left angular	L_AG	−45	−54	24	27.88
Right angular	R_AG	51	−60	30	28.05
Left superior frontal gyrus	L_SFG	−17	33	48	18.13
Right superior frontal gyrus	R_SFG	17	33	48	16.31
Left middle temporal gyrus	L_MTG	−48	−56	19	24.13
Right middle temporal gyrus	R_MTG	48	−39	0	17.91
Left precuneus	L_prec	−6	−64	28	25.72
Right precuneus	R_prec	6	−64	28	24.65
Left parahippocampal cortex	L_PHC	−21	−36	−12	13.01
Right parahippocampal cortex	R_PHC	24	−35	−12	9.61
Left cerebellar tonsil	L_CT	−42	−59	−45	11.47
Right cerebellar tonsil	R_CT	42	−59	−45	16.32
Left cuneus	L_cuneus	−12	−99	−3	8.12
Right cuneus	R_cuneus	18	−99	−3	8.78

Note: ROI coordinates are reported in Montreal Neurological Institute (MNI) space. Peak t statistics were obtained from the group-level one-sample t-test of the condition-averaged PCC seed-based functional connectivity maps ($n = 47$, $df = 46$; voxel-level FWE-corrected $p < 0.01$).

2.7. Network characteristic metrics

After thresholding, we quantified the topological properties of the resulting binary graphs using graph-theoretical analysis. Network measures were computed across a range of sparsity levels with the Brain Connectivity Toolbox (Rubinov and Sporns, 2010). We examined global efficiency (GE) as a global metric, and clustering coefficient (CC), node degree centrality (DC_{node}), eigenvector centrality (EC_{node}), and node betweenness centrality (BC_{node}) as regional (nodal) metrics. Methodological details and formal definitions of these measures are provided in Rubinov and Sporns (2010).

2.8. Hub node identification

To identify critical hub nodes within the DMN, we integrated three key node centrality measures: node degree centrality (DC_{node}), node betweenness centrality (BC_{node}), and eigenvector centrality (EC_{node}) (Zhang et al., 2016). Since network topological features depend on threshold selection, we computed each node's centrality measure across all thresholds (6%–40%), and then aggregated these measures for robust identification of hub nodes.

First, for each node i , we calculated the integrated node centrality score $S_{node}(i)$ across the entire range of sparsity thresholds T , as follows:

$$S_{node}(i) = \sum_{t \in T} [DC_{node}(i, t) + BC_{node}(i, t) + EC_{node}(i, t)] \quad (1)$$

where $DC_{node}(i, t)$, $BC_{node}(i, t)$, and $EC_{node}(i, t)$ represent node degree centrality, node betweenness centrality, and eigenvector centrality of node i at sparsity threshold t , respectively.

Next, to ensure comparability across participants and nodes, we normalized the integrated node centrality scores across all nodes and participants as follows:

$$NS_{node}(i) = \frac{S_{node}(i)}{\sum_{j=1}^N \sum_{m=1}^M S_{node}(j, m)} \quad (2)$$

where $NS_{node}(i)$ is the normalized integrated centrality score of node i , N is the total number of nodes, and M is the total number of subjects.

Finally, a node was classified as a hub node if its normalized integrated centrality score $NS_{node}(i)$ exceeded the mean plus one standard deviation across all nodes:

$$NS_{node}(i) > \text{mean}(NS_{node}) + SD(NS_{node}) \quad (3)$$

This procedure allowed us to robustly identify critical nodes (hub nodes) within the DMN that significantly contributed to network connectivity and information integration during EO/EC resting-state conditions.

2.9. Key edge identification

To identify critical edges (connections) within the DMN, we computed the edge betweenness centrality (BC_{edge}), which quantifies how frequently an edge participates in the shortest paths between all pairs of nodes (Rubinov and Sporns, 2010). Considering that network topology characteristics are sensitive to the choice of sparsity threshold, we aggregated the edge betweenness centrality across the entire range of thresholds (6%–40%) to ensure robustness and reliability of our results.

Specifically, for each edge e connecting nodes i and j , we calculated the integrated edge centrality score $S_{edge}(e)$:

$$S_{edge}(e) = \sum_{t \in T} BC_{edge}(e, t) \quad (4)$$

where $BC_{edge}(e, t)$ represents the edge betweenness centrality of edge e at sparsity threshold t .

To facilitate comparison across all edges and subjects, we then

normalized the integrated edge centrality scores as follows:

$$NS_{edge}(e) = \frac{S_{edge}(e)}{\sum_{k=1}^E \sum_{m=1}^M S_{edge}(k, m)} \quad (5)$$

where $NS_{edge}(e)$ denotes the normalized integrated centrality score for edge e , E is the total number of edges, and M is the number of participants.

Finally, edges were identified as key connections (edge hubs) if their normalized integrated edge centrality score exceeded the mean plus two standard deviations across all edges:

$$NS_{edge}(e) > \text{mean}(NS_{edge}) + 2 \times SD(NS_{edge}) \quad (6)$$

This rigorous identification approach allowed us to reliably pinpoint critical edges that play pivotal roles in maintaining DMN connectivity and information transfer during eyes-open and eyes-closed resting-state conditions.

2.10. Statistical analysis

To quantify the overall similarity of DMN functional connectivity patterns, FC matrices were averaged across participants separately for EO and EC. Pearson's correlation coefficient between the two matrices was used as a descriptive measure of pattern similarity. For connection-level comparisons, two-tailed paired-sample t -tests were performed on Fisher-Z-transformed FC values for each of the 153 connections. Multiple comparisons were controlled using false discovery rate (FDR) correction, with significance defined as FDR-corrected $p < 0.05$. Global topological metrics, including global efficiency and clustering coefficient, were compared between EO and EC using two-tailed paired-sample t -tests at each sparsity threshold. Nodal centrality metrics and edge betweenness centrality were integrated across sparsity thresholds and used to identify hub nodes and key edges according to the pre-defined criteria described above. These hub- and edge-level analyses were descriptive and were not treated as inferential between-condition tests. Statistical significance was set at $p < 0.05$.

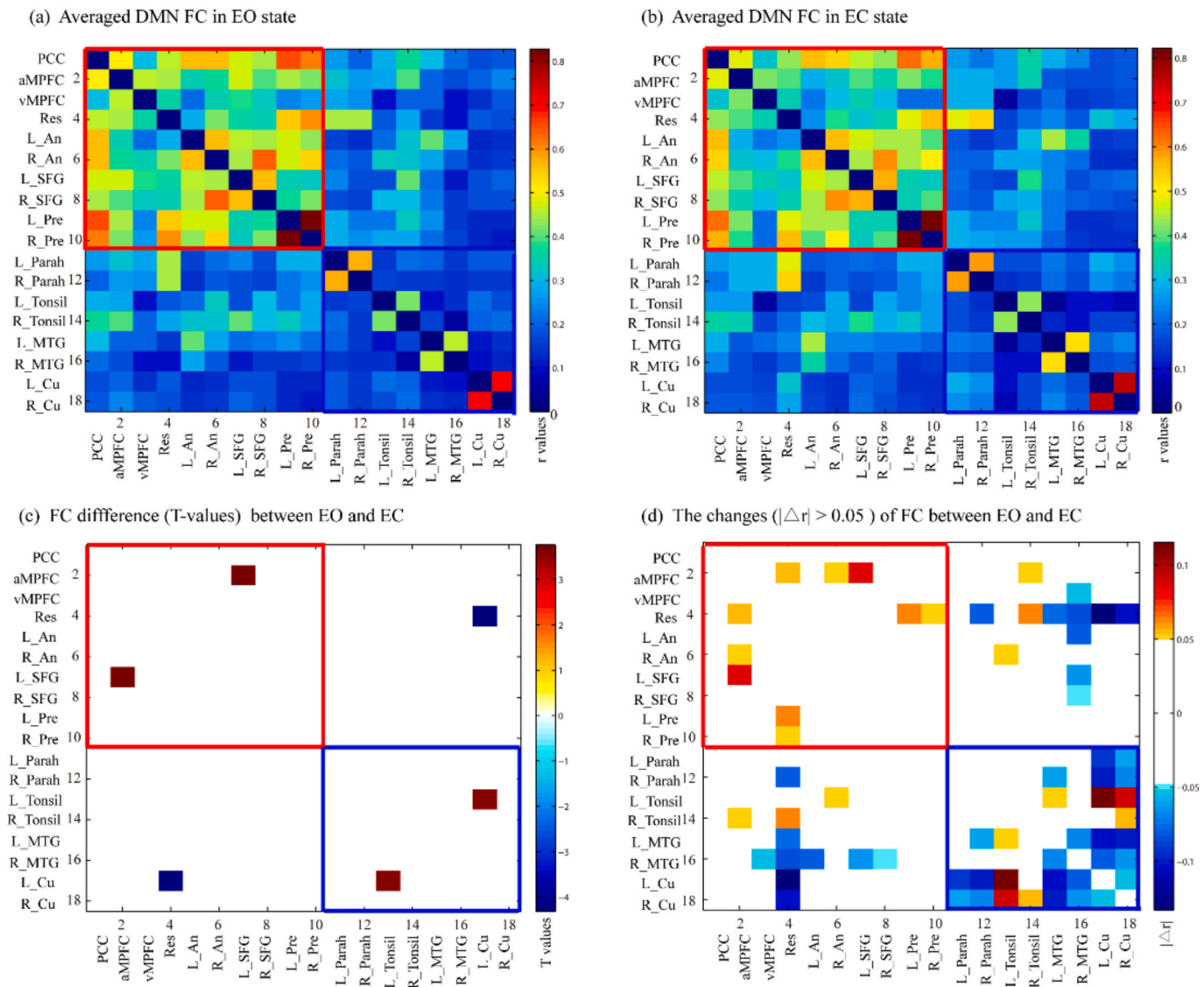


Fig. 2. The DMN FC patterns and differences in EO and EC states. (a) The mean FC during the EO state. (b) The mean FC during the EC state. (c) FC differences between EO and EC states. (d) FC strength changes between the EO and EC states. The red and blue rectangles indicate two literature-informed ROI blocks used to facilitate visual inspection of within- and between-block connectivity patterns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. DMN FC pattern similarity and differences between EO and EC states

We first computed the group-averaged FC matrices of the DMN for the EO and EC resting-state conditions, respectively. For matrix visualization, the DMN ROIs were arranged according to a literature-informed anatomical-functional order. The red and blue rectangles in Fig. 2 indicate two prespecified ROI blocks used only to facilitate visual inspection of within- and between-block connectivity patterns. Visual inspection and correlation analysis revealed a high similarity between the overall FC patterns across the two states (Pearson's $r = 0.96$), indicating a largely preserved large-scale connectivity architecture of the DMN under both conditions (Fig. 2a and 2b).

Using paired t-tests, we found that FC between the anterior medial prefrontal cortex (aMPFC) and the left superior frontal gyrus (L.SFG) ($t(46) = 3.66, p = 0.0006$, FDR-corrected $p < 0.05$), as well as between the left cerebellar tonsil and the left cuneus ($t(46) = 3.56, p = 0.0009$, FDR-corrected $p < 0.05$), was significantly increased in the EO state compared with the EC state. In contrast, FC between the retrosplenial cortex and the left cuneus was significantly decreased during EO relative to EC ($t(46) = -4.25, p = 0.0001$, FDR-corrected $p < 0.05$). These results indicate that while the global FC configuration of the DMN remains largely stable across resting-state conditions, consistent and region-specific modulations in connectivity strength can be detected across subjects. To further characterize the magnitude of connectivity changes between conditions, we calculated the absolute differences in FC strength ($|\Delta r|$) for each DMN connection. Fig. 2c and 2d illustrate the spatial distribution of FC differences and the corresponding strength changes between EO and EC states.

3.2. Differences in DMN global topological properties between EO and EC states

We examined differences in global topological properties of the DMN between the EO and EC conditions. Global efficiency and clustering coefficient were computed for each subject across the full range of sparsity thresholds (6%–40%). Paired t-tests were then performed to compare these network measures between conditions at each threshold. Across the examined sparsity range, the EC condition generally exhibited higher global efficiency and clustering coefficient than the EO condition. Paired comparisons at individual sparsity thresholds identified significant EO–EC differences at several thresholds ($p < 0.05$), as

indicated by the asterisks in Fig. 3.

3.3. Hub nodes of DMN in EO and EC resting-state conditions

Based on the integrated node centrality measures, distinct hub configurations of the DMN were identified under the EO and EC conditions. In the EO condition, three regions met the criteria for hub nodes: the posterior cingulate cortex (PCC), the retrosplenial cortex (RSC), and the right precuneus. These hubs were distributed primarily along the posterior midline and adjacent medial regions of the DMN. In the EC condition, two regions were identified as hub nodes: the PCC and the RSC. Compared with the EO state, the right precuneus did not meet the hub criterion in the EC condition, resulting in a reduced number of hub nodes within the DMN. No additional regions emerged as hubs uniquely in the EC state. The spatial distribution and relative centrality of hub nodes for each condition are shown in Fig. 4, with node size proportional to the integrated centrality value.

3.4. Key edges of DMN in EO and EC resting-state conditions

Based on the integrated edge centrality measures, distinct hub configurations of the DMN were identified under the EO and EC conditions. In the EO condition, a total of nine connections met the criteria for key edges. These connections primarily involved interactions between posterior midline regions and occipital areas, as well as connections linking medial cortical regions within the DMN. In the EC condition, ten connections were identified as key edges. Compared with the EO state, the EC condition exhibited a partially overlapping but non-identical set of key connections. Several key edges observed in the EO state were also present in the EC state, whereas additional connections emerged uniquely in the EC condition. The spatial distribution and relative centrality of key edges in the EO and EC conditions are illustrated in Fig. 5, with edge thickness representing the integrated edge centrality value.

4. Discussion

In this study, we systematically examined EO/EC-related differences in FC and topological organization within the DMN. The overall DMN FC pattern was highly similar across conditions, indicating a largely preserved intrinsic architecture. Against this stable background, EO and EC differed in a limited set of intra-DMN functional connections and in global topological metrics, while descriptive analyses further revealed differences in hub-node and key-edge configurations. Thus, eye

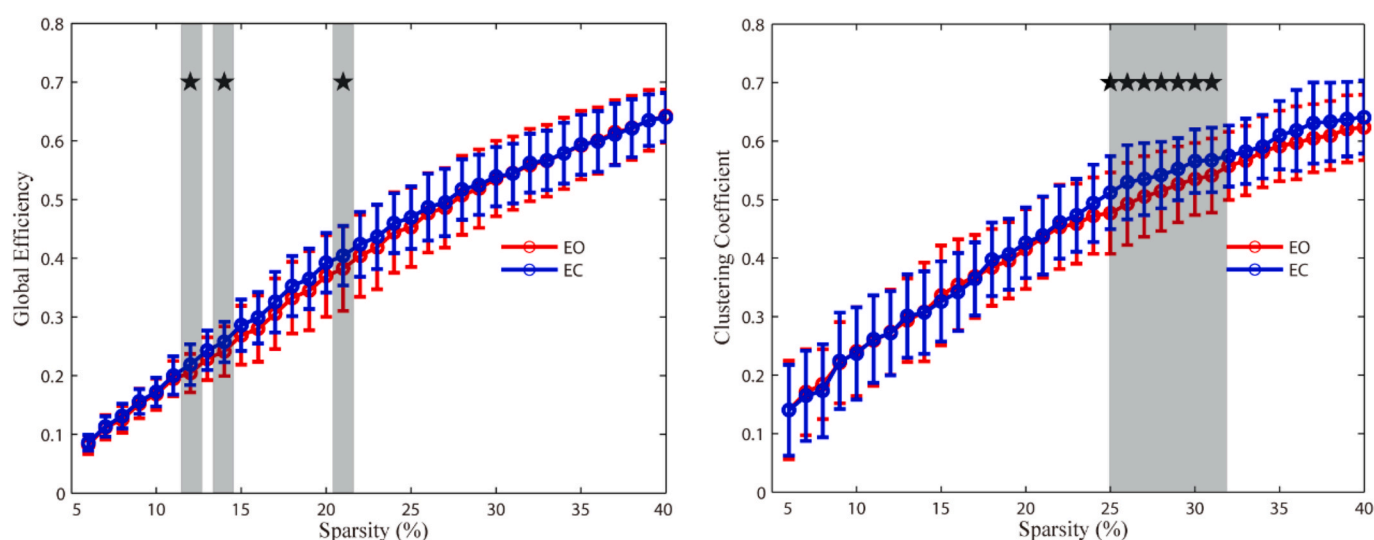
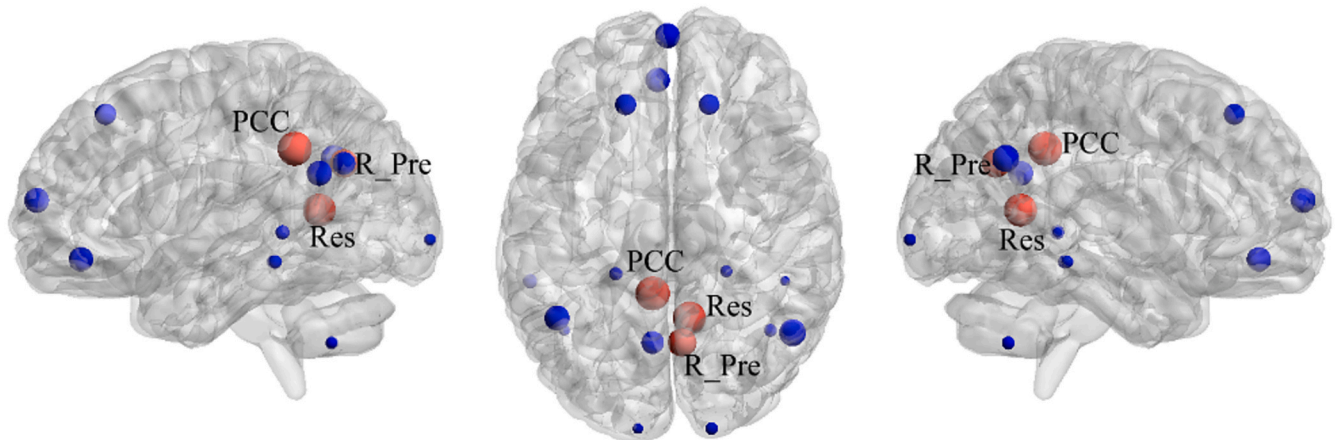


Fig. 3. Global topological properties of the DMN across sparsity thresholds in the EO and EC conditions. Data are presented as mean $\pm$ SD. Asterisks indicate sparsity thresholds at which significant differences between EO and EC were identified using paired-sample t-tests ($p < 0.05$).

(a) The hub nodes in EO state



(b) The hub nodes in EC state

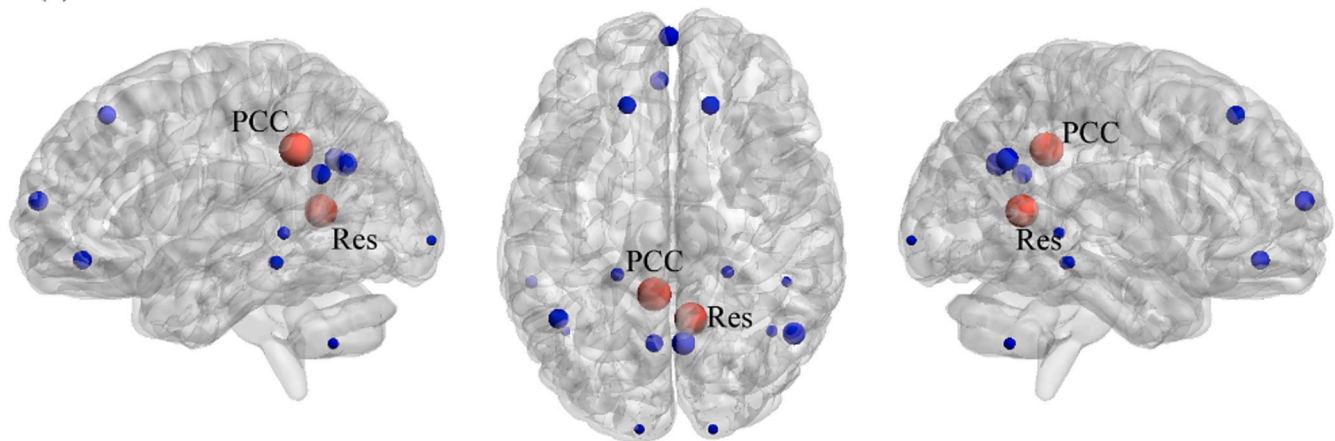


Fig. 4. Key nodes within DMN during EC and EO states. The size of the ROI represents the node centrality.

condition appears to selectively modulate specific aspects of DMN organization rather than reorganizing the network. By providing a DMN-focused, multilevel characterization of EO/EC-related variation, the present study extends previous whole-brain investigations and highlights the importance of considering eye condition when interpreting or comparing resting-state DMN measures across studies and datasets.

Previous resting-state fMRI studies have demonstrated that eye condition influences spontaneous DMN activity and functional connectivity, with recent evidence further showing that EC-related effects are concentrated in selective subsets of connections involving the DMN and visual systems (Agcaoglu et al., 2019, Liu et al., 2020, Han et al., 2023, Zhang et al., 2025b). In the present study, these condition-related effects were confined to a limited set of intra-DMN connections. Compared with EC, EO showed increased FC between the aMPFC and L_SFG and between the left cerebellar tonsil and left cuneus, whereas FC between the RSC and left cuneus was decreased. Notably, two of the three significant connections involved the cuneus, suggesting that posterior visual-related components of the PCC-positive DMN architecture may be particularly sensitive to eye condition. This interpretation is consistent with previous evidence that opening and closing the eyes alters functional coupling between visual cortex and the DMN (Costumero et al., 2020), and with evidence that spatial visual information is represented within the default network itself (Szinte and Knapen, 2020). More recent work further indicates that distinct DMN subdivisions contribute differently to the integration of incoming perceptual information and internally generated representations (Zhang et al., 2026). Thus, the observed medial frontal and cuneus-related differences may

reflect selective adjustments in DMN coupling across different sensory contexts rather than a global alteration of network architecture.

At the topological level, the EC condition was associated with higher global efficiency and clustering coefficient than EO, indicating greater global communication efficiency together with stronger local clustering within the DMN. The higher global efficiency observed during EC is consistent with previous whole-brain graph-theoretical evidence showing reduced global efficiency during EO relative to EC (Xu et al., 2014, Liu et al., 2020). However, Xu et al. also reported greater cliquishness and local efficiency during EO, rather than EC, suggesting that eye-condition effects on network segregation may depend on the spatial scale and network definition examined. Similarly, dynamic DMN analyses have shown that EO–EC differences in clustering and efficiency vary across transient connectivity states rather than following a uniform direction (Liu et al., 2020). More recent network-level evidence nevertheless supports a broader shift toward enhanced functional integration during EC. For example, Han et al. (2023) reported increased connectivity among most large-scale networks during EC, whereas Zhang et al. (2024) demonstrated enhanced modular integration during eye closure, with particularly pronounced effects in network hubs located predominantly within the DMN. Together, these findings suggest that eye condition influences DMN topology in a scale- and metric-dependent manner, with the present results indicating increased global efficiency and local clustering specifically within the PCC-defined DMN during EC.

Further insight into the internal organization of the DMN was provided by the descriptive analysis of hub configurations. The PCC and RSC met the predefined hub criterion under both EO and EC, whereas

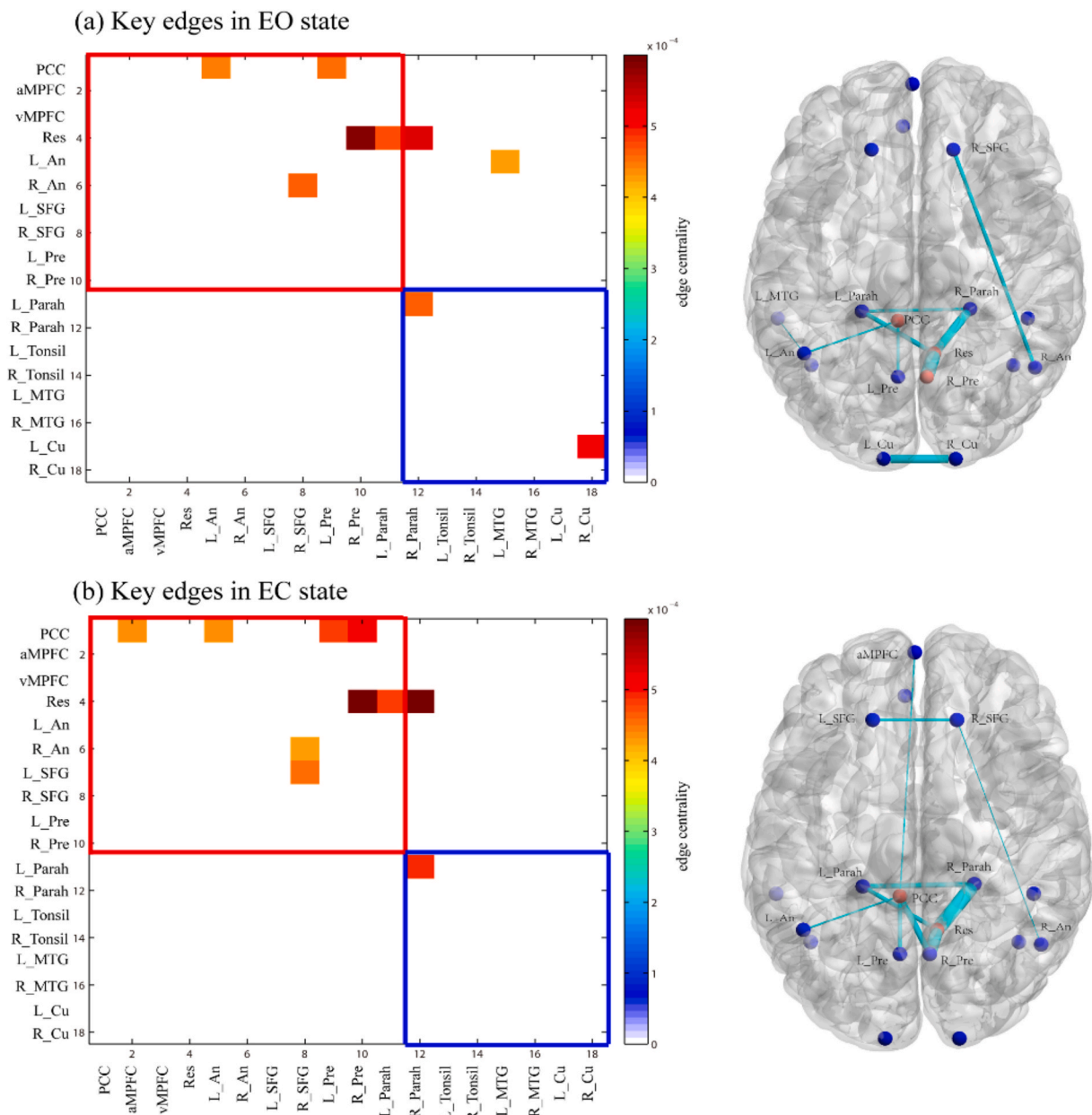


Fig. 5. Key edges within DMN during EC and EO states. The size of the edge represents the edge centrality. The red and blue rectangles indicate two literature-informed ROI blocks used to facilitate visual inspection of within- and between-block connectivity patterns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the right precuneus met this criterion only under EO. The persistence of PCC- and RSC-centered hubs across conditions is consistent with the central role of posteromedial regions in DMN organization, whereas the condition-specific classification of the right precuneus suggests greater topological prominence of this region during EO (Foster et al., 2023, Paquola et al., 2025). The precuneus is well positioned to integrate higher-order and sensory information, and recent functional neuroimaging evidence has demonstrated coupling of the precuneus with visual cortical regions during externally driven perceptual processing (Yazin et al., 2025). Together with earlier evidence linking the right precuneus to visuospatial representation and visual-attentional processing (Schott et al., 2019), these findings provide a plausible context for its hub classification under EO. Nevertheless, because hub status was determined using a predefined centrality criterion rather than an inferential EO–EC comparison, and because visuospatial attention was not directly measured, this interpretation should remain tentative.

The descriptive key-edge analysis further suggested condition-related differences in the topological distribution of highly central connections. Under EO, the bilateral cuneus connection met the predefined key-edge criterion, indicating a prominent position of this visual-related pathway in shortest-path communication within the DMN. This pattern is compatible with previous evidence that eye opening and closing modulate functional interactions between visual cortex and the DMN (Costumero et al., 2020, Han et al., 2023), and with recent evidence that sensory information can access specific components of the DMN rather than the network uniformly (Paquola et al., 2025). In contrast, key edges under EC more frequently involved the bilateral superior frontal regions, suggesting a shift in the topological distribution of central communication pathways toward frontal components of the network. Given the absence of direct measures of internally generated cognition, however, this pattern should not be taken as direct evidence for enhanced self-generated thought or mental imagery during EC.

Overall, the condition-specific hub and key-edge configurations occurred within a largely preserved DMN architecture, supporting the view that EO and EC are associated with selective redistribution of topological prominence rather than wholesale reorganization of the network.

Several limitations should be acknowledged. First, EO and EC differ not only in sensory input but potentially also in vigilance, arousal, and physiological state. Because the present dataset did not include eye tracking, electrophysiological recordings, or cardiorespiratory monitoring, the observed differences should be interpreted as condition-related modulation rather than effects attributable specifically to visual input or arousal. Future studies combining resting-state fMRI with eye tracking or pupillometry, simultaneous EEG-fMRI, and respiratory and cardiac monitoring could help distinguish neural effects from vigilance- and physiology-related contributions (Kung et al., 2024). Second, the relatively limited scan duration may have reduced sensitivity to subtle or temporally variable network effects. Longer or repeated resting-state acquisitions could improve the reliability of future EO/EC comparisons. Third, the present study focused specifically on intra-DMN organization and therefore did not characterize EO/EC-related interactions between the DMN and other large-scale networks. Whole-brain or multi-network analyses could provide a more comprehensive account of condition-dependent network reconfiguration. Finally, the current analyses were conducted primarily at the group level and did not explicitly characterize inter-individual variability in EO/EC-related modulation. Subject-specific and longitudinal approaches may help determine the stability and heterogeneity of these effects across individuals.

5. Conclusion

In conclusion, the present study demonstrates that the DMN exhibits a highly preserved large-scale functional architecture across eyes-open and eyes-closed resting-state conditions, while also showing reliable condition-related differences at multiple organizational levels. Specifically, EO and EC states were associated with differences in selected intra-DMN functional connections, global network properties, and the distribution of highly central nodes and edges. These findings indicate that commonly used resting-state acquisition conditions are associated with systematic modulation of DMN organization embedded within an otherwise stable intrinsic architecture. By applying graph-theoretical analyses at both connection and network levels, the present work provides a DMN-focused characterization of how resting-state condition influences intrinsic functional organization, offering a useful framework for interpreting and comparing DMN measures obtained under different resting-state paradigms.

CRedit authorship contribution statement

Fei Wang: Writing – original draft, Visualization, Resources, Investigation, Formal analysis, Data curation, Conceptualization. **Tao Zhang:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jiawang Ma:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Shunjie Yin:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Fen Xu:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Bharat B. Biswal:** Writing – review & editing, Supervision, Methodology, Conceptualization. **X. San Liang:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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