

Exploring brain functional plasticity in world class gymnasts: a network analysis

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Abstract Long-term motor skill learning can induce plastic structural and functional reorganization of the brain. Our previous studies detected brain structural plasticity related to long-term intensive gymnastic training in world class gymnasts (WCGs). The goal of this study was to investigate brain functional plasticity in WCGs by using network measures of brain functional networks. Specifically, we acquired resting-state fMRI data from 13 WCGs and 14 controls, constructed their brain functional networks, and compared the differences in their network parameters. At the whole brain level, we detected significantly decreased overall functional connectivity (FC) and decreased local and global efficiency in the WCGs compared to the controls. At the modular level, we found intra- and inter-modular reorganization in three modules, the cerebellum, the cingulo-opercular and fronto-parietal networks, in the WCGs. On the nodal level, we revealed significantly decreased nodal strength and efficiency in

several non-rich club regions of these three modules in the WCGs. These results suggested that functional plasticity can be detected in the brain functional networks of WCGs, especially in the cerebellum, fronto-parietal network, and cingulo-opercular network. In addition, we found that the FC between the fronto-parietal network and the sensorimotor network was significantly negatively correlated with the number of years of training in the WCGs. These findings may help us to understand the outstanding gymnastic performance of the gymnasts and to reveal the neural mechanisms that distinguish WCGs from controls.

Keywords Brain functional network · Cerebellum · Fronto-parietal network · Cingulo-opercular network

Introduction

Motor skill training refers to the process by which movements come to be performed effortlessly through repeated practice and interactions with the environment (Willingham 1998). The acquisition of a motor skill is characterized first by a short-term fast learning stage in which the performance improves rapidly, and then followed by a long-term slow learning stage in which the performance gains are incremental. Motor skill training can induce brain structural and functional plasticity (Doyon et al. 2009; Dayan and Cohen 2011), and short- and long-term motor skill training involve distinct brain networks (Dayan and Cohen 2011). Previous studies (Floyer-Lea and Matthews 2005; Dayan and Cohen 2011) suggested that the short-term motor skill training is associated primarily with a cortical network specific for learned movements, whereas the long-term motor skill training involves a bihemispheric cortical–subcortical network.

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Professional athletes typically undergo long-term motor skill training, beginning their skill learning from very early in childhood, practicing several hours a day, and maintaining the training for their entire careers. Through this long-term intensive training, they acquire excellent abilities in perception, stimulus discrimination, decision making, motor preparation, and execution (Nakata et al. 2010). Neuroimaging techniques have revealed brain structural or functional plasticity in a number of types of professional athletes, including skilled golfers (Jancke et al. 2009), world class mountain climbers (Di Paola et al. 2013), formula racing-car drivers (Bernardi et al. 2013), badminton players (Di et al. 2012), and world class archers (Kim et al. 2008). These studies revealed that long-term motor skill training indeed caused plastic reorganization in brain structure and function and suggested that the reorganization may vary in different types of athletes.

Professional gymnasts perform a variety of exercises which require physical strength, flexibility, power, agility, coordination, grace, balance, and control. Because world class gymnasts (WCGs) have extraordinary balance, strength, and flexibility, they can excel in gymnastics competition (Wang et al. 2013a). We previously investigated the brain structural plasticity of gymnasts by analyzing their brain diffusion-weighted and structural magnetic resonance imaging (MRI) data (Wang et al. 2013a; Huang et al. 2013). In those studies, we found that WCGs showed structural plasticity in the network parameters of the whole brain structural network and especially in the brain regions responsible for motor, attention, and cognitive control (Wang et al. 2013a; Huang et al. 2013). Structural connectivity networks have been shown to be the physical substrate of functional connectivity networks (van den Heuvel et al. 2008; Greicius et al. 2009; van den Heuvel et al. 2009). But inconsistencies exist between structural and functional networks (Zhang et al. 2011; Skudlarski et al. 2010). However, up to now, we have no knowledge about the brain functional network of the WCGs.

A variety of human brain network models derived from resting-state fMRI (R-fMRI) data have been widely used to detect the plasticity of brain functions (Guerra-Carrillo et al. 2014; Duan et al. 2012; Taubert et al. 2011; Luo et al. 2012). Graph theory analysis can be used to characterize the topological properties, including the local and global efficiency of information communication, of whole brain functional networks (Sporns 2013; Newman 2012). Because whole brain networks can be divided into a set of sparsely interconnected (but densely intra-connected) functional modules, modularity analysis can help to reveal intra- and inter-modular connectivity properties (He et al. 2009). In addition, since nodes and inter-nodal connections are basic elements of brain functional networks, the

network-based statistic (NBS) approach can be used to determine changes in inter-nodal connections (Zalesky et al. 2010), and rich club analyses can be used to determine the organization of vital nodes in networks (van den Heuvel and Sporns 2011).

In this study, we acquired R-fMRI data from 13 world class gymnasts and 14 normal controls, constructed their functional networks, and determined the differences in their network parameters (Zalesky et al. 2010; Sporns 2013; Newman 2012; van den Heuvel and Sporns 2011). Our earlier findings revealed that brain structural plasticity of WCGs exists throughout the whole brain structural network, especially in the brain regions responsible for motor, attention, and cognitive control (Wang et al. 2013a; Huang et al. 2013). Besides, previous studies by other groups (Floyer-Lea and Matthews 2005; Dayan and Cohen 2011) suggested that long-term motor skill training involves a bihemispheric cortical-subcortical network. Thus, we hypothesized that brain functional plasticity of WCGs exists throughout the whole brain network, especially in brain regions responsible for motor, attention, and cognitive control functions. Further, rich club regions or hub regions have been found mainly in the bilateral precuneus, superior frontal and superior parietal cortex, and insula (van den Heuvel and Sporns 2011; Collin et al. 2014a; van den Heuvel et al. 2013). Considering the rich club regions less overlapped with brain regions showing brain functional plasticity induced in motor skill learning, we hypothesized the brain functional plasticity of WCGs may mainly occur in non-rich club regions. In addition, we investigated whether these reorganized network parameters were significantly correlated with the number of years of training of the WCGs and whether they were sufficient to allow us to distinguish the WCGs from the controls.

Materials and methods

Subjects

Thirteen world class gymnasts (6 M/7 F, age 17–26 years, mean \pm SD = 20.5 \pm 3.2 years) participated in this study. Table 1 lists the detailed demographics for all of these champions. Each gymnast had won at least one gold medal in the Gymnastics World Cup or the Olympic Games since 2007. Each had started gymnastic training at about 4.5 years old and had been in training for more than 12.5 years by the time of this experiment, with a mean training time of 6 h per day. All of them were right-handed according to their self-report. We also recruited 14 healthy undergraduate/graduate volunteers (7 M/7 F, aged 19–28 years, mean \pm SD = 20.3 \pm 2.5 years) who were age-, gender-, and handedness-matched to the gymnasts. No

Table 1 Characteristics of the world class gymnasts (WCGs) participating in this study

| Champions | Best medal record since 2007 | Sex | Age (years) | Age of commencement (years) | Years of training |
|---------------|------------------------------|-----|----------------|-----------------------------|-------------------|
| sub01 | OC | M | 24 | 4.5 | 19.5 |
| sub02 | WC | M | 24 | 4.5 | 19.5 |
| sub03 | WC | M | 23 | 4.5 | 18.5 |
| sub04 | WC | M | 26 | 4.5 | 21.5 |
| sub05 | WC | M | 21 | 4.5 | 16.5 |
| sub06 | WC | M | 23 | 4.5 | 18.5 |
| sub07 | WC | F | 19 | 4.5 | 14.5 |
| sub08 | OC | F | 18 | 3.5 | 14.5 |
| sub09 | OC | F | 21 | 4.5 | 16.5 |
| sub10 | WC | F | 17 | 4.5 | 12.5 |
| sub11 | OC | F | 17 | 4.5 | 12.5 |
| sub12 | OC | F | 17 | 4.5 | 12.5 |
| sub13 | OC | F | 17 | 4.5 | 12.5 |
| Mean \pm SD | | | 20.5 \pm 3.3 | 4.4 \pm 0.3 | 16.1 \pm 3.3 |

All gymnasts had won individual or team gold medals in the Gymnastics World Cup or Olympic Games since 2007

OC Olympic Champions, WC World Champions or World Cup Champions

significant between-group difference was found either in age (two-sample t test, $t = -1.33$, and $p = 0.20$) or in gender (χ^2 -test, $\chi^2_{(1)} = 0.04$, and $p = 0.84$).

None of the subjects had a history of neurological or psychiatric disorders or brain injuries. The study was approved by the Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University (BNU). Written informed consent was obtained from each subject prior to the study.

Data acquisition

All MRI datasets were obtained on a 3T Siemens Trio Tim MR scanner with the use of a 12-channel phased-array receiver-only head coil. The R-fMRI datasets were acquired using a gradient echo EPI sequence with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 90°, field of view (FOV) = 224 mm \times 224 mm, data matrix = 64 \times 64, thickness/gap = 3.6 mm/0.7 mm, 33 transverse slices covering the whole brain, and 240 volumes acquired in 8 min. During the R-fMRI scan, each subject was asked to keep their eyes closed but not to fall asleep and to relax their minds but not to think about anything in particular. In addition, we also acquired high-resolution brain structural images (1 mm³ isotropic) for each subject using a T1-weighted 3D magnetization-prepared rapid gradient echo (MP-RAGE) sequence. The sequence parameters were TR/TE = 1900 ms/3.44 ms, inversion time (TI) = 900 ms, slice thickness = 1 mm, flip angle = 9°, FOV = 256 mm \times 256 mm, data matrix = 256 \times 256, BW = 190 Hz/pixel,

and 176 sagittal slices acquired over about 10 min. For each subject, the R-fMRI data and 3D high-resolution brain structural images were acquired in the same session.

Data preprocessing

The R-fMRI data were preprocessed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>) and DPARSF (Yan and Zang 2010). For each subject, the first ten volumes of the R-fMRI dataset were discarded to allow for MR signal equilibrium, leaving 230 volumes for further analysis. The remaining images were first corrected for the acquisition time delay between slices within the same TR and were then realigned to the first volume to correct for inter-TR head motions. This realigning calculation provided a record of head motions within the R-fMRI scan. All of the subjects in this study satisfied our criteria for head motion, displacement <2 mm in any plane and rotation <2° in any direction. In order to test the influence of head motion on the functional images (Mowinckel et al. 2012), we compared the root mean squares of the head displacements and the head rotations, respectively, between the two subject groups. Statistical analyses showed no significant between-group differences in either head displacement ($p = 0.58$) or head rotation ($p = 0.11$). The R-fMRI data were spatially normalized to the T1-weighted brain structural images in the standard MNI-152 template and were resampled to a voxel size of 3 \times 3 \times 3 mm³. The waveform for each voxel was detrended and passed through a band-pass filter within 0.01–0.08 Hz to reduce the effects of low-frequency drift and high-frequency physiological noise.

Constructing brain functional networks

Using the GREYNA toolbox (<http://www.nitrc.org/projects/gretna/>), we constructed the brain functional network for each subject according to the Dos-160 template, which consists of 160 regions of interest (ROIs) derived from an fMRI meta-analysis (Dosenbach et al. 2010) and is regarded as an optimal template for constructing brain functional networks (Yao et al. 2015). The names and the abbreviations of these ROIs are listed in Table S1 (Supplementary Materials). We calculated the time series for each ROI (spherical radius of 5 mm) by averaging the time courses of all the voxels within a ROI, and performed a linear regression to remove the effects of the following eight nuisance covariates: signals from the brain white matter and cerebrospinal fluid as well as three translation and three rotation parameters of head motion (Wang et al. 2014; Jiang et al. 2013). Due to controversy about removing the global signal when preprocessing R-fMRI data (Fox et al. 2009; Murphy et al. 2009), we did not regress out the global signal (Wang et al. 2013b; Lynall et al. 2010).

For each subject, we first used the residuals of the time series for each ROI to calculate a Pearson's linear correlation and the significance level (i.e., p value) of a given inter-regional correlation. Then we obtained a 160×160 symmetric correlation matrix and the corresponding p value matrix for each subject. To de-noise spurious correlations, we retained only those correlations whose corresponding p values passed through a statistical threshold $p < 0.05$ (Bonferroni correction); otherwise, we set the correlations to zero (Cruse et al. 2011). By taking the remaining Pearson's coefficients as edge weights, we obtained a weighted 160×160 FC matrix, which was used to conduct the subsequent analysis for each subject. The flowchart for constructing a brain functional network is presented in Fig. S1 (Supplementary Materials).

Network analysis

Global parameters

Graph theory was used to analyze the topological properties of the human brain functional networks. We used six parameters, the clustering coefficient (C_w), characteristic path length (L_w), normalized clustering coefficient (γ), normalized characteristic path length (λ), global efficiency (E_{glob}), and local efficiency (E_{loc}), to characterize the global topological properties of the brain networks. Their definitions and descriptions can be found in Table S2 (Supplementary Materials) and in Rubinov and Sporns (2010). The small-world properties of a network can be characterized by the normalized clustering coefficient,

$\gamma = C_w^{\text{real}}/C_w^{\text{rand}}$, and normalized characteristic path length, $\lambda = L_w^{\text{real}}/L_w^{\text{rand}}$, where C_w^{real} and L_w^{real} are the clustering coefficient and characteristic path length of the real brain network, in which C_w^{rand} and L_w^{rand} are the mean values of the corresponding parameters derived from 100 matched random networks with the same number of nodes, edges, and distribution of degrees as the real brain network. Typically, a small-world network satisfies the following criteria: $\gamma \gg 1$ and $\lambda \approx 1$, or $\sigma = \gamma/\lambda > 1$ (Uehara et al. 2014).

Nodal parameters

We also used two parameters, nodal strength (S_i^w) and nodal efficiency (E_i^w), to characterize the nodal properties of the brain networks. Their definitions and descriptions are also listed in Table S2 (Supplementary Materials).

Modular parameters

To provide more information about the Dos-160 template, Dosenbach et al. (2010) have performed a community detection analysis according to the modularity optimization algorithm proposed by Newman (2006) and classified these 160 ROIs into six modules, the default mode network (DMN), fronto-parietal network (FPN), cingulo-opercular network (CON), sensorimotor network (SMN), occipital network (ON), and the cerebellum (CN). These six modules are shown in Fig. S2 (Supplementary Materials). We calculated the values of the intra- and inter-modular FC for both the WCG and control groups. For any subject, the strength of the intra-modular FC was defined as the mean of all the inter-nodal FCs within the selected module, while the strength of the inter-modular FC was defined as the mean of the FCs between any two nodes of the two selected modules.

Rich club organization and connection density

The rich club nodes are brain regions with a high degree, low clustering, short path length, and a high degree of centrality and participation in modules across a network and which are more densely connected among themselves than with others. Previous studies (van den Heuvel and Sporns 2011; de Reus and van den Heuvel 2013b) indicated that the presence or absence of rich club organization can provide important information about the level of resilience, hierarchical ordering, and specialization of a network. In this study, we identified the 'rich club' regions for the weighted networks based on the normalized rich club coefficient $\phi_{\text{norm}}^w(k)$, where k is the degree that represents the number of links from a given node to other nodes in the

network. A network is considered to have a rich club organization if $\phi_{\text{norm}}^w(k) > 1$ for a specific degree k . The $\phi_{\text{norm}}^w(k)$ is described in the Supplementary Materials and in van den Heuvel and Sporns (2011).

The rich club organization was determined using the method from these previous studies: van den Heuvel and Sporns (2011, 2013) and Ray et al. (2014). We first obtained the group-averaged correlation matrix and the nodal degrees for each subject group. Then we sorted all the nodal degrees and took the nodes in the top 12 % of the ranked nodes as the rich club nodes ($k \geq 11$). The remaining brain regions were classified as non-rich club nodes. On the basis of this categorization, we classified the network edges into three types: ‘rich club’ connections linking rich club nodes to each other, ‘feeder’ connections linking rich club nodes to non-rich club nodes, and ‘local’ connections linking non-rich club nodes to each other (Collin et al. 2014b; Harriger et al. 2012). For a given connection type, we determined its FC strength by averaging all the inter-nodal FCs of this connection type.

Statistical analysis

Between-group comparisons: A non-parametric permutation test (van den Heuvel et al. 2010; Nichols and Holmes 2002) was used to detect between-group differences in the number and strength of existing connections in the FC matrices for each of the global parameters (C_w , L_w , E_{loc} , E_{glob} , γ , λ , and δ) and nodal parameters (S_i^w and E_i^w), for each parameter derived from the rich club analysis (rich club, local, and feeder connections), and for each of the intra- and inter-modular FCs. For a given parameter, we first computed the t value of the between-group difference and then obtained an empirical distribution of the difference. Specifically, we randomly assigned the parameter values for all subjects in this study into two groups and recalculated the differences in the mean values of the parameter between the two re-sampled groups. This permutation was repeated 10,000 times, resulting in a null distribution of the between-group differences for this parameter. Finally, we set a threshold of $p = 0.05$ to determine the significance level of the between-group differences at 95 % of the empirical distribution in a two-tailed test. In the calculations, we took age, gender, and age-gender interaction as nuisance covariates throughout the entire analysis to regress out any potential covariate-related effects (Wang et al. 2013b; Tian et al. 2011). Once a significant between-group difference was observed for a parameter, we estimated its effect size (Cohen d) and statistical power according to the Cohen’s definition (1992).

Based on each individual FC network, we also used a network-based statistic (NBS) approach (Zalesky et al.

2010) to identify subnetworks, clusters of connections, in which each edge showed a significant between-group difference. This approach can control the family-wise error rate when mass-univariate testing is performed at every connection comprising the subnetwork (Zalesky et al. 2010). A detailed description of the NBS is presented in the Supplementary Materials and can also be found in Zalesky et al. (2010). For the NBS-derived subnetwork, we estimated the average value across all the FCs in this subnetwork as its FC strength. When performing the NBS calculation, we set the primary threshold for each inter-nodal FC as $t > 3.42$ and $p < 0.001$ (5000 permutations).

Correlations between network parameters and years of training

For any of the network parameters that showed a significant between-group difference, we performed a partial correlation to describe their relationships with the number of years of training for the WCG group, controlling for age, gender, and age-gender interactions ($p < 0.05$). If the network parameters were significantly correlated with the number of years of training, we calculated its correlation with age to estimate the age effect, since the age and the number of years of training are closely correlated for the obvious reason that most gymnasts started gymnastic training at about 4.5 years of age (Table 1).

Robustness analysis

The robustness of the network parameters is a key issue in network analysis (Zuo et al. 2014; Zuo and Xing 2014; Liang et al. 2012; Deuker et al. 2009; Telesford et al. 2013). To determine if the observed differences in the network parameters reflected true differences, not artifacts, we repeated the network analysis by adopting different preprocessing strategies, different brain templates, and a binary network type.

Preprocessing strategies: Previous studies (Braun et al. 2012; Wang et al. 2011; Garrison et al. 2015) revealed that different preprocessing strategies may affect the calculated network parameters of brain network. To test the robustness of the findings, besides of the main strategy (both the positive and negative correlations after thresholding were included in the FC matrices, and the global signal was not regressed out), we also took four other preprocessing strategies, (1) Sparsity, (2) Regressing-Global, (3) Smoothing, and (4) Positive-Only, as defined below, to repeat the network analysis. In the Sparsity strategy, we estimated a threshold range by using a measure of sparsity (the ratio of the total number of edges to the possible maximum number of edges in a network) and applied different values of sparsity as the thresholds for the FC

matrices. In the Regressing-Global strategy, we constructed brain networks using the functional signal but regressed out the global brain signal. In the Smoothing strategy, we constructed brain networks using the functional signals after smoothing (FWHM = 6 mm) the functional images. Finally, in the Positive-Only strategy, we constructed the network by using the positive-only inter-nodal FCs, i.e., we assumed that no inter-nodal FC existed if the inter-nodal FC was non-positive.

Parcellation templates: The choice of a nodal definition can affect the calculated network parameters of a brain network (de Reus and van den Heuvel 2013a; Wang et al. 2009). To test the robustness of our findings derived from the main strategy (nodes defined from Dos-160), we also repeated the network analysis by defining the nodes according to three additional templates, the automated anatomical labeling (AAL-90) template (Tzourio-Mazoyer et al. 2002), Power-264 template containing 264 ROIs obtained from an fMRI meta-analysis (Power et al. 2011), and a high-resolution AAL-1024 template (1024 ROIs of equal size) (Dosenbach et al. 2010).

A binary network: Following previous studies (Wang et al. 2014; Jiang et al. 2013), we also obtained a binary functional network to assess the robustness of our findings.

Cross-validation

The cross-validation method was performed by repeating the same analysis by adopting leave-one-dataset-out approach from these fMRI datasets at a time to establish whether the results remain significant. The rationale of this test is that if a previous significant result remains in all or most of the combinations of subjects, we may conclude that the finding is highly replicable (Nakao et al. 2011; Aoki et al. 2015). In this study, we excluded a gymnast from the WCG group at a time and thus had 13 combinations of subjects. The repeated analysis was performed and the result was presented.

Network classification

For those network parameters that showed significant between-group differences, we plotted the receiver operating characteristic (ROC) curve to determine which of these parameters could clearly distinguish the WCGs from the controls. The ROC curve, which is widely used in medical science, is a fundamental plot in signal detection theory (Pencina et al. 2008; Desco et al. 2001). A ROC, a scatter plot showing the relationship between false alarm rates and hit rates, describes the relationship between the underlying distribution of the places where signals were absent and places where signals were present. This analysis was performed using public MATLAB codes (<http://www.mathworks.com/matlabcentral/fileexchange/199500-roc-curve>; by Giuseppe Cardillo).

[mathworks.com/matlabcentral/fileexchange/199500-roc-curve](http://www.mathworks.com/matlabcentral/fileexchange/199500-roc-curve); by Giuseppe Cardillo).

Results

For the thresholded FC matrix of each subject, we calculated the total number of links and the mean FC weights for all the existing connections ($p < 0.05$, Bonferroni correction). The statistical analysis revealed that the WCG group had a significantly smaller number of connections ($p = 0.01$) and lower overall connectivity weights ($p = 0.03$) compared to the controls.

Global parameters

Figure 1 shows the values of the global parameters (C_w , L_w , E_{loc} , E_{glob} , γ , λ , and δ) for the brain functional networks for the WCG and control groups, as well as their between-group differences. The calculations indicated that the functional networks for the WCG and control groups satisfy the small-world criteria, $\gamma > 1$ and $\lambda \approx 1$, or $\delta > 1$. Additionally, we detected that the WCG group showed a significantly lower C_w ($p = 0.032$), E_{loc} ($p = 0.013$), and E_{glob} ($p = 0.0088$) but a significantly higher L_w ($p = 0.0076$) compared to the control group.

Inter- and intra-modular connectivity

For the six modules determined by Dosenbach et al. (2010), we calculated the intra- and inter-modular FCs for each subject and compared their between-group differences ($p < 0.05$). Figure 2 shows that of the 15 inter-modular FCs (six modules give $C_6^2 = 15$ inter-modular FCs), 11 were uniformly significantly lower in the WCG group

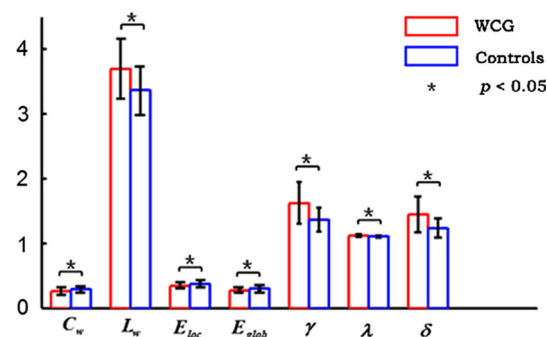


Fig. 1 Bar plots showing statistical comparisons of the global parameters between the world class gymnasts (WCGs) and the controls ($p < 0.05$) in the whole brain functional networks. Significant between-group differences were found in the weighted clustering coefficient (C_w), characteristic path length (L_w), local efficiency (E_{loc}), global efficiency (E_{glob}), normalized clustering coefficient (γ), normalized shortest path length (λ), and small-worldness (δ)

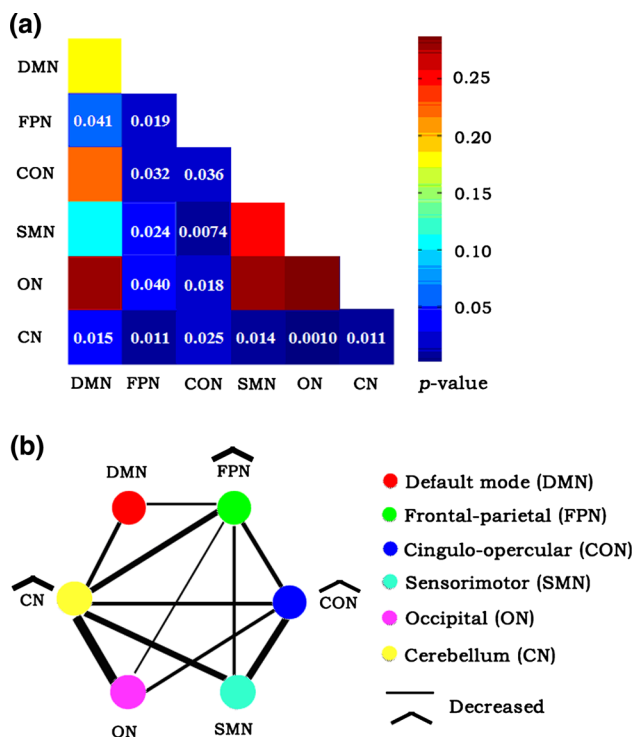


Fig. 2 Statistical comparisons of the intra- and inter-modular functional connectivity (FC) between the world class gymnasts (WCGs) and the controls. **a** The correlation matrix displaying the p values of the between-group differences in the intra- and inter-modular FCs. The *colorbar* indicates the corresponding p value. Compared to the control group, the WCG group showed not only uniformly significantly lower intra-modular FCs within each of three modules (the cerebellum, fronto-parietal, and cingulo-opercular networks) but also uniformly significantly lower inter-modular FCs between these modules. **b** Illustration of the FCs that showed a significant between-group difference. The *bent* (straight) line corresponds to the intra-modular (inter-modular) FC. The thickness of the line is inversely proportional to the p value of the between-group difference. The thicker the line, the lower the FC in the WCG compared to the controls

compared to the control group. In addition, the WCG group showed uniformly significantly lower intra-modular FCs compared to the controls in three modules, FPN ($p = 0.019$), CON ($p = 0.036$), and CN ($p = 0.011$). The detailed results of the between-group comparisons of the intra- and inter-modular FCs are listed in Table S4 (Supplementary Materials).

Inter-nodal functional connectivity

Figure 3a displays the NBS-derived subnetwork ($p = 0.0033$), which contained twenty nodes and twenty inter-nodal FCs. The distribution of FC values in this subnetwork is shown in Fig. 3b. All the FCs in this subnetwork were significantly lower in the WCG group compared to the controls. Of these twenty FCs, twelve were related to the CON module and nine to the CN

(Fig. 3c), and eighteen belonged to ‘local’ connections (Table S5 in Supplementary Materials).

Rich club analysis

Figure 4a shows the normalized rich club coefficient $\phi_{\text{norm}}^w(k)$ for both groups over the range of degrees from $1 \leq k \leq 16$. Figure 4b indicates the rich club nodes at $k = 11$ by following several previous studies: (van den Heuvel and Sporns 2011; van den Heuvel et al. 2013; Ray et al. 2014). Of these 16 rich club nodes, 11 were located in the DMN module, 4 in the SMN, and 1 in the ON. A statistical analysis revealed a significantly smaller number of ‘local’ connections ($p = 0.032$) in the WCG group compared to the control group but no significant between-group differences in either the ‘rich club’ connections ($p = 0.20$) or the ‘feeder’ connections ($p = 0.12$) (Fig. 4c). The rich club nodes and the values for the ‘rich club’, ‘feeder’ and ‘local’ connections at each value of k from 1 to 16 are listed in Table S6 (Supplementary Materials).

Nodal parameters

Figure 5 shows the brain regions with significant between-group differences in their nodal parameters. We found that in the WCG group, nodal strength (S_i^w) was uniformly significantly lower in seven regions and nodal efficiency (E_i^w) was also uniformly significantly lower in 16 regions, compared to the control group [$p = 0.0063$ using a false positive correction for multiple testing (Meng et al. 2014; Lynall et al. 2010)]. These regions are also listed in Table S7 (Supplementary Materials). We noticed that, of these 23 involved regions, only one region was a rich club node but the other 22 were non-rich club nodes, and most of them were located in the CN, FPN, and CON modules (Fig. 5).

Relationship between network parameters and years of training

Of all the network parameters that showed significant between-group differences, we found that the inter-modular FC between the FPN and the SMN was significantly negatively correlated with their number of years of training ($r = -0.645$, $p = 0.044$) but not with their age ($r = -0.231$, $p = 0.470$) in the WCG group (Fig. 6).

Robustness analysis

Table 2 shows the network results derived from different preprocessing strategies, different brain templates and a binary network. The calculation indicated that most of our

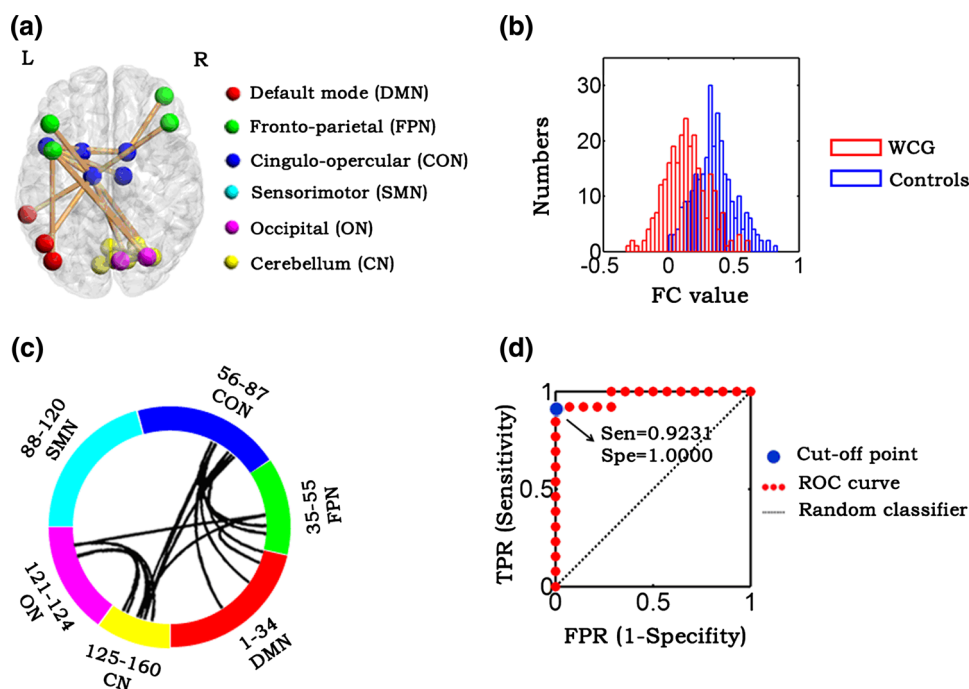


Fig. 3 The NBS-derived subnetwork showing significantly decreased functional connections (FCs) in the WCGs compared to the controls. **a** Plots of these FCs rendered using BrainNet Viewer (<http://www.nitrc.org/projects/bnv/>). **b** Histograms showing the distribution of the FC values in this subnetwork for the WCGs and the controls. **c** A circular plot of the twenty lower inter-nodal FCs. Each number indicates the index for a single node. See Table S1 in the

Supplementary Materials for more information about each region. **d** ROC curve based on the functional connectivity within the NBS-derived subnetwork. It shows that the mean FC strength of the NBS-derived subnetwork had a strong ability to discriminate the WCGs from the controls ($AUC > 0.9$). *TPR* true positive rate, *FPR* false positive rate, *Sen* sensitivity, *Spe* specificity, *AUC* area under curve

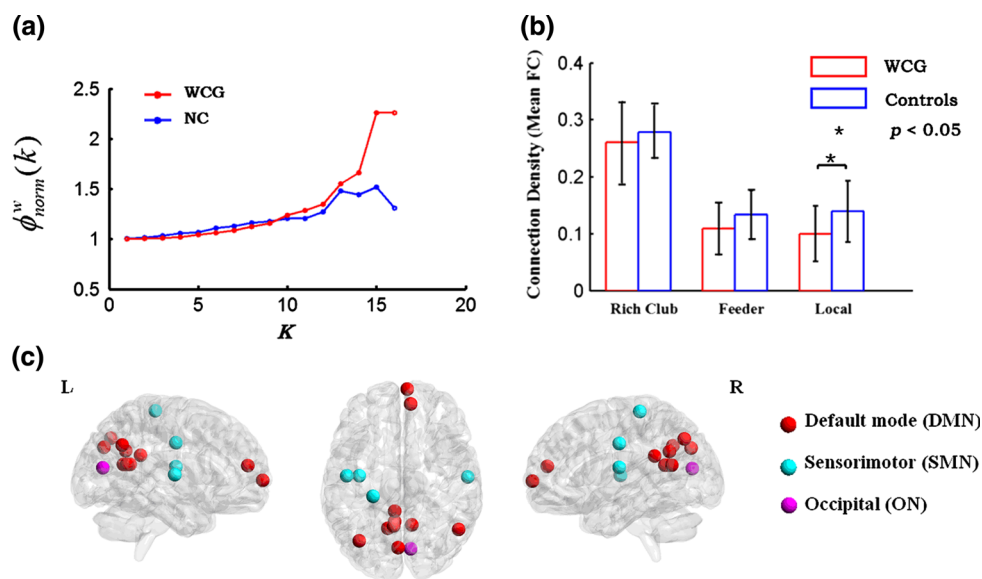


Fig. 4 Rich club organization of the world class gymnasts (WCGs) and the controls. **a** Group-averaged rich club curve for the gymnasts (red) and controls (blue). Both groups had a rich club organization $\phi_{norm}^w(k) > 1$ in the range of $1 \leq \text{degree } k \leq 16$. **b** Rich club regions occurring in both the WCG and control groups. These were rendered on the brain using BrainNet Viewer (<http://nitrc.org/projects/bnv/>). The group-averaged functional network for a given subject group was used to identify the rich club regions ($k \geq 11$). We found that the

shared rich club regions were located primarily in two modules, the DMN and SMN. **c** Barplot showing between-group differences in the strength of the 'rich club', 'feeder', and 'local' functional connections. We found significantly lower connectivity strength in the 'local' connections ($p = 0.032$) in the WCG group compared to the controls, but no significant between-group difference in either the 'rich club' or the 'feeder' connections

Fig. 5 Rendering plots of the brain regions that showed significantly lower nodal parameters for the brain functional networks in the WCG group compared to the control group ($p < 0.0063$ based on false positive correction for multiple testing). **a** Nodal strength. **b** Nodal efficiency. The regions with significantly lower nodal parameters were primarily located within three modules, the cerebellum (CN), fronto-parietal network (FPN), and cingulo-opercular network (CON). The size of the nodes is inversely proportional to the p value of the between-group difference in the given nodal parameter

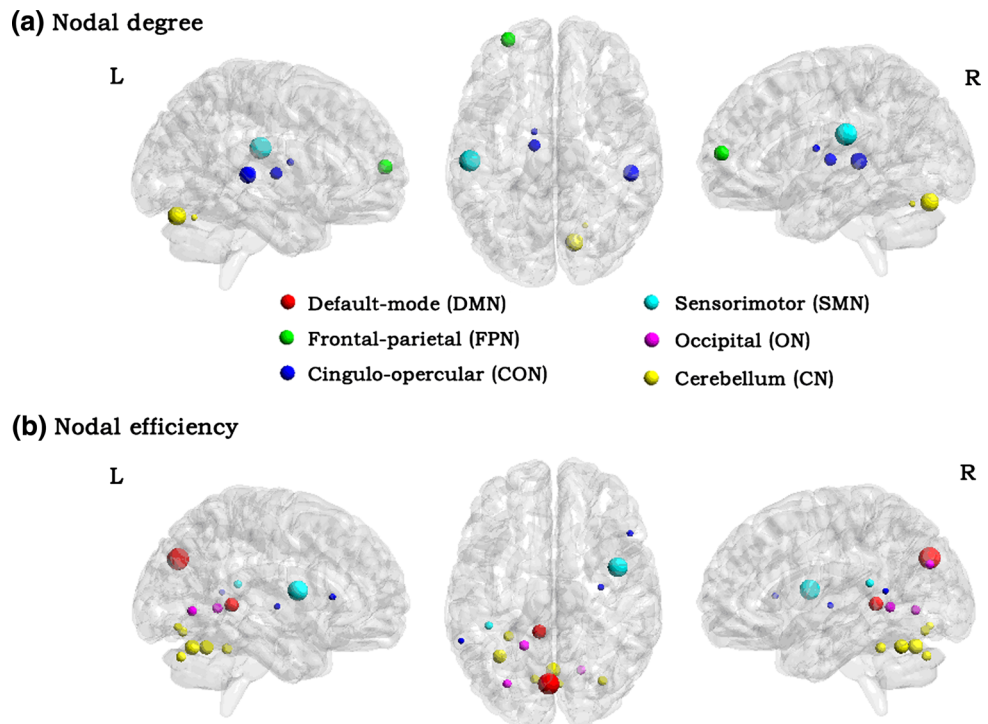


Table 2 Robustness of the alterations in brain functional network parameters of the world class gymnasts (WCGs) compared to the normal controls

| Different processing strategies | C_w | L_w | E_{loc} | E_{glob} | δ | ϕ_{norm}^w | NBS |
|--|-------|-------|-----------|------------|----------|-----------------|-----|
| Main processing strategy in this study | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Other preprocessing strategies | | | | | | | |
| Sparsity | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Global regressing | – | – | – | – | >1 | >1 | ↓ |
| Smoothing | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Positive only | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Other brain templates | | | | | | | |
| AAL-90 | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Power-264 | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| H-1024 | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |
| Network type | | | | | | | |
| Binary | ↓ | ↑ | ↓ | ↓ | >1 | >1 | ↓ |

The ‘↓’ (↑) symbol indicates a significantly lower (higher) value for a global parameter in the WCG group compared to the controls; ‘–’ indicates no significant between-group difference. ‘Sparsity’ stands for estimating a threshold range (0.10–0.35) by using a measure of sparsity (the ratio between the total number of edges and the maximum possible number of edges in a network). We applied these thresholds to each of the FC matrices. ‘Global Regressing’ refers to a network analysis based on a connectivity matrix which was constructed from the R-fMRI data after regressing out the global signal. ‘Smoothing’ refers to a network analysis based on a connectivity matrix which was obtained from the smoothed R-fMRI data (FWHM = 6 mm). ‘Positive Only’ refers to a network analysis based on a connectivity matrix which was derived from the positive-only inter-nodal correlations. And ‘Binary’ refers to connectivity matrices that were converted into binary matrices at a selected threshold when constructing the networks. AAL-90 is the Automatic Anatomical Labeling atlas that parcellates the brain into 90 regions. Power-264 is an atlas obtained from a meta-analysis of fMRI data and R-fMRI connectivity data. H-1024 is a high-resolution atlas which was generated from the AAL atlas and randomly parcellates the whole brain into 1024 equal volume cortical and sub-cortical regions. NBS, network-based statistic

findings were relatively stable across the various strategies. Specifically, small-worldness and rich club organization were always found in both the WCGs and the controls. For

the global parameters, the WCGs consistently showed significantly lower C_w , E_{loc} and E_{glob} , but higher L_w , compared to the controls. In addition, a NBS-derived

subnetwork that had a significantly low FC in the WCGs compared to the controls was always detected.

Cross-validation

The cross-validation analysis showed that the reported between-group differences in this study were highly replicable, as these findings were almost preserved in the 13 combinations of subjects (Table S9 in Supplementary Materials).

Classification

For the network parameters showing significant between-group differences, most can discriminate the WCGs from controls significantly ($p < 0.05$) (Table S9 in Supplementary Materials). Further, the mean FC of the subnetwork with significantly decreased FC has the highest ability to distinguish the WCGs from the controls (AUC = 0.997; Sensitivity = 0.923; Specificity = 1.000; Efficiency = 0.963; $p = 1.0e-9$) (Fig. 3d).

Discussion

In this study, we constructed brain functional networks for both the WCGs and control groups and compared between-group differences in the network parameters. At the whole brain level, we found that the FC, local efficiency, and global efficiency were uniformly significantly lower in the WCG group compared to the controls, though both groups showed small-worldness and rich club properties. At the modular level, the WCG group showed not only significantly lower intra-modular FC within each of three functional modules (the cerebellum, fronto-parietal, and cingulo-opercular networks) but also significantly lower inter-modular FCs in these three modules in the WCGs compared with the controls. At the nodal level, we detected significantly lower nodal strength and nodal efficiency in several non-rich club nodes within these three modules in the WCG group compared to the controls. Among all of the reorganized network parameters, we also found that the inter-modular FC between the fronto-parietal network and the sensorimotor network was significantly negatively correlated with number of years of training in the WCG group, and the NBS-derived subnetwork was well able to distinguish the WCGs from the controls.

Plasticity in the whole brain functional networks of the WCGs

At the whole brain level, the WCG group showed uniformly significantly lower FC, clustering coefficient, local

efficiency, and global efficiency, but greater characteristic path length, compared to the controls (Fig. 1; Table 2; S3). This may reflect a decrease in the amount of local and global transfer of information in the WCGs after long-term intensive training. This apparent plasticity in the whole brain network level was in line with previous studies (Hikosaka et al. 2002; Doyon and Benali 2005; Dayan and Cohen 2011; Schendan et al. 2003; Floyer-Lea and Matthews 2005) which suggested that widespread cortical-subcortical regions are crucial for mediating long-term motor skill training. In addition, these results are parallels to our previous findings of structural plasticity in the WCGs (Wang et al. 2013a), which showed changes in the network parameters of the whole brain anatomical networks, including the local and global efficiency as well as the shortest path length.

The lower local and global information transfer in the WCGs may be related to an increase in their neural efficiency after long-term, intensive gymnastic training. Motor skill learning can allow people to achieve very skilled behaviors, and repetitive skill practice can allow people to possess a degree of automaticity. With long-term motor skill training, the performance becomes more precise and automatic. In this study, we may logically assume that the gymnastic skills of the WCG group have a high degree of automaticity as they have been in intensive professional gymnastic training for more than 10 years and have gained an outstanding performance. Previous studies (Wu et al. 2004; Haslinger et al. 2004) suggested that automatic behaviors are associated with increased neural efficiency and correspond to a lessening of the neuronal resources involved.

However, our results were inconsistent with several studies reporting increased brain functional connectivity after long-term motor skill training. This inconsistency may be due to the intensity, period, or discipline of motor skill training. Table 3 summarizes the findings of previous studies on detecting brain functional connectivity changes after motor skill learning from 2010 to 2015, and shows both decreased and increased functional connectivity. These studies provided cues that different practice schedules and different amount of practice periods for specific motor skills may influence the directions of brain plasticity (decrease or increase). High intensity and amount of training may lead to negative correlation, but low-to-moderate intensity and amount of training may lead to positive correlation between the brain plasticity and the training period. The possible reason for this divergence is that different practice would elicit different cellular mechanisms (Sampaio-Baptista et al. 2014, 2015) or make subjects at different stages of learning (Sampaio-Baptista et al. 2015; Dayan and Cohen 2011). In our study, all gymnasts have received long-time intensive professional

Table 3 Overview of previous studies on revealing the plasticity of brain functional connectivity (FC) after motor skill learning

| References | Training task | Training time | fMRI scan | Main findings in trainers |
|--------------------------------|--------------------|--|-----------|--|
| Hamzei et al. (2012) | Left hand practice | 30 min/day for 5 days | R-fMRI | ↑ FC between striatum and cortical regions |
| Ma et al. (2011) | Finger movement | 15 min/day for 4 weeks | R-fMRI | ↑ FC between PoCG.R and SupraMarginal_R in 0–2nd week ↑ FC between PoCG.R and SupraMarginal_R in 3rd–4th week |
| Ma et al. (2010) | Finger movement | 15 min/day for 4 weeks | T-fMRI | ↑ FC between BG and cortical regions ↓ FC between CB and cortical regions |
| Coynel et al. (2010) | Finger movement | 10–20 min/day for 4 weeks | T-fMRI | ↓ FC in associative/premotor networks ↑ FC between associate/premotor and SMN |
| Taubet et al. (2011) | Dynamic balance | 42.5 min once a week for 6 weeks | R-fMRI | ↑ FC between frontal and parietal regions |
| Sampaio-Baptista et al. (2015) | Juggling practice | 30 min/day (high intensity group) 15 min/day (low intensity group) for 6 weeks | R-fMRI | ↑ FC in motor network in low intensity group ↓ FC in motor network in high intensity group |
| Di et al. (2012) | Badminton | ≥3 years | R-fMRI | ↓ FC between medial CB and ACC.R ↓ FC between left parietal and IFG.L ↓ FC between left parietal and MFG.L/R ↑ FC between left parietal and ACC.R |
| Bernardi et al. (2013) | Racing-car | ≥4 years | T-fMRI | ↑ FC related to brain areas responsible for motor reaction and visuo-spatial tasks |
| Current study | Gymnastics | ≥10 years | R-fMRI | ↓ FC related to the CB, FPN and CON |

FC functional connectivity, *PoCG.R* right postcentral gyrus, *BG* basal ganglia, *ACC.R* right anterior cingulate cortex, *IFG.L* left inferior frontal cortex, *MFG.L/R* bilateral middle frontal cortex, *CB* Cerebellum, *SMN* sensorimotor network, *FPN* fronto-parietal network, *CON* cingulo-opercular network

gymnastic training, over 10 years, and have gained an outstanding performance, world-level. By now, very few studies reported brain plasticity in professional subjects experienced over 10 years intensive motor skill training (exception of the motor plasticity in musicians). Thus, our result seems consistent with these previous studies. But we must point out that this is only a possible explanation. No doubt, a better way to validate this explanation is that we need to conduct a longitudinal study to detect the dynamic effects of plasticity.

Plasticity in the functional modules of WCG

In this study, we also found that the WCGs showed significantly larger numbers of lower intra- and inter-modular FCs (Figs. 2, 3; Tables S4, S5 in Supplementary Materials), and lower nodal degree and efficiency (Fig. 5, Table S6 in Supplementary Materials) in three modules (the cerebellum, frontal-parietal network, and cingulo-opercular network), compared to the controls. These results are in line with several previous studies (Hikosaka et al. 2002; Doyon and Benali 2005; Dayan and Cohen 2011;

Doyon et al. 2002; Miller and Cohen 2001; Hardwick et al. 2013), which all concluded that the fronto-parietal network, cerebellum, thalamus, and basal ganglia are critical for long-term motor skill training.

The cerebellum is thought to be related to motor functions. It receives inputs from the sensory system of the spinal cord or from cortical and subcortical regions and then integrates these inputs to fine tune motor activity (Fine et al. 2002). It has been validated that the cerebellum plays important roles in motor timing and motor execution (Mauk et al. 2000) and that activity in the cerebellum can be used to predict the sensory consequences of movements and to detect errors in these predictions (Hardwick et al. 2013; Krakauer and Mazzoni 2011; Penhune and Steele 2012). In addition, a review by Manto et al. (2012) concluded that the cerebellum is involved in the control of motor speech, oculomotor functions, grip forces, voluntary limb movement, and classical conditioning.

Furthermore, previous studies (Di et al. 2012; Di Paola et al. 2013; Bernardi et al. 2013; Walz et al. 2015) revealed an effect of long-term motor skill training on the cerebellum. Di et al. (2012) detected significantly increased gray

matter density in the cerebellum in professional badminton players compared to controls. Di Paola et al. (2013) revealed that world class mountain climbers showed significantly greater volumes of the vermal lobules I–V of the cerebellum compared to controls. Bernardi et al. (2013) demonstrated that professional car drivers had less activation in the cerebellum compared to naïve drivers when performing a motor reaction and a visuo-spatial task. In addition, Walz et al. (2015) used an arm ability training paradigm to train the left hand of right-handed healthy participants over 2 weeks and found that activation in the lateral cerebellar regions decreased over the training time. Our detected changes in the cerebellum of the WCGs appears to validate the effects of long-term motor skill training on the cerebellum and can help us understand the high level of motor performance in gymnasts.

The fronto-parietal network (FPN) may be divided into dorsal and ventral sections, both of which are thought to be involved in the control of attention (Corbetta and Shulman 2002). The dorsal part of the FPN, including the intraparietal cortex and superior frontal cortex, has been suggested to be involved in preparing and applying goal-directed (top–down) selection for stimuli and responses; whereas the ventral part, including the temporoparietal cortex and inferior frontal cortex, has been proposed to specialize in the detection of behaviorally relevant stimuli, such as salient or unexpected stimuli (Corbetta and Shulman 2002). Some studies (Cole et al. 2013; Zanto and Gazzaley 2013) also suggested that the FPN takes a central role in cognitive control and adaptive implementation of task demands. Sridharan et al. (2008) revealed a critical role for the FPN in switching between the central-executive and the default-mode networks. Rizzolatti and Luppino (2001) proposed that the FPN is responsible for controlling the coordination and planning of complex motor functions. A clinical study (Leiguarda and Marsden 2000) also suggested that lesions in the FPN may result in severe deficits in coordinating complex visuomotor movements.

Also, the FPN has been shown to reorganize after long-term motor skill training (Jancke et al. 2009; Di et al. 2012; Taubert et al. 2011; Albert et al. 2009). Jancke et al. (2009) found that the gray matter volumes in the FPN were larger in skilled golfers than in less-skilled golfers. Di et al. (2012) showed an alteration of the FPN in professional badminton players compared to controls. Taubert et al. (2011) revealed that connectivity in the FPN gradually increased during 6 weeks of learning a dynamic balancing task. Albert et al. (2009) revealed that motor training, but not motor performance, can modulate resting state activity in the FPN. The differences in the FPN between the WCGs and the controls may help us understand gymnasts' excellent motor attention and motor control in gymnastics. This result was also consistent with our previous work on

structural plasticity in WCGs (Wang et al. 2013a; Huang et al. 2013), which detected that the nodal degree and efficiency, as well as the fractional anisotropy and gray matter density in brain regions responsible for motor attention were also changed in the WCGs.

The cingulo-opercular network (CON), which includes the dACC, anterior insula, operculum, anterior prefrontal cortex, inferior parietal cortex, basal ganglia, and thalamus (all bilaterally), is believed to be involved in attention and executive control (Dosenbach et al. 2007; Seeley et al. 2007). Dosenbach et al. (2007, 2008) proposed that the FPN may serve to initiate and adjust cognitive control whereas the CON may provide 'set initiation', stable 'set-maintenance', and 'error monitoring' over the duration of a group of task blocks. In this study, we detected significantly lower intra-modular FC and nodal parameters within the CON (Figs. 1, 2, 5; Tables S3, S4, S6 in Supplementary Materials), as well as lower inter-modular FCs between the CON and other brain regions (Fig. 3 and Table S5 in Supplementary Materials). In addition, we found the reorganization of the CON were primarily in the basal ganglia and thalamus. Previous studies (Picard and Strick 1996; Tanji 1996) suggested that two distinct cortical-subcortical circuits, a cortico-basal ganglia-thalamo-cortical loop and a cortico-cerebello-thalamo-cortical loop, are responsible for motor skill training. As a relay station, the thalamus provides the specific channels for transferring signals from the basal ganglia and cerebellum to the cortical motor regions (Kurata 2005; Sakai et al. 2002). The basal ganglia are responsible for monitoring the consequences of behavioral variations produced by other brain regions (Charlesworth et al. 2012) and for allowing training and automaticity (Ashby et al. 2010). Thus, functional reorganization in the thalamus and basal ganglia in WCGs may contribute to their outstanding performance in gymnastic competitions.

In fact, several studies (Walz et al. 2015; Floyer-Lea and Matthews 2005) reported that long-term motor skill training can influence the brain functional activity in the basal ganglia. Walz et al. (2015) used the arm ability training paradigm to train the left hand of right-handed healthy participants over 2 weeks and found that activation in the basal ganglia decreased over the training time. Floyer-Lea and Matthews (2005) asked their subjects to learn how to track the development of a demanding variable isometric force between the fingers and thumbs of the right hand and compared the brain activation networks between short- and long-term training. They found that the long-term motor skill training increased the activation of the motor cortical-basal ganglia loop.

In this study, we also found that most of the brain regions in the NBS-derived subnetwork as well as the brain regions showing significantly different nodal parameters were non-rich club nodes (Tables S5, S7 in the

Supplementary Materials). We also detected that the ‘local’ connections were significantly lower in the WCG group than in the controls (Fig. 5c). However, no significant training effect on the rich club nodes was found in the WCG group. This may indicate the stability of rich club organization even after long-term extensive gymnastic training.

Relationship between network parameters and the number of years of training

A statistical analysis showed a significantly negative correlation between the inter-modular FC of the FPN-SMN and the number of years of training in the WCG group (Fig. 6). This may indicate that intensive gymnastic training indeed induced plastic functional changes in the brain in that the WCGs with more years of training tended to have a weaker FC between the FPN and the SMN. Previous studies suggested that both the FPN and SMN play important roles in long-term motor skill learning (Floyer-Lea and Matthews 2005; Dayan and Cohen 2011). Specifically, the FPN seems to be involved in attention control and the SMN appears to be related to motor execution and control. As the number of years of training increased, the number of links between the attention control region and the motor execution region decreased in the WCG group. This may help us to understand their great physical agility, coordination, and control in gymnastic performance.

Potential indicators of WCG

There are gifted athletes, but there may not be totally natural athletes. Without professional skill training before adolescence, people seem to find it nearly impossible to participate in competitions. For athletes who have had

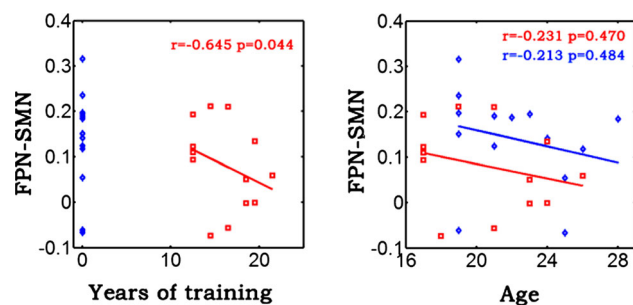


Fig. 6 Scatter plots of the inter-modular connectivity between the fronto-parietal network (FPN) and the sensorimotor network (SMN) against the number of years of training or against the age. The functional connectivity between the FPN and the SMN was significantly negatively correlated with the number of years of training in the WCG group ($r = -0.645$, $p = 0.044$). The *red square* stands for a gymnast and the *blue diamond* for a control subject

long-term, extensive gymnastic training, coaches would like to be able to use their gymnastic performance during routine competitions to identify the ones that have the potential to participate in world-level sports competitions. Actually, the selection criteria by which coaches make subjective evaluations of the gymnasts’ behavioral performance is not easy to ascertain and ignores their inner abilities. Thus, we tested to see whether we could detect an objective evaluation index that could serve as a neuroimaging indicator of WCGs based on their network parameters. Such an index could provide extra information for the selection of WCGs. For this portion of the study, we plotted ROC curves based on different network parameters and found that the mean FC of the NBS-derived subnetwork easily discriminated the WCGs from the controls (Fig. 3d). These results suggest that FC in the NBS-derived subnetwork can potentially be regarded as a neuroimaging indicator of WCGs.

Limitations

Several limiting factors need to be addressed. First, the sample size of the subjects in this study was small (only 13 world class gymnasts) which may bias the findings of this study. Of course, we were limited in our ability to recruit more world gymnastic champions. For the limited sample size, we calculated the statistical power and effect size, conducted the cross-validation analysis, and plotted the ROC curve for network parameters showing significant between-group differences. Results revealed that their statistical power and effect size were quite high (Tables S3, S4, S5, S7, S8 in Supplementary Materials). The cross-validation analysis indicated that our findings were highly replicable as these were almost preserved in the 13 combinations of subject (Table S9 in Supplementary Materials). The ROC curve also showed that most of these parameters had significant discrimination ability to distinguish the WCGs from controls (Table S9 in Supplementary Materials). In addition, in order to test the robustness of our findings, we repeated the network analysis by applying various strategies, including different preprocessing strategies and different brain templates, for both the weighted and binary networks. The calculations showed that our main findings were robust under these various strategies. Second, the results of the modularity analysis in this study were based on the six modules reported in Dosenbach et al. (2010) that were obtained by analyzing 238 subjects. This may bias our results due to individual differences. Thus, we conducted a modularity analysis using Newman’s algorithm (2006) based on our own R-fMRI data. The results revealed seven modules (Fig. S3 in Supplementary Materials) with the functional plasticity of the WCGs primarily located in the modules of the FPN, CON, and subcortical regions (the basal ganglia and thalamus)

(Table S8 in Supplementary Materials), findings which were similar to the main results reported in this study. Third, because we were unable to perform a longitudinal study, we cannot completely rule out the possibility that maturation and/or innate traits from birth (such as genes) could have caused or contributed to the differences between the WCGs and the controls. In subsequent studies, we will collect longitudinal data to exclude these confounding effects and to try to reveal the dynamic features of brain functional plasticity throughout the years of gymnastics training. Fourth, as the gymnasts may be more fit than the controls during the fMRI scan, the artifacts related to respiration, heart rate and fitness may affect network analysis. In the calculations, we performed a band-pass filtering (0.01–0.08 Hz) to remove artifacts related to respiration and heart rate in data processing. In subsequent studies, we need to collect and record physiological data (peripheral pulse, respiration, and electrocardiography data) during the fMRI scan and to use them as nuisance regressors. Fifth, some studies (Zuo et al. 2014; Zuo and Xing 2014; Liang et al. 2012; Deuker et al. 2009; Telesford et al. 2013) have discussed that the replicability of brain functional networks may be affected by many factors. And these factors can be included in two aspects, the data quality (such as head motion, artifacts, scanning time, sequence parameters, etc.) and the processing strategies (node definition, edge definition, temporal filtering size, global signal, etc.). Although we have used several strategies, such as selecting different preprocessing strategies, different brain atlases, and different network types, to validate our results in this study (Table 2), we are far from using all the possible strategies. Finally, the champions were not classified into discipline-specific subgroups. Although the dominant disciplines differed between these champions, their routine training regimes were quite similar, other than during periods directly tied to preparation for competition.

Conclusion

This study analyzed brain functional plasticity that appears to have been induced by long-term intensive gymnastic training in gymnasts. Our results indicated that gymnastic training induced significant changes in the brain network parameters, especially in the cerebellum, fronto-parietal, and cingulo-opercular networks. We also found that the FC between the fronto-parietal network and the sensorimotor network was significantly negatively correlated with the number of years of training. These findings may help us to understand the outstanding performance of gymnasts in competitions and to reveal the neural mechanisms that distinguish WCGs from non-athletes.

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Compliance with ethical standards

Competing interest The authors declare that they have no competing financial interests.

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