Cost-efficiency trade-offs of the human brain network revealed by a multiobjective evolutionary algorithm

Junji Ma, Jinbo Zhang, Ying Lin*, Zhengjia Dai*

Department of Psychology, Sun Yat-sen University, Guangzhou 510006, China

ABSTRACT

Keywords:
Cost-efficiency trade-off
Diffusion MRI
Human brain
Connectome

It is widely believed that the formation of brain network architecture is under the pressure of optimal trade-off between reducing wiring cost and promoting communication efficiency. However, the questions of whether this trade-off exists in empirical human brain structural networks and, if so, how it takes effect are still not well understood. Here, we employed a multiobjective evolutionary algorithm to directly and quantitatively explore the cost-efficiency trade-off in human brain structural networks. Using this algorithm, we generated a population of synthetic networks with optimal but diverse cost-efficiency trade-offs. It was found that these synthetic networks could not only reproduce a large portion of connections in the empirical brain structural networks but also embed a resembling small-world organization. Moreover, the synthetic and empirical brain networks were found similar in terms of the spatial arrangement of hub regions and the modular structure, which are two important topological features widely assumed to be outcomes of cost-efficiency trade-offs. The synthetic networks had high robustness against random attacks as the empirical brain networks did. Additionally, we also revealed some differences between the synthetic networks and the empirical brain networks, including lower segregated processing capacity and weaker robustness against targeted attacks in the synthetic networks. These findings provide direct and quantitative evidence that the structure of human brain networks is indeed largely influenced by optimal cost-efficiency trade-offs. We also suggest that some additional factors (e.g., segregated processing capacity) might jointly determine the network organization with cost and efficiency.

1. Introduction

The brain is a complex system that can be characterized as a network with numerous connections linking brain regions, namely the brain connectome (Bullmore and Sporns, 2009, 2012; Sporns et al., 2005). Graph theoretical approaches in network neuroscience have revealed several pronounced topological features of the brain connectome, including small-worldness (for review see Bassett and Bullmore, 2006, 2017; Liao et al., 2017), modular organization (Meunier et al., 2010; Meunier et al., 2009), and the presence of hub regions (for review see van den Heuvel and Sporns, 2013). Although these features do provide a systematic description of brain network architecture, the underlying mechanism that shapes the human brain structural network remains poorly understood.

The wiring cost has long been recognized as one fundamental factor that shapes the brain network structure. Embedding within the limited space of the skull, construction and maintenance of anatomical connections in brain networks consume a high material cost (Ahn et al., 2006; Mitchison, 1991). Considering the cost constraint, previous studies have pointed out that several features of brain networks might be the outcome of cost minimization. First, it was commonly found that close region pairs had a much higher probability of connecting than remote region pairs that require costly long connections to be interconnected (Klyachko and Stevens, 2003; Markov et al., 2013; Young, 1992). Moreover, the existence of some topological features (e.g., high modularity and hierarchical organization) was also attributable to the pressure of minimizing cost (Samu et al., 2014). However, in silico, the wiring cost of empirical brain networks was found to be nearly minimal but not strictly minimized compared with simulated networks (Kaiser and Hilgetag, 2006). Hence, minimizing cost is one, but not the only, fundamental factor shaping brain network organization.

Efficient information processing and communication are also required for brain networks (Laughlin and Sejnowski, 2003). The small-worldness of brain networks enables them to achieve an optimal balance between local processing (i.e., high clustering coefficient) and global communication efficiency (i.e., short characteristic path length) (for review, see Bassett and Bullmore, 2006, 2017; Liao et al., 2017). Moreover, the existence of long-distance connections (Kaiser and Hilgetag, 2006) that promote communication between remote regions, modular structure (Meunier et al., 2010; Meunier et al., 2009), and highly

* Corresponding author.
E-mail addresses: linying23@mail.sysu.edu.cn (Y. Lin), daizhengji@mail.sysu.edu.cn (Z. Dai).

https://doi.org/10.1016/j.neuroimage.2021.118040.
Received 31 December 2020; Received in revised form 15 March 2021; Accepted 4 April 2021
Available online 20 April 2021.
1053-8119/© 2021 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license
(http://creativecommons.org/licenses/by-nc-nd/4.0/)
connected hubs (van den Heuvel and Sporns, 2013) that promote segregated and integrated information processing, all reflect an optimal arrangement for efficient network communication. However, these features inevitably increase the cost of the brain network. Therefore, the network structure configuration does not simply minimize cost or promote efficiency but seeks the optimal trade-off between these two factors (Bullmore and Sporns, 2012).

Recent studies have attempted to examine the hypothesis of optimal cost-efficiency trade-off in non-human brain structural networks (Chen et al., 2013, 2017). They defined an optimization objective that described the cost-efficiency trade-off as a weighted sum of the cost and efficiency measures, and then generated synthetic brain networks by employing the simulated annealing algorithm to approximate the optimal solution under the above objective. The comparison between the synthetic networks and the empirical brain structural network of macaque/ Caenorhabditis elegans (C. elegans) found that the synthetic networks could reproduce the modular organization and the spatial location of several hubs in the empirical network. Such findings strongly supported the hypothesis of optimal cost-efficiency trade-off in non-human brain structural networks. However, whether optimizing the cost-efficiency trade-off is also the underlying force that drives the formation of human brain structural networks remains an open question. Moreover, using fixed weights to quantify the relative importance of cost and efficiency, as did in previous research (Chen et al., 2013, 2017), could induce biased or incomplete conclusions when discussing the effect of cost-efficiency trade-off in the formation of brain networks. First, the relative importance of cost and efficiency is unknown. Presuming their weights may hinder full exploration of possible cost-efficiency trade-offs in empirical brain networks. Second, using fixed weights to define the cost-efficiency trade-off inherently denies the possibility of variation in the trade-off. However, the diversity of brain network structure is an adaptive property from an evolutionary perspective, which can prevent the risk of extinction in species while confronting environmental changes (Frankel et al., 2014; Schindler et al., 2010). Hence, the variation in the corresponding cost-efficiency trade-off may also exist and is worth further consideration.

In human brain structural network, several previous studies employed computational models to generate brain-like networks, such as generative models that combine regional topological and geometric features (Betzel et al., 2016; Betzel and Bassett, 2017) and modified models of random networks (Gollo et al., 2018; Samu et al., 2014). Although some of the descriptive features revealed by these models reemphasized the importance of cost or efficiency, there is still no straightforward or quantitative evidence for how and how well cost-efficiency trade-off shapes the human brain network. On one hand, the focus of these computational studies was how to generate brain-like networks, rather than to directly examine the fundamental factors (i.e., cost-efficiency trade-off) that induce these descriptive features. On the other hand, most of these models analyzed the effect of a single factor or several factors separately. The important term “trade-off”, as in our research question, is rarely investigated. It has been widely acknowledged that none of these factors (e.g., wiring cost or communication efficiency) could independently shape the empirical brain network. Change in one factor (e.g., cost) would inevitably cause change in the others (e.g., efficiency) (Bassett and Bullmore, 2006; Bullmore and Sporns, 2012; Stiso and Bassett, 2018).

In the current study, we explored the cost-efficiency trade-off in the human brain network using a novel approach that can avoid explicitly defining the relative importance between cost and efficiency. First, we modeled the cost-efficiency trade-off in the network as a multiobjective optimization problem that aimed at minimizing the wiring cost while simultaneously maximizing the communication efficiency. Then, we employed a multiobjective evolutionary algorithm (MOEA) to solve the above problem, which generated a set of synthetic networks with different but equally good trade-offs (namely, the non-dominated set) between the cost and efficiency objectives by imitating the evolution-
brain extraction, correction for eddy-current distortion, head motion, and b-matrix (Leemans and Jones, 2009). The diffusion tensor and fractional anisotropy (FA) were computed through the pipeline. Furthermore, to obtain the white matter (WM) binary mask in native diffusion space for a constraint mask for subsequent WM tractography, the T1-weighted images were reoriented manually to the AC-PC line and then segmented with SPM8 software. The resultant WM binary masks (with WM probability threshold > 0) in the T1 native space were further transformed into the native diffusion space for each participant with the inverse transformation matrix estimated during the coregistration of the FA image to T1.

Nodes and edges are two basic network elements. In this study, ninety nodes covering the whole brain were defined by Automated Anatomical Labeling parcellation (AAL, Tzourio-Mazoyer et al., 2002). The AAL atlas was originally defined in the standard Montreal Neurological Institute (MNI) space and was transformed into the native diffusion space for each participant with the typical procedure of previous studies (Gong et al., 2009). Specifically, individual FA images were coregistered to the T1-weighted images, and the T1-weighted images were normalized to the ICBM152 T1 template in the MNI space. These two transformation matrices were then inverted to warp the AAL atlas from MNI space to native diffusion space for each participant. To define network edges, we performed deterministic tractography based on fiber assignment by continuous tracking (FACT) using the Diffusion Toolkit (http://trackvis.org) (Wang et al., 2007). In the tracking procedure, a seed was distributed at the center of each voxel with an FA value greater than 0.2 in the WM mask. A streamline was started from each seed and terminated if the streamline reached a voxel with a turning angle greater than 45°, the FA value was less than 0.2, or the streamline entered a voxel out of the WM mask. For each pair of nodes, the edge was defined as one if there was at least one streamline between them; otherwise, it was set to zero. Therefore, for each participant, we obtained one 90 by 90 binary structural network.

2.4. Objective functions of brain network

In this study, to construct synthetic networks with the optimal cost-efficiency trade-offs, we first defined two objective functions to evaluate the wiring cost and the processing efficiency of brain networks. The first objective $F_c$, which measured the total wiring cost of the brain network, was calculated as follows:

$$ F_c(A) = \frac{1}{2} \sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij} a_{ij}, \quad i \neq j = 1, 2, 3, \ldots, N $$

where $d_{ij}$ is the Euclidean distance between the centroids of nodes $i$ and $j$; $A = [a_{ij}]_{N \times N}$ is the adjacency matrix of the binary structural network, and $a_{ij}$ is the indicator for the existence of the edge between nodes $i$ and $j$, where one-entry indicates existence and zero-entry indicates none; $N$ is the total number of nodes in the network (here, $N = 90$). To be noted, we used the Euclidean distance between two regions to approximate the wiring cost of their connection. This is because edges in synthetic networks established by the simulation process might not correspond to actual connections in empirical brain networks, which makes it hard to evaluate the fiber length (i.e., actual wiring cost) of these edges.

The second objective measured the processing efficiency of brain networks. Notably, to unify the optimization direction with the cost objective (i.e., minimization), we used the path length of the synthetic network to define the efficiency objective $F_e$. The smaller the $F_e$ value is, the higher efficiency the network possesses. The detailed calculation of $F_e$ is shown below:

$$ F_e(A) = \frac{1}{2} \sum_{i=1}^{N} \sum_{j=1}^{N} l_{ij}, \quad i \neq j = 1, 2, 3, \ldots, N $$

where $l_{ij}$ is the shortest path length between nodes $i$ and $j$ according to the binary network adjacency matrix $A$ and $N$ is the total number of nodes in the network (here, $N = 90$).

2.5. Cost-efficiency balanced network construction

After defining the two objective functions as above, we adopted the nondominated sorting genetic algorithm (NSGA-II; Deb et al., 2002; https://www.egr.msu.edu/~kdeb/codes.shtml), a popular multiobjective evolutionary algorithm (MOEA), to construct synthetic networks with optimal cost-efficiency trade-offs. Without predefining the weight of relative importance between cost and efficiency, the MOEA evolves a population of candidate networks to seek the best trade-off between these two objectives. The overall procedure of NSGA-II we implemented is described below (for pseudocode see Algorithm S1):

Step 1) Population initialization. The population of an MOEA is a set of individuals in which each individual represents a candidate solution to the optimization problem. Herein, each individual in the MOEA population was a binary and symmetric 90 by 90 matrix that represented a synthetic network of the 90 brain regions regarding the AAL parcellation. An individual was initialized by randomly assigning a value (one or zero) to each entry beyond the main diagonal of the matrix, where one represented an edge existing between the corresponding nodes and zero represented the opposite. The probability of adding edges was set to 0.1 to ensure that the connection density of the initial matrix was approximately 10%, which was in accordance with the connection density of the empirical structural network at the group level (density $= 9.69\%$). Then, the upper triangle of the matrix was flipped by the main diagonal to ensure symmetry, and the entries on the main diagonal were all set as zeros to avoid loop edges. After initializing the matrix, we evaluated the fitness of the individual’s performance using the above cost and efficiency objective functions. According to the problem dimension (i.e., the number of decision variables to be optimized), we set the population size to 200. A population of 200 candidate network matrices was thus generated at the current step.

Step 2) Reproduction of the population. To retain high-quality gene blocks for subsequent generations, MOEAs design crossover operators to imitate the reproduction procedure in the natural evolutionary process. More specifically, the crossover operator generates promising new solutions (i.e., offspring) by inheriting and recombining elements from several previous solutions (i.e., parents). Herein, the crossover operator first selected two high-quality individuals from the previous generation as parental solutions. Then, one of the following two crossover methods was applied: (1) exchange a random section of edge values of the two parental solutions and (2) exchange the edge values at several random positions of the two parental solutions. The probabilities of applying the two methods were set equal. Although both the two crossover operators generated offspring by exchanging edges of parents, their ways to conduct exchange were different. The first crossover operator could retain the integrity of a consecutive section of edge values while exchanging, which helped keep certain information of local connection patterns. In contrast, the second crossover operator exchanged the edge values in a more random and discrete manner, which might bring more diversity into the offspring. Using multiple crossover methods enabled us to explore the solution space more thoroughly. The crossover step produced 200 offspring in total and composed a new population, namely, the offspring population. The offspring population was also evaluated using the cost and efficiency objective functions.

Step 3) Mutation of the population. Mutation is another important operator of MOEAs, aiming to imitate the mutation of chromosomes in nature. From the perspective of optimization, the mutation operator can improve the global search ability of the algorithms by imposing subtle changes in the solutions and thus relieve the risk of getting trapped in local optima. Specifically, for each edge of each individual from the parental and offspring populations, it had a relatively low probability (here, probability $= 0.1$) to flip into the other value (i.e., one to zero or vice versa). The mutated individuals were also added to the offspring population. After mutation, the mutated individuals were further evaluated by the cost and efficiency objectives.
Step 4) Selection of the population. The selection operator of MOEAs is designed to imitate the natural selection procedure. Candidate solutions with higher quality, indicated by better objective values, are given a higher chance to enter the population of the next generation. Herein, the selection operator selected 200 elites from the parental and offspring populations to generate the new population of the next generation. More specifically, the elites were selected using the fast nondominated sorting approach (Deb et al., 2002), which ranked the considered solutions according to their performance (i.e., the cost and efficiency objective values) and local diversity (i.e., crowding distance between solutions in the cost-efficiency objective space). The performance of a solution was measured based on the mutual dominance relationship with the other solutions. That is, the fewer counterparts one solution got dominated by, the higher rank this solution had.

Step 5) Termination check. This algorithm was terminated when one of the following conditions was satisfied. (1) The population stopped evolving for 10 consecutive generations. The term “stop evolving” was defined as less than 5% individuals were changed or the maximum difference in the objective values was less than 0.1% of mean objective values. (2) The number of generations reached 2,000. If neither of the conditions was satisfied, the algorithm returned to Step 2) and started a new iteration. The population of the final iteration was returned as the result.

Since MOEA is a probabilistic algorithm, the results can vary across different runs. We ran the algorithm 30 independent times and then used the fast nondominated sorting approach to select the nondominated solutions among the results of all the runs for subsequent analyses.

2.6. Recovery rate of synthetic networks

The above NSGA-II generated synthetic networks that approximated the optimal trade-off between cost and efficiency. To measure the similarity between the synthetic networks and the empirical human brain networks, we computed the recovery rate $R$ of the synthetic networks by calculating the ratio of overlapping entries between synthetic and empirical adjacency matrices (Chen et al., 2013; Costa Lda et al., 2007). The recovery rate was computed as follows:

$$ R = \sqrt{R_0 \cdot R_1}; \quad R_0 = \frac{K_{00}}{K_0}, \quad R_1 = \frac{K_{11}}{K_1} $$

where $R_0$ and $R_1$ are the recovery rates of zero- and one-entries of the matrix, respectively; $K_{00}$ and $K_{11}$ are the numbers of zero- and one-entries in the matrix of the empirical brain network (without considering the diagonal entries); $K_0$ and $K_1$ are the numbers of overlapping zero- and one-entries between the synthetic and empirical networks. To verify whether recovery rates of these synthetic networks were driven by cost-efficiency trade-off rather than just random redistribution of connections, we further calculated the recovery rate on two types of random models and compared the recovery rate between the synthetic networks and random networks. The first random model is the topological random network (Maslov and Sneppen, 2002), which randomly rewires the connections while preserving the number of nodes and edges, and the degree distribution of the group-level empirical network. The second random model is the geometrical random network (Sizemore et al., 2017). Specifically, this model randomly chooses $N$ nodes ($N = 90$) in the original MNI space and evaluates the Euclidian distance between each two nodes. Then connections of the $K$ shortest node pairs were generated, where $K$ is equal to the number of connections in the group-level empirical network. Different from the topological random network, this type of random network preserves the spatial dependence of wiring that closer region pair has higher possibility to be mutually connected.

According to previous studies (Chen et al., 2013, 2017), edges with different physical distances or from different modules might play different roles in the cost-efficiency trade-off. We further calculated the recovery rate on different subgroups of edges: distance subgroups according to the Euclidean distance between region pairs and modular subgroups according to the network partition obtained by the method detailed in the “Modular structure” section.

2.7. Topological characteristics of the synthetic networks

To further examine whether the synthetic networks could capture the topological features of empirical brain networks, we calculated the graphical metrics at the whole-brain level, including the small-world metrics [i.e., clustering coefficient (Cp), characteristic path length (Lp), normalized clustering coefficient ($\gamma$), normalized characteristic path length ($\lambda$), and small-worldness ($\sigma$)], efficiency metrics [i.e., global efficiency (Eg) and local efficiency (El)] and modularity metrics [i.e., modularity (Q) and the number of modules (Mn)]. High values of clustering coefficient, normalized clustering coefficient, local efficiency, modularity, and a large number of modules reflect a good capacity of segregated processing in the network. Low characteristic path length and normalized characteristic path length, and high global efficiency characterize a good capacity of integrated processing in the network. High small-worldness shows an optimal balance between segregated and integrated processing in the brain network. Calculation of the above graphical metrics was performed using the Graph Theoretical Network Analysis toolbox (GRETNAs; Wang et al., 2015) and Brain Connectivity Toolbox (BCT; Rubinov and Sporns, 2010). Detailed definitions of these graph metrics are presented in the Supplementary Materials. Notably, considering the potential effect of cost on these metrics, only the synthetic networks whose cost objective values were distributed in the cost range of the SCNU sample were selected for comparison. All seventy-five synthetic networks within this cost range were finally selected in the current analysis (see Results section).

2.8. Extraction of the representative network

To examine more specifically how the cost-efficiency trade-off shapes the topological characteristics of brain networks, we further extracted a representative network from the nondominated synthetic networks and the empirical brain networks, respectively. The representative synthetic network was the one that resembled most of the others. It was derived through the following steps: (1) calculated the mutual information (Meilă, 2007) between every pair of the synthetic networks to evaluate their pairwise similarity, (2) computed the mean mutual information of each synthetic network with the other synthetic networks, and (3) selected the synthetic network with the highest mean mutual information as the representative network. The representative network of the empirical brain networks was the group-level network retaining edges that existed in more than 50% of the participants’ structural networks. Subsequent analyses were all performed on these two representative networks. Three specific aspects of network features were analyzed, including the presence of hubs and modular structure, which were previously assumed as the outcome of cost-efficiency trade-off, and network robustness, which is a necessary property of human brain networks.

2.9. Degree centrality and hubs

Hub regions, which have a relatively large number of connections, are commonly suggested to have high cost and high communication capacity in human brain networks (for review, see van den Heuvel and Sporns, 2013). Therefore, the existence of hub regions might be the outcome of the cost-efficiency trade-off. To examine this hypothesis, we compared the generation and spatial arrangement of hub regions between synthetic and empirical networks. In the current study, we first computed the degree centrality (i.e., number of nodal connections) of all 90 regions and examined the similarity in the degree distribution between the representative synthetic and empirical networks. Then, the regions that ranked in the top 20% in descending order of degree centrality (Zuo et al., 2012) were identified as hubs of each representative
network, and their spatial locations were compared. We also assessed the effects of different thresholds (top 5%, 10%, 15%, and 25%) on the overlapping pattern of the hub regions.

2.10. Modular structure

The human brain network is organized into a modular structure with clusters (i.e., modules) of densely connected nodes and sparse connections between these clusters (Meunier et al., 2009). In this section, we investigated whether the synthetic network with optimal cost-efficiency trade-offs also possessed a modular structure and how similar the modular partition was with that of the empirical brain network. First, we applied the Louvain community detection algorithm (Blondel et al., 2008) on the representative empirical and synthetic networks to obtain their modular partitions respectively. Then, we computed the mutual information between the two partitions to evaluate the similarity in the modular structure. Furthermore, to examine whether different modules were differently influenced by the cost-efficiency trade-off, we computed the recovery rate on connections within and between modules based on the modular partition of the empirical brain network, respectively. To evaluate the recovery ability under different functional modules, we also computed the modular level recovery rate on a commonly used template that was derived from functional networks (Shen et al., 2013). By assigning each region to the module with the maximum area of overlapping voxels, the 90 regions were assigned to seven functional modules, including the medial frontal network (MFN), frontoparietal network (FPN), default mode network (DMN), subcortical network (subcortical), motor network (motor), visual network (visual), and visual association network (VAN).

2.11. Robustness of network

Robustness is an adaptive property of brain networks, which reflects the ability to preserve normal network functions under attacks (e.g., lesions). To investigate whether robustness also existed in the synthetic networks constructed under the optimal trade-offs between cost and efficiency, we performed computational attacks on the representatives of synthetic and empirical brain networks respectively, and compared the resulting network degradation in terms of global efficiency and local efficiency. Two types of computational attacks were conducted: random attacks and targeted attacks. For the random attacks, we randomly deleted nodes step by step with a step of 10% nodes in the entire network. Since node deletion involved certain randomness, at each step, we ran the procedure for 100 times and obtained 100 attacked networks. For the targeted attacks, we deleted nodes in descending order of degree centrality step by step, with the step length set the same as that in the random attacks.

2.12. Citation diversity statement

Recent work in neuroscience (Dworkin et al., 2020) and other fields (Caplar et al., 2017; Dion et al., 2018; Maliniak et al., 2013; Mitchell et al., 2013) has identified a bias in citation practices, such that papers from women and other minorities are under-cited relative to the number of such papers in the field. Here we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, and other factors. We obtained the predicted gender of the first and last author of each reference by using databases that store the probability of a name being carried by a woman or man (Dworkin et al., 2020; Zhou et al., 2020). Result of this measure, excluding self-citations, revealed that, our references contain 8.0% woman (first author)/woman (last author), 5.3% man/woman, 24.0% woman/man, 62.7% man/man. We hope future work that could help us to better understand how to support equitable practices in science.

3. Results

3.1. Global properties of synthetic networks under optimal cost-efficiency trade-offs

Using the NSGA-II algorithm, we obtained a set of 263 synthetic networks optimized under the cost-efficiency trade-off. Fig. 1A displays the distribution of these synthetic networks (blue points) and the empirical networks (orange points) in the cost-efficiency morphospace. Notably, for direct observation of the cost-efficiency relationship, we transformed the Fc objective into the efficiency metric. Specifically, for each network, the Fc value was divided by the number of all possible node pairs (here, the number of all possible node pairs is 4,005), and its reciprocal was used as the vertical coordinate. As can be seen, the 263 synthetic networks composed a nondominated front, implying that they achieved diverse but equally good cost-efficiency trade-offs. The 93 empirical brain networks also composed a front along a similar direction but were relatively narrower and were fully dominated by that of the synthetic networks. Together, visual inspection showed that the synthetic networks and empirical brain networks had similar distributions within the cost-efficiency morphospace, but the synthetic networks achieved better and more diverse cost-efficiency trade-offs.

To quantify the similarity between the synthetic networks and the empirical brain networks, we employed the recovery rate to evaluate the ratio of overlapping edges at the whole-brain level. Note that to avoid the potential effect of cost, we only analyzed the results in the 75 synthetic networks whose cost objective values were in the same range as the empirical data (cost range: 15,958–27,544). The difference between the cost of the selected synthetic networks and empirical networks was not significant (two-sample test: t = -0.912, p = 0.360). As shown in Fig. 1B, the synthetic networks had a high overall recovery rate of the empirical networks’ connections (R = 0.587 ± 0.066). As mentioned in the Method, in addition to these synthetic networks, we also generated two types of random networks (i.e., topological random network and geometrical random network) for comparison. Consistent with the number of selected synthetic networks, 75 random networks of each type were generated. We observed that both types of the random networks were positioned at the sub-optimal area of the morphospace and had a low diversity. The topological random networks (green points; Fig. 1A) had similar efficiency as empirical networks and relatively higher cost than empirical networks, which is consistent with the previous definition of random networks (Watts and Strogatz, 1998). Since the propensity of connecting short region pairs, the geometrical random networks showed a relatively lower cost and relatively lower efficiency than empirical networks (red points; Fig. 1A). The two-sample t-test revealed that the synthetic networks achieved a significantly higher recovery rate than the random networks (Fig. 1B; topological random network: t = 31.476, p < 0.001; geometrical random network: t = 35.893, p < 0.001), which supported the claim that synthetic networks are similar to empirical networks.

In addition to the recovery rate of connections, we also examined the topological characteristics of the synthetic networks at the whole-brain level. To avoid the potential effect of cost on these metrics, we only selected the 75 synthetic networks whose cost objective values were in the same range as the empirical data for analyses. For the small-world related metrics (Fig. 1C), both the synthetic networks and the empirical brain networks were organized as small-world networks (mean σ > 1; one-sample test: t > 5.029, p < 0.001), but some differences did exist between the two groups. The two-sample t-test showed that the synthetic networks scored lower in terms of the clustering coefficient (two-sample test: t = -18.688, p < 0.001), characteristic path length (two-sample test: t = -40.379, p < 0.001), normalized clustering coefficient (two-sample test: t = -52.910, p < 0.001) and normalized characteristic path length (two-sample test: t = -70.784, p < 0.001) than the empirical brain networks. Moreover, the small-worldness was also lower in the synthetic networks than in the empirical brain networks (two-sample test: t = -50.942, p < 0.001). For efficiency metrics (Fig. 1D),
3.2. Distance-dependent connections pattern of synthetic network under cost-efficiency trade-offs

The above results on the recovery rate revealed that the synthetic networks had a higher connection similarity with the empirical brain networks than the random networks. However, the detailed features of the recovered connections remained unknown. To address this issue, we

synthetic networks showed higher global efficiency (two-sample test: $t = 43.354, p < 0.001$) but relatively lower local efficiency (two-sample test: $t = -11.156, p < 0.001$) than the empirical brain networks. For modularity metrics (Fig. 1E), the synthetic networks showed a weaker modular structure ($t = -92.839, p < 0.001$) and had fewer modules (two-sample test: $t = -12.387, p < 0.001$) compared to the empirical brain networks.
performed further analyses on the representatives of synthetic networks (density = 13.71%) and empirical brain networks (density = 9.69%). The adjacency matrices and the brain maps of both representative networks are shown in Fig. 2A. A visual inspection found that the patterns were quite similar between the two networks, except that the synthetic network had some obvious global hubs (i.e., regions connected with almost all other regions in the network) in subcortical area (e.g., caudate, putamen and thalamus). The overall recovery rate of the representative synthetic network also supported its similarity with the empirical brain network ($R = 0.638$).

Although the overall recovery rate was high, we found that the recovery of connections was not uniform across the entire network. After dividing the edges into several distance intervals (Fig. 2B), we observed that the representative synthetic network recovered a large proportion of short-distance edges (Euclidian distance <= 40 mm, 0.510 < Rs < 0.860) but a relatively small proportion of middle- or long-distance edges (Euclidian distance > 40 mm, Rs < 0.455). We then divided the entries in the synthetic adjacency matrix into two subgroups based on whether they represented connections (one-entries) or not (zero-entries) in the empirical brain network. Similar to the pattern in Fig. 2B, the recovery rate of one-entries (R1) was higher in short-distance edges than in the middle- or long-distance edges (Fig. 2C). The recovery rate of zero-entries (R0) was high in most distance subgroups, except for the distance range of 20–40 mm (Fig. 2C), indicating a relatively high proportion of false-positive edges within this range. As shown in Fig. 2D, except for very short edges (distance < 20 mm), the number of edges in the empirical brain network decreased as a function of distance, and only a few long-distance edges existed. Thus, the number of unrecovered edges, especially long-distance edges, was relatively small under the optimization of the cost-efficiency trade-off. In general, the above findings suggested that local connections are preferable while trading off between cost and efficiency, which leads to the recovery of most local connections in the human brain network.
3.3. Degree distribution and hub regions of synthetic network under cost-efficiency trade-offs

After examining the recovery rates of connections, we further investigated the specific topological characteristics that emerged with the recovered connections. The first one we investigated was the presence of hubs. To identify hub regions, we first computed the degree centrality of the 90 brain regions and sorted them according to their degree centrality. As shown in Fig. 3A, the overall pattern of the degree distribution was similar between the representatives of synthetic networks and empirical brain networks. That is, in both distributions, most regions had relatively low degree centrality, while a small number of regions owned a disproportionately large number of connections. The Kolmogorov-Smirnov test further supported the similarity between these two distributions ($p = 0.675$). Nonetheless, the two degree distributions showed some difference in the scale of degree centrality. After identifying the hub regions (i.e., the top 20% regions with the highest degree centrality) in the two representative networks, Fig. 3B compared their spatial locations. The hub regions largely overlapped in the left precuneus, left olfactory cortex, left insula, left caudate and bilateral putamen (Fig. 3B right panel). Additionally, to further examine how the thresholds influence the overlapping pattern of hub regions, we reanalyzed the degree centrality of synthetic and empirical networks and defined hubs with several different thresholds, ranging from the top 5% to 25% with a step of 5%. As expected, the number of overlapping hub regions increased from 2 (threshold = 5%) to 7 (threshold = 25%) as the threshold increased (Fig. S1). Although the absolute number of overlapping hubs increased with threshold, the Dice coefficient ($0.320 \pm 0.049$) was consistent across different thresholds, which suggested a stable overlapping extent of hubs. Several hub regions were robustly detected under different thresholds, including bilateral putamen and precuneus. Notably, although several overlapping hub regions were revealed, the correlation of overall regional degree between synthetic and empirical networks was relatively low ($r = 0.111$, $p = 0.299$).

3.4. Modular structure of synthetic network under cost-efficiency trade-offs

Another topological feature we considered is the network modular structure, which is commonly suggested to be associated with the cost-efficiency trade-off (Bullmore and Sporns, 2012). Applying the Louvain community detection algorithm, we obtained the modular partitions of the representative synthetic network (modularity values = 0.330) and the group-level empirical brain network (modularity values = 0.521, Fig. 4A). The modular partitions were similar between these two networks, with mutual information at 0.434. Based on the modular partitions of the empirical brain network, we examined the recovery of intra- and inter-module connections in the synthetic network, and found that the recovery rates were not uniform across modules (Fig. 4B). Even
in the same module, the recovery rates were quite different between inter- and intra-module connections. Module-1 at the left frontal area achieved higher recovery of within-module connections than its inter-module connections and the intra-module connections of other modules. In contrast, the recovery rates of Module-3 and Module-4 at the right occipital and frontal areas were dominated by inter-module connections. Furthermore, Fig. 4C shows that the recovery rate also varied obviously across functional modules defined by Shen et al. (2013). Specifically, intra-module connections had a relatively higher recovery rate \( (R = 0.691) \) than inter-module connections \( (R = 0.605; \text{Fig. 4C right panel}) \). This pattern was particularly obvious in modules such as DMN and FPN, which carry a large proportion of high-cost hub regions and are responsible for considerable information integration in the functional network. The variety in recovery rate across modules suggested that different modules were affected by cost-efficiency trade-offs to different degrees.

3.5. Network robustness of synthetic network under cost-efficiency trade-offs

Finally, we investigated the robustness, which is an important property of the brain network, of both the representatives of synthetic networks and empirical brain networks. Previous studies suggested that human brain networks were almost as resilient as random networks under random attacks but suffered from more severe deterioration under targeted attacks on high-degree regions (Crossley et al., 2014). As shown in Fig. 5A, under almost every step of the random attacks, the synthetic network had slightly better robustness than the empirical brain network in terms of both global efficiency \( (t > 2.710, ps < 0.007) \) and local effi-
ciency ($t > 2.411, ps < 0.017$) degeneration. The two networks achieved similar degeneration in terms of local efficiency ($t = 1.761, p = 0.080$) only at the step that removed 80% of the nodes. However, the synthetic network was much more vulnerable to targeted attacks on high-degree regions than the empirical brain network (Fig. 5B), where global and local efficiency degenerated more rapidly. In other words, high-degree regions, especially those global hubs, played a much more important role in the synthetic network communication, leading to higher overall fragility of the network.

4. Discussion

In this study, we adopted an MOEA approach to reconstruct a population of synthetic networks that simultaneously optimized wiring cost and communication efficiency. These synthetic networks showed a good recovery of connection patterns in the empirical brain networks. Through a comparison between the synthetic networks and the empirical brain networks, we revealed a series of important network features that are related to cost-efficiency trade-offs. First, most of the connections in the empirical brain networks, especially the local connections, were recovered in the synthetic networks. Second, similar to the empirical brain networks, the synthetic networks showed a clear small-world property. Third, the modular structure and the spatial distribution of hub regions in the synthetic network were also similar as the empirical brain networks. Fourth, compared to the empirical brain networks, the synthetic networks achieved similar or even better robustness under random attacks. The synthetic networks also deviated from the empirical brain networks on a few aspects, including relatively weaker segregated processing capacity (i.e., lower average clustering coefficient and local efficiency) and weaker robustness under targeted attacks.

4.1. Cost-efficiency trade-off in human brain networks

Studies have accumulated to support the hypothesis that the evolution of brain structural networks is driven by trade-offs between minimizing wiring cost and promoting communication efficiency (for review see Bullmore and Sporns, 2012; Stiso and Bassett, 2018). However, it remains unclear whether this hypothesis is true in human brain networks and how this cost-efficiency trade-off shapes the structure in human brain networks. Our work, instead of simply rediscovering the existence of cost-efficiency trade-off, provided a rather straightforward and quantitative answer for the above question. Here, we used a well-designed MOEA approach to generate a nondominated set of synthetic networks that approximated the Pareto front in the space of the two competitive dimensions (i.e., cost and efficiency) (Avena-Koenigsberger et al., 2015). The Pareto front represents the optimal area of multiobjective solution space. Every solution on the Pareto front dominates the other legal solutions outside the front by winning on all the optimization objectives,
whilst every two solutions on the front are mutually nondominated as one is better than the other on at least one objective and vice versa. These synthetic networks showed significantly higher recovery of the empirical brain networks than random networks. This high similarity between synthetic and empirical networks partially and quantitatively supports the hypothesis that human brain networks are organized under the cost-efficiency trade-off. Moreover, we found considerable variation in the cost-efficiency trade-off among the empirical brain networks, suggesting that the trade-off between cost and efficiency might not be unique. This suggestion is consistent with the hypothesis of a recent review (van den Heuvel and Sporns, 2019). Notably, none of the empirical brain networks were distributed on the approximated Pareto front outlined by the synthetic networks. Instead, the empirical networks were closely distributed to the approximated Pareto front along the same direction but in a suboptimal area. The implication of such suboptimality is two-fold. On the one hand, the suboptimality implies that the current implementation of the cost-efficiency trade-off framework is missing something critical, either in terms of the definitions of cost and efficiency or in terms of a third optimization objective. Our subsequent analyses over the synthetic and empirical networks highlighted the importance of local connections in the cost-efficiency trade-off and further pointed out two potential factors (i.e., segregated processing capacity and robustness) that could complement the current cost-efficiency trade-off framework. On the other hand, from the evolutionary perspective, the suboptimality may imply that the organization of the human anatomical brain network might not reach the optimal cost-efficiency trade-off but a suboptimal or near-optimal stage (Gollo et al., 2018). The above findings provided novel insight of cost-efficiency trade-off that human brain networks have diverse but remain suboptimal cost-efficiency trade-off.

### 4.2. Distance-dependent connections pattern of synthetic network under cost-efficiency trade-off

Several studies have found that a large proportion of connections in structural brain networks are short-distance connections, which reflects a strategy of minimizing material cost (Chen et al., 2006; Hagmann et al., 2007). In the current study, we found that the synthetic networks generated by optimizing the cost-efficiency trade-off could also reproduce most of the short-distance connections in human brain networks. This finding provided direct evidence to support the notion that the cost-efficiency trade-off plays a significant role in shaping the arrangement of local connections. Despite the economic local connections, the human brain network also has a small number of long-distance connections. However, we found that the recovery rate of long-distance connections was relatively low, which is similar to the pattern observed in macaque and C. elegans brains (Chen et al., 2013, 2017). In contrast to the drive to minimize cost, costly long-distance connections have been widely considered topological “shortcuts” that allow direct and efficient communication between remote areas (Bassett and Bullmore, 2017; van den Heuvel and Sporns, 2011). Given the advantage in promoting communication efficiency, why were long-distance connections in human brain networks still poorly recovered in the optimization of the cost-efficiency trade-off? One possible explanation is that the efficiency gain of adding these long-distance connections is not high enough to make up the penalty of their wiring cost. One recent study has argued about the role of long-distance connections in promoting rapid communication (Betzel and Bassett, 2018). Instead, they found that long-distance connections were necessary for supporting other important functions in the complex brain network, such as robustness and functional diversity.

### 4.3. Topological features of synthetic network under cost-efficiency trade-off

Apart from the recovery of connections, the synthetic networks also reproduced several important topological characteristics of human brain networks. The first was small-worldness, which is an early proposed concept characterized by short characteristic path length and high clustering coefficients in the network (Watts and Strogatz, 1998). Such an architecture has been widely reported in brain networks of C. elegans (Watts and Strogatz, 1998), mouse (Rubinov et al., 2015), macaque (Latora and Marchiori, 2001), and human (Bassett and Bullmore, 2006; Bassett and Bullmore, 2017; Liao et al., 2017). Moreover, the small-world architecture emerges early and is preserved across the human lifespan (Cao et al., 2017; Collin and van den Heuvel, 2013). With these cross-species and cross-age consistencies of small-worldness, many researchers have assumed that the small-world architecture might be an outcome of some general evolutionary pressures (e.g., trade-offs between cost and efficiency; for review, see Liao et al., 2017). Our findings provide direct evidence that cost-efficiency trade-offs lead to the formation of small-world networks. Notably, the small-worldness of the synthetic network, although significantly larger than one, was significantly lower than that of the empirical network (Fig. 1C), which was attributed to the shorter characteristic path length and the lower clustering coefficient of the synthetic networks. The main reason behind this is that the current model of cost-efficiency trade-off did not account for the effect of segregated processing capacity, which would be discussed below in the subsection of Additional factors that shape human brain network.

In addition to small-worldness, two important topological features of the human brain network have also been widely reported: the emergence of hubs and modular organization. Hubs are costly but crucial for network communication (van den Heuvel and Sporns, 2013). With the large number of connections, the spatial distribution of hubs is particularly important for achieving the optimal trade-offs between minimizing cost and promoting efficiency (Gollo et al., 2018). An appropriate arrangement allows hub regions to achieve efficient information transmission at the cost of a short total wiring length. In our analysis, the synthetic network sourced from the optimization of the cost-efficiency trade-off could reveal the presence of hub regions and successfully reproduce several hubs of human brain structural networks, such as the precuneus and insula. These hub regions were also commonly found in previous studies (for review, see van den Heuvel and Sporns, 2013). However, the synthetic network revealed an additional group of “global hubs” in subcortical areas. This might be due to the central spatial location of subcortical regions in the three-dimension brain volume. From the perspective of our model, connections to these spatially central areas could allow efficient interregional communication of the whole network by consuming relatively low wiring costs. For the modular organization, this structure in human brain networks could not only promote efficient local communication but also save the cost of building connections among remote modules (Meunier et al., 2010; Meunier et al., 2009). In our present work, the synthetic network also showed a similar modular structure as the empirical brain network. However, the recovery rates of connection were not uniform across modules. Connections related to high-level modules such as the DMN and FPN, especially intra-module connections, achieved better recovery. This might be due to the large proportion of costly hub regions in these modules and their responsibility to process a large amount of global information (Cole et al., 2013; Raichle, 2015; van den Heuvel and Sporns, 2013), which made their connections more dependent on the trade-off between cost and efficiency. In general, the recovery of modular structure and hubs in the synthetic network suggested that the cost-efficiency trade-off could partially influence the organization of modular structure and arrangement of hub regions.
4.4. Additional factors that shape human brain network

Despite all the above similarities, we also noted some differences between the synthetic networks and the empirical brain networks, which may imply additional factors that shape the human brain network. The first notable difference is segregated (or local) processing capacity. When referring to the cost-efficiency trade-off, we used to focus on the balance between cost and global efficiency (Avena-Koenigsberger et al., 2014; Chen et al., 2013; Fornito et al., 2011). In the current study, we found that compared to the empirical brain networks, the synthetic networks optimized under the cost-efficiency trade-off were significantly lower in terms of local efficiency, clustering coefficients, and modularity score, which were all associated with segregated communication in the brain network (Rubinov and Sporns, 2010). Moreover, several unexpected global hubs were observed in the representative synthetic network, which might be the outcome of overestimating the importance of global efficiency. These findings suggest that we might have neglected the balance between global and local communication in the generation of synthetic networks. Segregated processing ability is crucial for several human brain functions, such as task switching (Cohen and D’Esposito, 2016; Wig, 2017). In line with our speculation, previous studies based on generative models have revealed that regional clustering-based metrics, which are also associated with segregated processing, had a considerable effect in determining edge generation of brain networks (Betzel and Bassett, 2017; Betzel et al., 2016). However, although convergent observations were revealed, the problem of how the trade-off between cost and efficiency, including the efficiency of global and local communication, shapes the network structure remains unsolved. Unlike the current study, the main objective of optimization in these generative models was to generate brain-like networks based on topological/geometric features, regardless of the underlying principle (i.e., cost-efficiency trade-off). In future work, we still need to adopt the MOEA approach with improved efficiency measure that combines global and local efficiency to examine the human brain cost-efficiency trade-off mechanism more precisely.

The other important difference is the robustness under targeted attacks on high-degree regions. Our analysis revealed that compared with the empirical brain network, the robustness of the synthetic network was slightly higher under random attacks but lower under targeted attacks. This might be due to the existence of dominant hubs, the failure of which will lead to considerable damage to network communication. Another possible reason might be the poor recovery of long-distance connections. A recent study suggested that long-distance connections tended to link regions with similar connectivity profiles (Betzel and Bassett, 2018). Following this suggestion, if one of two remotely connected regions is damaged, some of its functions could be compensated by the other region, which might benefit the robustness against targeted attacks. The existence of the dominant hubs and poor recovery of long-distance connections might jointly lead to low robustness of the synthetic network against targeted attacks. Actually, in empirical human brain networks, it is vital to have high resilience under targeted attack on high-degree regions. According to previous studies on neuropsychiatric disorders, high-degree regions are more vulnerable to degeneration caused by diseases (Buckner et al., 2009; Crossley et al., 2014; Dai et al., 2015; Gong and He, 2015). High robustness against targeted attacks could help reduce the functional degradation induced by diseases. Therefore, allocations of hubs should consider their contributions not only to minimize cost and promote efficiency but also to maintain network robustness towards damage.

4.5. Methodological considerations

MOEAs are a spectrum of optimization algorithms that search for a nondominated set of solutions for multiobjective problems by imitating the evolutionary process in nature. In addition to inheriting the general adaptability and the strong global search capacity of traditional evolutionary algorithms, MOEAs have specific advantages in exploring multiobjective trade-offs, as they do not require predefinition of the optimization weights among objectives. MOEAs have already been applied to some fields in neuroscience (Avena-Koenigsberger et al., 2014; Lin et al., 2018) but never to the topic of cost-efficiency trade-off in the human connectome. Here, using an MOEA approach NSGA-II (Deb et al., 2002), we approximated the Pareto front of the cost-efficiency trade-off and revealed the influence of this trade-off on human brain structural networks. Following the new avenue from this fundamental work, future studies can use MOEAs to further investigate other important aspects of the cost-efficiency trade-off in brain networks, including individual differences in the trade-off, deviation in the trade-off due to the abnormal connectome of disorders (van den Heuvel and Sporns, 2019) and the trade-off that involves more factors (e.g., robustness). Despite the novelty of our work, some methodological limitations should also be considered. First, our current implementation of the MOEA algorithm is restricted to binary networks. The crossover and mutation operators are not fully applicable to the weighted condition. However, connection weights (e.g., number of streamlines) might reflect additional information on wiring cost and transmission efficiency (Bullmore and Sporns, 2012). Hence, future work on the cost-efficiency trade-off should extend the current algorithm to the optimization of weighted networks. Second, while examining the cost-efficiency trade-off, we only focused on the cost of white matter wiring in the structural brain network, which is related to the material cost of human brain (Ahn et al., 2006; Mitchison, 1991). Another important aspect of the cost, the metabolic cost (Laughlin et al., 1998), was not accounted for here. The metabolic cost of the human brain mainly emerges from the maintenance of coordinated activity between brain areas, which could be examined in the functional brain network. However, the relationship between the structural network and the functional network is complicated (Hermundstad et al., 2013; Honey et al., 2009) and modulated by the communication dynamics (Avena-Koenigsberger et al., 2018). Whether the current model is suitable for functional networks remains unknown. Considering that this was the first work to explore the optimal cost-efficiency trade-off in human brain networks, we only focused on the anatomical brain network. Future works could employ a modified version of the MOEA algorithm and objective functions to account for both the material cost and the metabolic cost in the cost-efficiency trade-off in functional networks. Third, we used the dMRI technique to acquire empirical structural brain networks, which is a widely used noninvasive method for mapping white matter trajectories in the human brain. Although this method could successfully detect most connections, the detection of relatively small or very long fiber bundles is still a technical challenge. This might affect the connection pattern of the empirical brain networks and thus further bias our findings derived from comparisons between the synthetic networks and the empirical ones. Future work using ultrahigh spatial resolution diffusion imaging techniques might be able to reduce the inaccuracy of mapping connections (Bassett et al., 2011). Fourth, the current findings showed that the correlation of overall regional degree between synthetic and empirical networks was not significant. The low correlation in regional degree might be due to the following two reasons: Firstly, the current implementation of the cost-efficiency mechanism did not take into account the spatial information of brain regions. This trade-off mainly focused on the relative distance between regions, which was directly related to cost, rather than their exact placement. The synthetic networks could thus resemble the empirical ones from an overall perspective, but lacked carving in the detailed spatial placement of regions, which is assumed to be related to their functional utility and gene expression (Stiso and Bassett, 2018). Secondly, the synthetic networks captured some global hubs that were not presented in empirical networks. These global hubs, which owned a large number of connections to almost all the other regions in the network, could benefit the network global efficiency, but also impaired the connectivity patterns of other brain regions. It might be the outcome of the fact that we had overestimated the importance of effi-
ciency of global communication and underestimated the effect of local efficiency. Therefore, in the future work, we might seek improvement in the consistency with empirical degree centrality by further introducing spatial information and local efficiency into the proposed cost-efficiency model. Fifth, in recent years, many studies have started challenging the assumption that communication takes place on only the shortest paths across the network (for review, see Avena-Koenigsberger et al., 2018).

Following this argument, recent studies have proposed several alternative communication models (e.g., diffusion model and navigation model; Avena-Koenigsberger et al., 2017; Avena-Koenigsberger et al., 2019; Estrada and Hatano, 2008; Goñi et al., 2013; Seguin et al., 2018). These new models might provide a more accurate evaluation of communication efficiency in the brain network. However, there are still no broadly recognized models for characterizing network communication, and the above alternative models still need unified validation and comparison in future studies. In future work, new efficiency metrics based on well-approved communication models are needed to better investigate the cost-efficiency trade-off in the human brain structural network.

Ethics statement

This study was approved by the Institutional Review Board in the Department of Psychology of Sun Yat-sen University and all participants provided informed consent before the experiment.

Data and code availability statement

The newly acquired SCNU dataset for the present study is available at an open platform https://osf.io/45cjy/?view_only=4f1a88db7a16471db5248806еб19466. The toolboxes and third-party code we used are all stated and cited appropriately, and relevant links of code are also provided in the Materials and Methods section. Pseudocode of our implemented NSGA-II algorithm could be found in Algorithm S1 in the Supplementary Materials.

Declaration of Competing Interest

None.

Credit authorship contribution statement

Junji Ma: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. Jinbo Zhang: Formal analysis, Writing – review & editing. Ying Lin: Conceptualization, Methodology, Supervision, Writing – review & editing. Zhengjia Dai: Conceptualization, Methodology, Supervision, Writing – review & editing.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (NSFC) (No. 61772569), the Guangdong Basic and Applied Basic Research Foundation (No. 2019A1515012148, 2021A1515010844), and the Fundamental Research Funds for the Central Universities (No. 19wkzd20, 20wkzd11).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118040.

References

Ahn, Y.-Y., Jeong, H., Kim, B.-J., 2006. Wiring cost in the organization of a biological neuronal network. Physica A 367, 521–537. Avena-Koenigsberger, A., Goñi, J., Betzel, R.F., van den Heuvel, M.P., Grifﬁa, A., Hagmann, P., Thiran, J.-P., Sporns, O., 2014. Using Pareto optimality to explore the topology and dynamics of the human connectome. Philos. Trans. R. Soc. B 369 20130530.
ping anatomical connectivity patterns of human cerebral cortex using in vivo diffusion tensor imaging tractography. Cereb. Cortex 19, 524–536.

Gong, Q., He, Y., 2015. Depression, neuroimaging and connectomics: a selective overview. Biol. Psychiatry 77, 223–235.

Gotlib, J., Avena-Koenigsberger, A., Velez de Mendizabal, N., van den Heuvel, M.P., Betzel, R.F., Sporns, O., 2013. Exploring the morphospace of communication efficiency in complex networks. PLoS One 8 (3), e58070.

Hagmann, P., Kurant, M., Gigandet, X., Thiran, P., Wedeen, V.J., Meuli, R., Thiran, J.P., 2007. Mapping human whole-brain structural networks with diffusion MRI. PLoS One 2, e597.

Hermundstad, A.M., Bassett, D.S., Brown, K.S., Aminiﬀ, E.M., Clewett, D., Freeman, S., ... Grafton, S.T., 2013. Structural foundations of resting-state and task-based functional connectivity in the human brain. Proc. Natl. Acad. Sci. 110 (15), 6169–6174.

Honey, C.J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J.P., Meuli, R., Hagmann, P., 2009. Predicting human resting-state functional connectivity from structural connectivity. Proc. Natl. Acad. Sci. 106 (6), 2035–2040.

Kaiser, M., Hilgetag, C.C. 2006. Nonoptimal component placement, but short processing paths, due to long-distance projections in neural systems. PLoS Comput. Biol. 2.

Klymchko, V.A., Stevens, C.F., 2005. Connectivity visualization and the positioning of cortical areas. Proc. Natl. Acad. Sci. 100, 7937–7941.

Latora, V., Marchiori, M.J., 2001. Efficient behavior of small-world networks. Phys. Rev. Lett. 87, 198701.

Laughlin, S.B., Sejnowski, T.J., 2003. Communication in neuronal networks. Science 301, 1870–1874.

Laughlin, S.B., van Steveninck, R.R.D.R., Anderson, J.C., 1998. The metabolic cost of neural information. Nat. Neurosci. 1 (1), 36–41.

Leemans, A., Jones, D.K., 2009. The B-matrix must be rotated when correcting for subject motion in DTI data. Magn. Reson. Med. 61, 1336–1349.

Liao, X., Vanlakerv, A., He, Y., 2017. Small-world human brain networks: perspectives and challenges. Neurosci. Biobehav. Rev. 77, 286–300.

Lin, Y., Ma, J., Gu, Y., Yang, S., Li, L.M.W., Dai, Z., 2018. Intrinsic overlapping modular organization of human brain functional networks revealed by a multiobjective evolutionary algorithm. Neuroimage 181, 430–445.

Malinak, D., Powers, R., Walter, B.F., 2013. The gender gap in citation in international relations. Int. Organ. 67 (4), 889–922.

Markov, N.T., Ercecy-Ravass, M., Lamy, C., Gomes, A.R.R., Magrou, L., Misery, P., Giroud, P., Barone, P., Dehay, C., Toroczkai, Z.J., 2013. The role of long-range connections on the specificity of the macaque interareal cortical network. Proc. Natl. Acad. Sci. 110, 5187–5192.

Maslov, S., Sneppen, K., 2002. Speciﬁcity and stability in topology of protein networks. Science 296 (5569), 910–913.

Melia, M., 2007. Comparing clusterings—an information based distance. J. Multivariate Anal. 98, 873–895.

Meunier, D., Lambiotte, R., Bullmore, E.T., 2010. Modular and hierarchically modular organization of brain networks. Front. Neurosci. 4, 200.

Meunier, D., Lambiotte, R., Fornito, A., Ersche, K., Bullmore, E.T., 2009. Hierarchical modularity in human brain functional networks. Front. Neuroinform. 3, 37.

Mitchell, S.M., Lange, S., Brus, H., 2013. Gendered citation patterns in international relations journals. Int. Stud. Perspect. 14 (4), 485–492.

Mitchison, G., 1991. Neuronal branching patterns and the economy of cortical wiring. Proc. R. Soc. Lond. 245, 151–158.

Raichle, M.E., 2015. The brain’s default mode network. Annu. Rev. Neurosci. 38, 433–447.

Rubinov, M., Sporns, O., 2010. Complex network measures of brain connectivity: uses and interpretations. Neuroimage 52, 1059–1069.

Rubinov, M., Ypma, R.J., Watson, C., Bullmore, E.T., 2015. Wiring cost and topological participation of the mouse brain connectome. Proc. Natl. Acad. Sci. 112, 10032–10037.

Sams, D., Seth, A.K., Nowotny, T.J., 2014. Inﬂuence of wiring cost on the large-scale architecture of human cortical connectivity. PLoS Comput. Biol. 10.

Seguin, C., Van den Heuvel, M.P., Zalesky, A., 2018. Navigation of brain networks. Proc. Natl. Acad. Sci. 115 (24), 6297–6302.

Schindler, D.E., Hilborn, R., Chasco, B., Bostridge, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio eﬀect in an exploited species. Nature 465, 609–612.

Shen, X., Tokoglu, F., Papademetris, X., Constable, R.T., 2013. Groupwise whole-brain parcellation from resting-state fMRI data for network node identiﬁcation. Neuroimage 82, 403–415.

Sporns, O., Tononi, G., Kötter, R., 2005. The human connectome: a structural description of the human brain. PLoS Comput. Biol. 1.

Stiso, J., Bassett, D.S., 2018. Spatial embedding imposes constraints on neuronal network architectures. Trends Cognit. Sci. 22, 1127–1142.

Sizemore, A., Giusti, C., Bassett, D.S., 2017. Classiﬁcation of weighted networks through mesoscale homological features. J. Complex Netw. 5 (2), 245–273.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15, 273–289.

van den Heuvel, M.P., Sporns, O., 2011. Rich-club organization of the human connectome. J. Neurosci. 31, 15775–15786.

van den Heuvel, M.P., Sporns, O., 2013. Network hubs in the human brain. Trends Cogn. Sci. 17, 683–696.

den Heuvel, M.P., Sporns, O., 2019. A cross-disorder connectome landscape of brain dysconnectivity. Nat. Rev. Neurosci. 20, 435–446.

Wang, J., Wang, X., Xia, M., Liao, X., Evans, A., He, Y., 2015. GRETRA: a graph theoretical network analysis toolbox for imaging connectomics. Front. Hum. Neurosci. 9, 386.

Wang, B., Benner, T., Sorensen, A.G., Wedeen, V.J., 2007. Diffusion toolkit: a software package for diﬀusion imaging data processing and tractography. In: Proceedings of the International Society for Magnetic Resonance in Medicine.

Watts, D.J., Strogatz, S.H., 1998. Collective dynamics of ‘small-world’ networks. Nature 393, 440–442.

Wig, G.S., 2017. Segregated systems of human brain networks. Trends Cognit. Sci. 21, 981–996.

Young, M.P., 1992. Objective analysis of the topological organization of the primate cortical visual system. Nature 358, 152–155.

Zhou, D., Cornblath, E.J., Stiso, J., Teich, E.G., Dworkin, J.D., Blevins, A.S., Bassett, D.S., 2020. Gender Diversity Statement and Code Notebook, v1. 0. Zenodo.

Zuo, X.-N., Ehmke, R., Mennes, M., Imperati, D., Castellanos, F.X., Sporns, O., Milham, M.P., 2012. Network centrality in the human functional connectome. Cereb. Cortex 22, 1862–1875.