

Long-term intensive gymnastic training induced changes in intra- and inter-network functional connectivity: an independent component analysis

Huiyuan Huang¹ · Junjing Wang¹ · Carol Seger^{1,2} · Min Lu³ · Feng Deng¹ · Xiaoyan Wu¹ · Yuan He¹ · Chen Niu¹ · Jun Wang⁴ · Ruiwang Huang¹

Received: 20 February 2017 / Accepted: 17 July 2017
© Springer-Verlag GmbH Germany 2017

Abstract Long-term intensive gymnastic training can induce brain structural and functional reorganization. Previous studies have identified structural and functional network differences between world class gymnasts (WCGs) and non-athletes at the whole-brain level. However, it is still unclear how interactions within and between functional networks are affected by long-term intensive gymnastic training. We examined both intra- and inter-network functional connectivity of gymnasts relative to non-athletes using resting-state fMRI (R-fMRI). R-fMRI data were acquired from 13 WCGs and 14 non-athlete controls. Group-independent component analysis (ICA) was adopted to decompose the R-fMRI data into spatial independent components and associated time courses. An automatic component identification method was used to identify components of interest associated with resting-state

networks (RSNs). We identified nine RSNs, the basal ganglia network (BG), sensorimotor network (SMN), cerebellum (CB), anterior and posterior default mode networks (aDMN/pDMN), left and right fronto-parietal networks (lFPN/rFPN), primary visual network (PVN), and extrastriate visual network (EVN). Statistical analyses revealed that the intra-network functional connectivity was significantly decreased within the BG, aDMN, lFPN, and rFPN, but increased within the EVN in the WCGs compared to the controls. In addition, the WCGs showed uniformly decreased inter-network functional connectivity between SMN and BG, CB, and PVN, BG and PVN, and pDMN and rFPN compared to the controls. We interpret this generally weaker intra- and inter-network functional connectivity in WCGs during the resting state as a result of greater efficiency in the WCGs' brain associated with long-term motor skill training.

Electronic supplementary material The online version of this article (doi:10.1007/s00429-017-1479-y) contains supplementary material, which is available to authorized users.

✉ Ruiwang Huang
ruiwang.huang@gmail.com

¹ School of Psychology, Institute of Brain Research and Rehabilitation (IBRR), Center for the Study of Applied Psychology and MRI Center, Key Laboratory of Mental Health and Cognitive Science of Guangdong Province, South China Normal University, Guangzhou 510631, P. R. China

² Department of Psychology and Program in Molecular, Cellular, and Integrative Neurosciences, Colorado State University, Fort Collins 80523, Colorado, USA

³ Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, P. R. China

⁴ State Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, P. R. China

Keywords Neuroplasticity · World class gymnasts · Independent component analysis (ICA) · Resting-state networks (RSNs) · Intra-network functional connectivity · Inter-network functional connectivity

Introduction

Motor skill learning refers to the acquisition of a motor ability as a result of repetition or long-term training (Nakata et al. 2010). Long-term intensive motor skill learning can induce structural and functional neuroadaptations (Dayan and Cohen 2011; Doyon et al. 2009). Usually, elite athletes begin training from a very early age in childhood, practice several hours a day, and maintain the training throughout the entire careers. As a result of this long-term intensive motor skill training, they possess

greater strength, speed, endurance, coordination, accuracy, consistency, automaticity, and efficiency than less proficient athletes (Nakata et al. 2010), making elite athletes an ideal model for studying training-induced brain plasticity. Our understanding of the neural substrates underpinning the acquisition and retention of motor skills has improved in recent years, owing in a large part to technological and methodological advances in neuroimaging, especially magnetic resonance imaging (MRI). Previous studies have identified structural and/or functional differences related to intensive motor skill training in elite athletes in a variety of sports, including distance running (Raichlen et al. 2016), basketball (Park et al. 2009, 2015), badminton (Di et al. 2012), golf (Jäncke et al. 2009), mountain climbing (Paola et al. 2013), archery (Chang et al. 2011; Kim et al. 2008, 2014), dance (Calvo-Merino et al. 2005; Giacosa et al. 2016; Hanggi et al. 2010), and formula racing (Bernardi et al. 2013). These studies found that long-term motor skill training was associated with neuroplastic adaptations in brain structure and function, which may, together with muscular and cardiovascular fitness, contribute to the exceptional abilities of elite athletes (Callan and Naito 2014). However, since the abilities or skills required for athletic performance (e.g., strength, accuracy, and artistry) depend on the particular sport, plastic reorganization may vary across different types of athletes.

World class gymnasts, who excel in gymnastics competition, have extraordinary abilities in physical strength, balance, coordination, grace, agility, and flexibility. They must precisely control their direction of movement, their speed of execution, and monitor their spatial location relative to objects in the surrounding environment (Huang et al. 2015; Wang et al. 2013a, 2016). Gymnastics relies on the ability of the nervous system to activate the correct muscles to the proper extent at the right time and in the right sequence (Nielsen and Cohen 2008). Gymnastics also requires integration of inputs from multiple sensory modalities (Calvert and Thesen 2004; Stein and Stanford 2008). Our previous studies identified neuroanatomical differences between gymnasts and nonathletic controls using diffusion-weighted and structural MRI data (Huang et al. 2015; Wang et al. 2013a). We found that the gymnasts showed morphological plasticity in white matter microstructure and gray matter density, especially for brain regions and networks related to motor, attention, and cognitive control functions. Furthermore, using resting-state fMRI (R-fMRI), we examined the topological properties of whole-brain functional networks and found significant differences between the gymnasts and controls in functional topological parameters, especially in the cerebellum, fronto-parietal, and cingulo-opercular networks (Wang et al. 2016).

However, this and other graph theoretical analyses of human brain functional networks show a strong reliance on the templates chosen (i.e., brain parcellation schemes) (Fornito et al. 2010; Liang et al. 2012; Wang et al. 2009; Zuo and Xing 2014; Zuo et al. 2014) and are sensitive to noise or artifacts (e.g., head motion and physiological noise related to respiratory and cardiac signals) (Wang et al. 2011). To overcome these limitations, in the present study, we analyzed the R-fMRI data using independent component analysis (ICA), a fully data-driven multivariate blind source separation method that does not require any prior assumption (Calhoun et al. 2001; McKeown et al. 1998), and has higher test-retest reliability than other commonly-used functional connectivity approaches (Zuo et al. 2010; Zuo and Xing 2014). It also offers the advantage of better isolating physiological artifacts from neuronal components. ICA applied to spontaneous brain activity measured during R-fMRI can be used to identify and characterize connectivity in different functional networks, referred to as intra-network functional connectivity. This method decomposes R-fMRI data into several sources or independent components which are spatially independent of each other. Many components identified across studies show substantial overlap with brain regions associated with particular cognitive functions (Smith et al. 2009). They are commonly referred to as resting-state networks (RSNs) or intrinsic connectivity networks (Beckmann et al. 2005; Damoiseaux et al. 2006; De Luca et al. 2006; Seeley et al. 2009). Other components, especially those located beyond the canonical locations of the functional networks, are often treated as noise and discarded from further analyses (Greicius et al. 2007). Thus, ICA can be used as an effective method to separate functionally interpretable components from noise and artifacts. Furthermore, ICA can be used to study inter-network functional connectivity, defined as the temporal dependency between the independent components or the temporal correlation between pairs of functional networks estimated from ICA (Jafri et al. 2008).

In the current study, R-fMRI data were acquired from 13 world class gymnasts (WCGs) and 14 demographically-matched non-athlete controls. Group ICA was adopted to decompose the R-fMRI data into distinct spatial independent components and associated time courses. An automatic component identification method was used to identify components of interest (COI) related to RSNs. Then, both intra- and inter-network functional connectivities were evaluated in the WCGs in comparison with those of the non-athlete controls.

Materials and methods

Subjects

Thirteen world class gymnasts (7 F/6 M, aged 17–26 years, mean \pm SD 20.5 \pm 3.2 years) participated in this study in 2010. Each gymnast had won at least one gold medal at the Gymnastics World Cup or the Olympic Games between 2007 and the time of the study. They started gymnastic training at an average age of 4.5 years and had been training on average for more than 12.5 years by the time of this experiment, with a mean training time of 6 h per day. In addition, we also recruited 14 healthy non-athletes (7 F/7 M, aged 19–28 years, mean \pm SD 20.3 \pm 2.5 years) as the controls. They were age and gender-matched to the gymnasts, with no significant between-group difference in age (two-sample t test, $t = -1.33$, and $p = 0.20$) and 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 or movement disorders, and the control subjects did not have any previous formal gymnastics training. Written informed consent was obtained from each subject prior to the study. The experiment protocol was approved by the Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University. Table 1 lists the detailed information about each of the world class

gymnasts. Additional informed consent was obtained from the WCGs for whom potentially identifying information is included in this article.

Resting-state fMRI acquisition

All MRI data 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 data sets 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, slice thickness/gap = 3.6 mm/0.7 mm, 33 transverse interleaved slices covering the whole brain, and in total 240 volumes acquired in 8 min. During the scanning, each subject was instructed to relax with eyes closed, without falling asleep and without thinking 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 as follows: 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 covering the whole brain acquired in 10 min. For each subject, the

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

Champions	Discipline	Best medal records since 2007	Gender	Age (years)	Age of commencement (years)	Years of training (years)
1	Pommel horse	OC	M	24	4.5	19.5
2	Still rings	WC	M	24	4.5	19.5
3	Parallel bars	WC	M	23	4.5	18.5
4	Horizontal bar, AA	WC	M	26	4.5	21.5
5	Vault	OC	F	21	4.5	16.5
6	Uneven bars, AA	WC	F	17	4.5	12.5
7	Uneven bars, AA	OC	F	18	3.5	14.5
8	Floor exercises	OC	F	17	4.5	12.5
9	Uneven bars, AA	OC	F	17	4.5	12.5
10	Parallel bars, AA	WC	M	21	4.5	16.5
11	Uneven bars, AA	WC	F	19	4.5	14.5
12	Pommel horse	WC	M	23	4.5	18.5
13	Balance beam, AA	OC	F	17	4.5	12.5
Mean \pm std				20.5 \pm 3.2	4.4 \pm 0.3	16.1 \pm 3.3

All of them have won individual or team gold medals in the Gymnastic World Championships or the Olympic Games since 2007. The second column represents the dominant discipline for each of the champion subjects

OC Olympic Champions, WC World Champions or World-Cup Champions, AA all around

R-fMRI data and 3D high-resolution brain structural images were acquired in the same session. Foam pads and noise-protection ear plugs were used to reduce head motion and suppress ambient scanner noise.

Data preprocessing

The R-fMRI data were preprocessed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>) and DPARSFAv2.3 (<http://rfmri.org/DPARSF>) (Chao-Gan and Yu-Feng 2010) in MATLAB 2013a (the MathWorks Inc., Natick, MA, USA). The following preprocessing steps were applied: (1) the first 10 volumes (i.e., 20 s of data) were discarded for fMRI signal to reach T1 equilibrium and to allow subjects to adapt to the scan, leaving 230 volumes for further analysis. (2) Slice-timing correction was applied to correct for within-scan acquisition time difference between slices using temporal sinc interpolation. (3) Head motion was corrected using a six-parameter rigid-body transformation. Our protocol called for exclusion of any subjects with excessive head motion (translation >2 mm in any plane or rotation >2° in any direction); however, no subjects exceeded these criteria and none were excluded. (4) The realigned R-fMRI images were spatially normalized to the high-resolution T1-weighted brain structural images in the standard MNI-152 space and were resampled to a voxel size of $3 \times 3 \times 3 \text{ mm}^3$. (5) The normalized images were spatially smoothed using an isotropic Gaussian kernel of 6 mm full-width at half-maximum (FWHM).

Extraction of ICA-based intrinsic connectivity networks

Group ICA was conducted to extract spatially independent components using the GIFT software package (<http://icatb.sourceforge.net/>, version 3.0a) (Egolf et al. 2004). First, data reduction was conducted to decrease computational complexity using a two-stage principal component analysis. The preprocessed data for each subject were first dimension-reduced temporally, and then, the reduced data from all subjects were concatenated into a single data set, referred to as the grouped data, along the temporal dimension and passed through another dimension reduction. Second, ICA was performed to decompose the grouped data into 30 independent components using an Infomax algorithm (Bell and Sejnowski 1995). This step was repeated 100 times using the ICASSO algorithm for assessing the repeatability or stability of independent components (Himberg et al. 2004). Finally, the independent components for each subject were derived from a GICA back reconstruction step and were converted into z scores (Calhoun et al. 2001). This provided subject-specific spatial maps and time courses which were further

used to make group-level random-effects inferences (one sample t test). Thus, for each independent component, a group-level t map was generated and was used to identify the brain regions involved. To identify COIs, we adopted “Discriminability Index-based Component Identification (DICI)”, an automatic component identification method. The DICI uses the “discriminability index (DI)” (DeCarlo 1998) to quantitatively evaluate the similarity of the spatial distribution of each independent component to a predefined spatial template for RSN identification (Huang et al. 2016; Zhang et al. 2013). In the current study, we selected the large-scale RSNs template provided by Shirer et al. (2012) as the reference template. Specifically, the t maps for all the group-level independent components were first converted to binary maps ($p < 0.01$, FDR corrected), and then, the DICI value for each IC was calculated by comparison with the RSNs template according to the following equation:

$$\text{DICI} = z(\text{hit rate}) - z(\text{false alarm rate}), \quad (1)$$

where the hit rate or sensitivity is the number of correctly identified voxels within a given independent component versus the total number of voxels in the RSN template, and false alarm rate ($1 - \text{specificity}$) is the number of mistakenly identified voxels within a given independent component versus the number of voxels outside the RSN template. DICI is calculated as the z transformed hit rate minus the z transformed false alarm rate. The independent component with the biggest DICI value was selected as the COI corresponding to the RSN template.

Intra-network functional connectivity

For each of the selected RSNs, we estimated the difference in intra-network functional connectivity between the WCGs and the controls. Specifically, a voxelwise one sample t test was conducted on the individual spatial z maps derived from ICA across subjects for each group, corrected for multiple comparisons (FDR corrected, q value = 0.01). Then, a two-tailed two-sample t test was performed to compare the group differences in the spatial z maps between the WCGs and the controls. Of note, we did not include voxels outside of the RSNs. To exclude outside voxels, we generated an RSN mask by combining the significant one sample t tests results from both groups for each RSN (i.e., the union of the maps). To avoid any spurious effects from white matter and ventricles on subsequent statistical analysis, we only included voxels falling in both the RSN masks and the gray matter mask (i.e., the intersection of the RSN masks and the gray matter mask). We entered age and gender as nuisance covariates throughout the entire analysis to regress out any potential covariate-related effects (Wang et al. 2013b). Group

difference maps derived from two-sample t tests were corrected for multiple comparisons using cluster-level thresholding at an uncorrected voxelwise $p < 0.01$ and a minimum cluster size threshold (see Tables S2–S6 of Supplementary materials) to maintain a corrected alpha threshold at the cluster level of $p < 0.05$. Cluster extents were computed via 1000 Monte Carlo simulations implemented in the 3dClustSim program (AFNI, <https://afni.nimh.nih.gov/>). The same procedures were applied to each of the selected RSNs.

Inter-network functional connectivity

A modified functional network connectivity method (Jafri et al. 2008) was used to study group differences in inter-network functional connectivity between the selected RSNs. The analyses procedure is briefly described as follows. First, the time courses for each of the nine RSNs were temporally band-pass filtered (0.01–0.1 Hz), followed by linear detrending for each subject, to remove any residual effect of low-frequency drift and high-frequency physiological noise. Second, the interaction of each pair of the selected RSNs was evaluated using Pearson's correlation coefficient (r) on the temporally filtered time courses. The r value indicates the spontaneous coherence level between RSNs. Third, the r value was transformed to z value using Fisher's r -to- z transformation to improve normality for further random-effects between-group analyses. Fourth, significance testing for the inter-network functional connectivity within each group and differences between the two groups was carried out using one sample t tests ($p < 0.05$, FDR corrected) and two-sample t tests ($p < 0.05$, FDR corrected), respectively.

Results

Components of interest

Figure 1 shows the nine COIs which were selected as the RSNs from the 30 independent components (one sample t test, $p < 0.01$, FDR corrected). These RSNs included the sensorimotor network (SMN), cerebellum (CB), basal ganglia network (BG), primary and extrastriate visual networks (PVN and EVN), anterior and posterior default mode networks (aDMN and pDMN), and left and right fronto-parietal networks (lFPN and rFPN). The location of each RSN was consistent with several previous studies (Beckmann et al. 2005; Calhoun et al. 2001; Damoiseaux et al. 2006; Smith et al. 2009). Detailed information about the regions in each RSN, such as cluster size, maximum t values, and coordinates, is listed in Table S1 (Supplementary Materials).

Intra-network functional connectivity

Figure 2 illustrates the significant between-group differences in intra-network functional connectivity. Compared to controls, the WCGs had significantly decreased intra-network functional connectivity in the left caudate (MNI: $-6, 7, 7$) within the BG (Fig. 2a), the bilateral medial superior frontal gyri (MNI: $-6, 36, 57$; BA 8) within the aDMN (Fig. 2c), the left superior frontal gyrus (MNI: $-18, 18, 57$; BA 8) within the lFPN (Fig. 2d), and the right middle frontal gyrus (MNI: $33, 60, 21$; BA 10) within the rFPN (Fig. 2e). In contrast, the WCGs showed significantly increased intra-network functional connectivity in the right middle occipital gyrus (MNI: $30, -84, 36$; BA 19) within the EVN (Fig. 2b) compared to the controls. No between-group difference in intra-network functional connectivity was found in other RSNs (i.e., SMN, CB, PVN, and pDMN). Table 2 gives detailed information for the brain areas with between-group difference in intra-network functional connectivity.

Inter-network functional connectivity

Figure 3 and Table 3 illustrate the significant between-group differences in inter-network functional connectivity (two-sample t test, $p < 0.05$, FDR corrected). We found that compared to the controls, the WCGs had significantly decreased correlation between SMN and BG ($t = 3.967$, $p = 0.0005$), CB and PVN ($t = 3.461$, $p = 0.0019$), BG and PVN ($t = 3.397$, $p = 0.0023$), and pDMN and rFPN ($t = 3.651$, $p = 0.0012$).

Discussion

In this study, we examined gymnastic training-related changes in functional connectivity: both intra-network functional connectivity within the RSNs and inter-network functional connectivity between the RSNs. For the intra-network functional connectivity, we found that intrinsic spontaneous activity was significantly reduced in four RSNs (BG, aDMN, lFPN, and rFPN), and significantly increased in one RSN (EVN) in the WCGs compared to the non-athletes. For the inter-network functional connectivity, the WCGs exhibited uniformly weaker interactions between SMN and BG, CB, and PVN, BG and PVN, and pDMN and rFPN compared to the non-athletes. The current study revealed that long-term intensive gymnastic training can cause reorganization in both the intrinsic brain activity of the RSNs and the interaction between the RSNs.

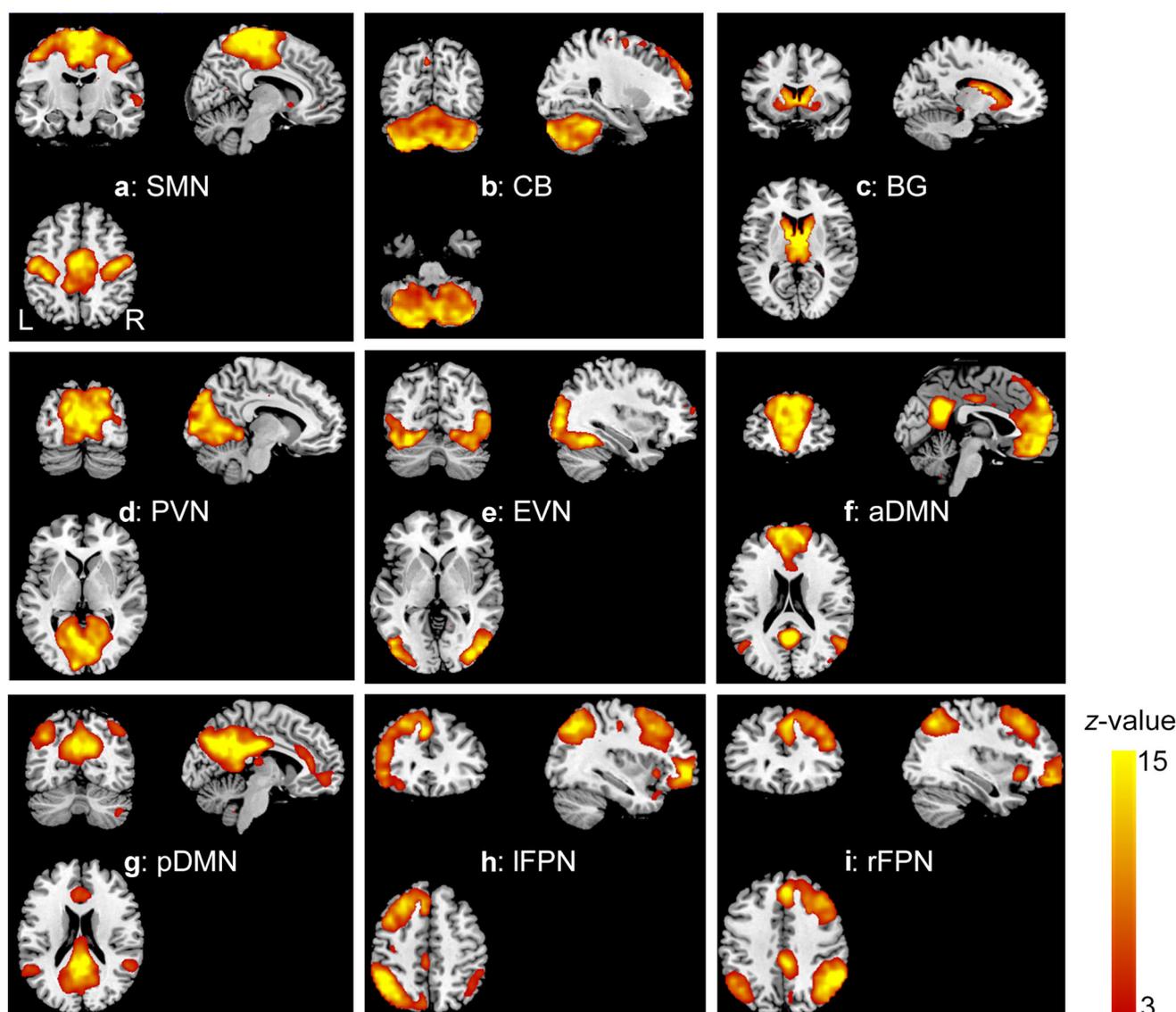


Fig. 1 Spatial distribution of the selected nine resting-state networks (RSNs) identified by Group ICA ($p < 0.01$, FDR corrected). **a** Sensorimotor network (SMN), **b** cerebellum (CB), **c** basal ganglia network (BG), **d** primary visual network (PVN), **e** extrastriate visual network (EVN), **f** anterior default mode network (aDMN), **g** posterior

default mode network (pDMN), **h** left fronto-parietal network (IFPN), and **i** right fronto-parietal network (rFPN). Images are shown on the three most informative orthogonal slices of the MNI standard space in neurological convention. The *color bar* indicates z value in each RSN

Intra-network functional connectivity

In the current study, the WCGs showed significantly decreased intra-network functional connectivity within parts of the BG, aDMN, IFPN, and rFPN compared to the non-athletes (Fig. 2; Table 2). These results are in line with several previous studies (Dayan and Cohen 2011; Hardwick et al. 2013; Hikosaka et al. 2002), finding training-induced plasticity in the basal ganglia, cerebellum, and fronto-parietal networks. The basal ganglia are involved in movement executing, programming, and control (Alexander and Crutcher 1990; Wu et al. 2004). The basal ganglia interact with motor cortical areas including primary motor

Fig. 2 Brain regions with significant between-group difference in intra-network functional connectivity. **a–e** Spatial maps and the boxplots of the RSNs with significant intra-network functional connectivity. The *color bar* indicates t value. *BG* basal ganglia network, *EVN* extrastriate visual network, *rMOG* right middle occipital gyrus, *aDMN* anterior default mode network, *mSFG* medial superior frontal gyrus, *IFPN* left fronto-parietal network, *ISFG* left superior frontal gyrus, *rFPN* right fronto-parietal network, *rMFG* right middle frontal gyrus

cortex, premotor area, supplementary motor area (SMA), pre-SMA, and cingulate motor area (Wu et al. 2004). These connections are also thought to be involved in acquiring and coordinating motor sequences (Nakano 2000).

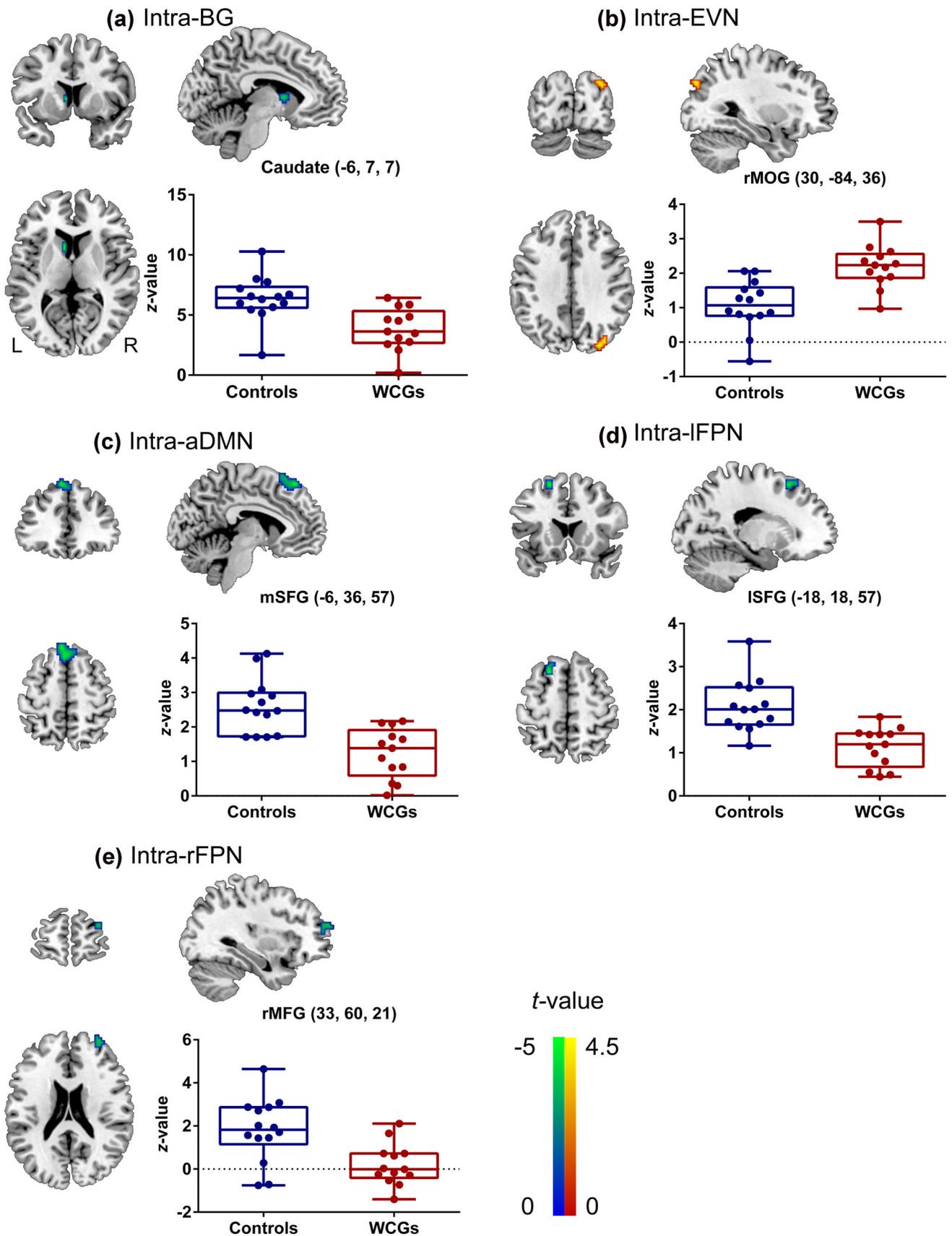


Table 2 Brain clusters with significant between-group difference in intra-network functional connectivity between the WCGs and the controls

RSN contrast	Cluster location	L/R	Location	Cluster size (# voxels)	<i>t</i> value	MNI coordinate		
						<i>x</i>	<i>y</i>	<i>z</i>
IC #5: Basal ganglia network (BG)								
WCGs < controls	Caudate	L	N/A	11	-3.04	-6	7	7
IC #12: Extrastriate visual network (EVN)								
WCGs > controls	Middle occipital gyrus	R	BA 19	24	4.37	30	-84	36
IC #21: anterior default mode network (aDMN)								
WCGs < controls	Medial superior frontal gyri	L/R	BA 8	63	-4.66	-6	36	57
IC #7: left fronto-parietal network (IFPN)								
WCGs < controls	Superior frontal gyrus	L	BA 8	24	-4.54	-18	18	57
IC #9: right fronto-parietal network (rFPN)								
WCGs < controls	Middle frontal gyrus	R	BA 10,46	19	-3.31	33	60	21

The results were corrected for multiple comparisons using cluster-level thresholding at an uncorrected voxelwise $p < 0.01$ and a minimum cluster size threshold to maintain a corrected cluster level $p < 0.05$. The MNI (Montreal Neurological Institute) coordinates correspond to the peak voxels of each cluster

IC # component number derived from the group ICA, BA Brodmann's area, L (R) left (right) hemisphere, WCGs world class gymnasts

Furthermore, the basal ganglia support learning by integrating motor selection with dopaminergic reinforcement. Decreased activity in the basal ganglia associated with extensive training and automaticity has been reported in previous studies (Braunlich and Seger 2013; Walz et al. 2015; Wu et al. 2004), suggesting that the BG may participate the function of shifting a learned performance to the automatic stage. The aDMN is associated with internally oriented thoughts and protecting the execution of long-term mental plans from distraction from immediate environmental demands (Ashby et al. 2010; Burgess et al. 2007; Gusnard and Raichle 2001; Koechlin and Hyafil 2007). Accomplishing a series of precise actions is usually the main goal of gymnasts, especially for WCGs. To achieve it, gymnasts need to maintain as internally oriented thoughts their goal and motor plans appropriate for the routine being performed and avoid distraction. The brain areas encompassed in the FPN have repeatedly been found to be active during external attention tasks and during tasks requiring cognitive control, especially for the coordination and planning of complex motor functions (Cole et al. 2013; Corbetta and Shulman 2002; Rizzolatti and Luppino 2001; Zanto and Gazzaley 2013). Intensive motor skill-training-induced reorganization of the FPN has been reported in several previous studies (Di et al. 2012; Jäncke et al. 2009; Taubert et al. 2011). Decreased activity within the FPN in this study was consistent with our previous works detecting training-induced structural plasticity (Wang et al. 2013a; Huang et al. 2015) and functional plasticity (Wang et al. 2016) in brain regions responsible for motor attention in the WCGs, which may suggest that long-term training may allow gymnasts to perform target behaviors in a more

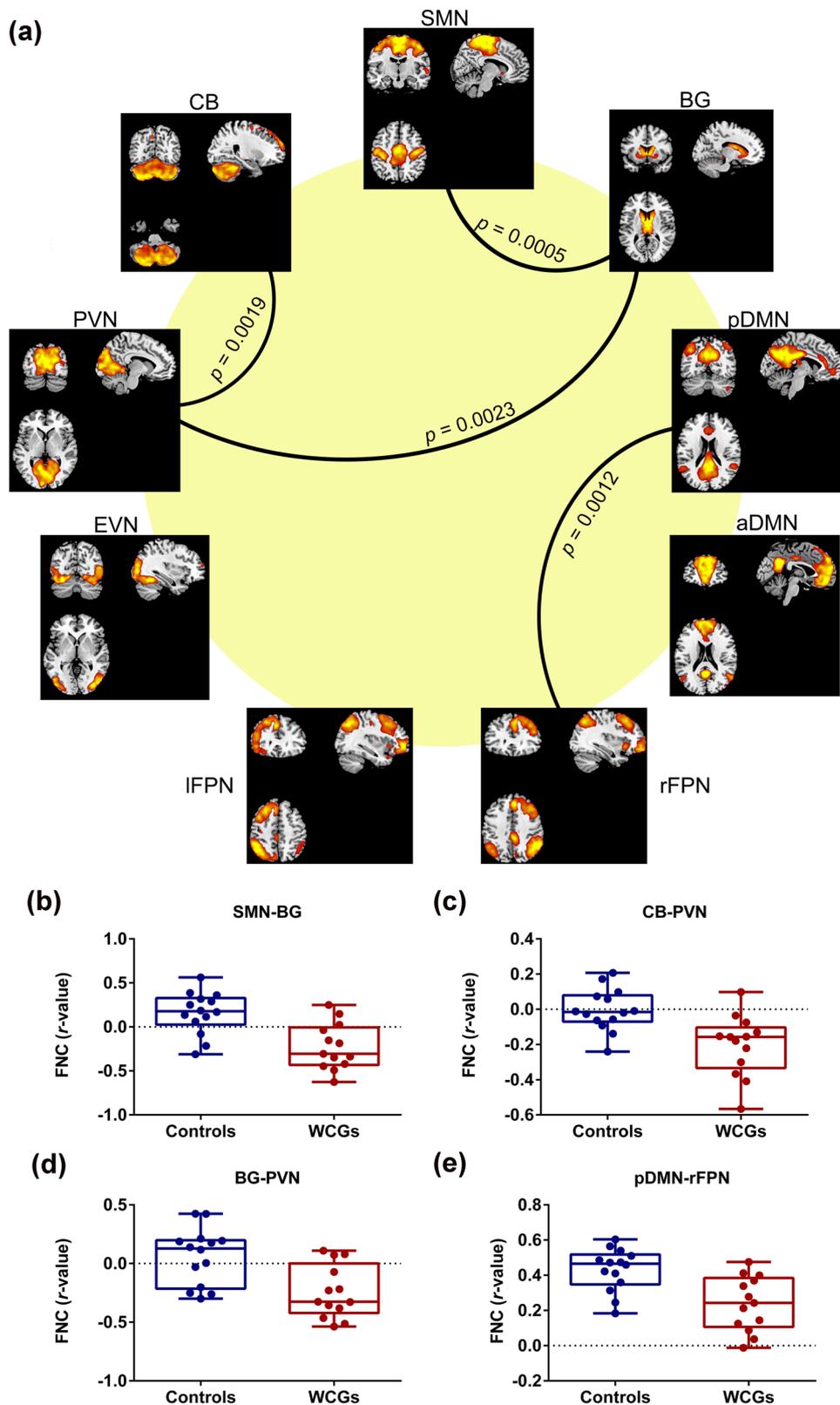
automatic fashion, reducing the need for attentional resources, and leading to the decreased intrinsic brain activity within the FPN.

Based on the results above, we speculate that the decreased intra-network functional connectivity in the WCGs may be due to an increase in their neural efficiency after long-term intensive gymnastic training. Previous studies have suggested that improvement in neural efficiency is related to a reduction in neural activity in specific brain regions as particular skills become more automated and less controlled (Callan and Naito 2014; Debarnot et al. 2014). Specifically, long-term repetitive skill practice can allow athletes to achieve very skilled and precise behaviors with a degree of automation (Doyon and Benali 2005; Wang et al. 2016; Wu et al. 2004). Such automatic behaviors are associated with increased neural efficiency and correspond to a lessening of neuronal resources expenditure (Haslinger et al. 2004; Naito and Hirose 2014; Nakata et al. 2010; Wu et al. 2004).

While a decreased brain response can be interpreted as a sign of enhanced neural efficiency in regional resource utilization, a number of studies have also reported reallocation of neuronal resources based on enhanced activity in some brain regions (Chein and Schneider 2005; Patel et al. 2013). In this study, we found that the intra-network functional connectivity in the EVN was increased in the WCGs compared to the non-athletes. Prior studies have suggested that the EVN is engaged in executing hand movements (Astafiev et al. 2004; Orlov et al. 2010), own-body perception (Heydrich and Blanke 2013), haptically exploring objects (Amedi et al. 2001), and responding to tactile stimulation (Beauchamp et al. 2009). It may be a

Fig. 3 Significant between-group difference in inter-network functional connectivity between the RSNs.

a Significantly correlated RSNs are connected by a *solid black line*. **b–e** Boxplots for the significant pairs as indicated by a two-sample *t* test ($p < 0.05$, FDR corrected). *SMN* sensorimotor network, *CB* cerebellum, *BG* basal ganglia network, *PVN* primary visual network, *EVN* extrastriate visual network, *pDMN* posterior default mode network, *aDMN* anterior default mode network, *IFPN* left fronto-parietal network, *rFPN* right fronto-parietal network



convergence zone of action representation embodying information across visual, haptic, proprioceptive, and motor domains (Weiner and Grill-Spector 2013). Indeed,

gymnastics is a special sport requiring the individual to accomplish a series of complex and elegant movements with the aid of required equipment (e.g., horizontal/parallel

Table 3 Inter-network functional connectivity in the WCGs and the controls

RSN pair: correlation	Controls			WCGs			Two-sample <i>t</i> test	
	<i>r</i> (mean ± SEM)	<i>t</i> value	<i>p</i> value	<i>r</i> (mean ± SEM)	<i>t</i> value	<i>p</i> value	<i>t</i> value	<i>p</i> value
SMN-BG	0.159 ± 0.064	2.320	0.0373	-0.225 ± 0.073	-3.079	0.0096*	3.967	0.0005*
CB-PVN	-0.003 ± 0.032	-0.677	0.510	-0.204 ± 0.048	-4.059	0.0016*	3.461	0.0019*
BG-PVN	0.060 ± 0.064	0.7948	0.441	-0.243 ± 0.063	-3.851	0.0023*	3.397	0.0023*
pDMN-rFPN	0.432 ± 0.032	8.551	1e-06*	0.239 ± 0.043	5.391	0.0002*	3.651	0.0012*

RSN resting-state network, *r* Pearson's correlation coefficient, *SEM* standard error of the mean, *SMN* sensorimotor network, *CB* cerebellum, *BG* basal ganglia network, *PVN* primary visual network, *pDMN* posterior default mode network, *rFPN* right fronto-parietal network, *WCGs* world class gymnasts

* *p* value surviving the false discovery rate (FDR) correction ($p < 0.05$)

bars, pommel horse, balance beam, and still rings), which involve complicated visuo-tactile-proprioceptive-motor interactions. Moreover, previous studies also suggested that attending to a particular location or to a particular object is often accompanied by response enhancement in extrastriate visual cortex as demonstrated in functional imaging and event-related potential studies in human (Baldauf and Desimone 2014; Kastner et al. 1998, 1999; Woldorff et al. 1997). Thus, we speculate that the stronger intrinsic functional connectivity in the EVN may suggest a reallocation of neuronal resources to actively promoting the integration of information across visual, haptic, proprioceptive, and motor domains, allowing gymnasts to make accurate motion response in time during gymnastic performance. However, future studies are needed that employ specific tasks for further verification of our findings.

Inter-network functional connectivity

We found that inter-network functional connectivity between SMN and BG, CB, and PVN, BG and PVN, and pDMN and rFPN was decreased in the WCGs compared to the non-athletes (Fig. 3; Table 3). Specifically, the functional connectivity between SMN and BG, CB and PVN as well as between BG and PVN was independent of the non-athletes, but was negatively correlated with the WCGs. While the neural mechanisms underpinning negative functional connectivity are not fully known, negative correlation in spontaneous neural activity may be related to active decoupling of different functional systems, which may prevent them from interacting with each other under task conditions (Lewis et al. 2009). It may reflect an efficient computational state that prevents two functional systems from interfering with each other and facilitates independent recruitment of each system. Deco et al. (2009) and Chen et al. (2011) argued that negative functional connectivity may result from phase accumulation along the shortest path in brain functional networks.

These results corroborate and extend our previous study indicating the complementary nature of the ICA approach taken in the present paper with the topological analyses in Wang et al. (2016). Our previous study examined functional connectivity during R-fMRI using graph theoretical techniques and found decreased functional connectivity and global and local efficiency overall in the WCGs compared with the controls. Both studies show decreased functional connectivity between cerebellar networks and visual cortex (CB and PVN in the present study, and cerebellum and occipital lobe nodes broadly in Wang et al. 2016). Our previous study did not examine connectivity with the basal ganglia, and therefore, the present results extend our previous results by finding that reduction of functional connectivity between basal ganglia and cortical networks (SMN and PVN) is also characteristic of the gymnasts. Basal ganglia, cerebellum, and motor cortex are the primary neural regions critical for motor skill learning. Previous studies (Doyon and Benali 2005; Hikosaka et al. 2002) have proposed that motor skill learning occurs within two sets of loop circuits, cortex-basal ganglia, and cortex-cerebellum. In this study, we found reductions in functional connectivity not only between BG and motor cortex (SMN), but also between both BG and CB and visual processing regions (PVN). During gymnastic performance, gymnasts need to attend either visual information or self-generated motor actions within a specific motor sequence. In this context, the negative correlations of PVN-CB and PVN-BG may operate to prevent the visual and motor systems from interfering with each other, enabling the gymnasts to flexibly estimate the direction of their movements, the speed of execution, and the identification of their own and surrounding objects' locations during gymnastic performance.

The FPN and DMN are two of the most important cognitive-related functional networks in human brain and the functional interaction between the FPN and DMN has been shown to control executive functions such as working

memory, attention, and cognitive flexibility (Bray et al. 2015; Chadick and Gazzaley 2011; Douw et al. 2016; Fornito et al. 2012; Hearne et al. 2015). Previous studies have found that FPN and DMN are typically anticorrelated across a range of experimental paradigms, reflecting the opposing cognitive functions of the two networks in externally focused task-related activity versus internally focused task-independent activity, respectively (Fox et al. 2005; Sridharan et al. 2008). We found that the WCGs showed decreased functional interaction between the pDMN and the rFPN. During the maintenance phase of working memory process, subjects are focused on the internal representation of the information and need to actively avoid or minimize any external or internal distraction (Piccoli et al. 2015). Therefore, one possible explanation for such weaker interaction in WCGs might be that for successful maintenance of information related to gymnastics skills, it is necessary to keep the FPN functionally separated from the DMN to keep maintenance operations undisturbed by typical internal cognition processes, such as self-awareness (Leech et al. 2011), mind wandering (Mason et al. 2007), and autobiographic memory (Svoboda et al. 2006).

Limitations

Several limitations need to be acknowledged. First, due to limitations in the number of world class gymnasts available to participate in the study, a relatively small sample size (total of 13 WCGs) was achieved, which may limit the statistical power for detecting group differences. Due to the small sample size, it was not possible to examine event-specific subgroups of the WCGs, e.g., those specializing in floor exercise versus those specializing in uneven parallel bars. Although the gymnastic events that each gymnast specialized in differed across the WCGs, their customary training regimes were very similar, other than during periods directly tied to preparation for competition. Second, because this is a cross-sectional study and subjects were not randomly assigned to conditions (e.g., gymnast or control), we cannot rule out the possibility that maturation and/or innate predispositions could have caused or contributed to the differences between the WCGs and the non-athletes. We also cannot rule out effects on brain plasticity due to the possibility of lower level of academic training in the WCGs, although all the subjects had at least high school-level education at the time of this study. Third, there are methodological limitations that are inherent to ICA. The functional components identified by ICA depend on the selection of model order, i.e., the number of meaningful components predetermined to exist in the data set (Abou-Elseoud et al. 2010; Kiviniemi et al. 2009). In this study, we set model order to 30, consistent with many previous

studies (Jafri et al. 2008; Wang et al. 2015). As an exploratory measure, we also tried other model order values, and tried using an automatic dimension estimation algorithm using the minimum description length (MDL) criteria (Li et al. 2007), but both these methods led to suboptimal decomposition in which COI either merged together commonly recognized RSNs or split RSNs into multiple subcomponents. More accurate dimension estimation methods are urgently needed to address this issue to support reliable decomposition across studies. Fourth, we used a correlational approach to measure the temporal synchronization of R-fMRI time series, which does not provide any information about causal relationships between the RSNs. One could also use other dependency measures, such as mutual information, Granger causality, or structural equation modeling techniques in future work to study multiple dependencies among networks in gymnasts versus non-athletes. Several studies have begun to examine the directional connectivity patterns of the RSNs (Jafri et al. 2008; Lewis et al. 2009). However, because of low EPI sampling rate, low signal-to-noise ratio (SNR), and non-neural contributions to temporal fluctuations in connectivity, whether methods that estimate directionality from R-fMRI data can meet criteria of reliability and statistical power is still under debate (Smith et al. 2011). Recent advances in data acquisition protocols, such as ultrahigh speed and ultrahigh field fMRI (Feinberg and Yacoub 2012), may support reliable and accurate directionality estimation in the future. Fifth, different significance thresholds and multiple comparison correction methods were used for intra- and inter-network functional connectivities. Although the multiple comparison correction method used for intra-network functional connectivity in this study, i.e., uncorrected voxelwise $p < 0.01$ together with a cluster size threshold to maintain a corrected threshold at the cluster level of 0.05 has been used for many previous studies (Cha et al. 2016; Cropley et al. 2015; Felger et al. 2016; Kong et al. 2015; Rice et al. 2016), it is not as conservative as that of FDR correction. Thus, we did not claim that the type-I (false positive) error was strongly controlled for these multiple exploratory analyses. In the future, larger sample size is preferred to improve the statistical power for detecting group differences. Sixth, we did not monitor hormonal status of the female subjects. Previous studies have found sex-hormonal effects on the intrinsic functional connectivity of specific cortical networks in women across the menstrual cycle (Filippi et al. 2013; Hjelmervik et al. 2014). However, De Bondt et al. (2015) performed a longitudinal fMRI study and suggested that different hormonal stages of the female menstrual cycle affect brain response in task fMRI, but leave resting-state networks relatively unaffected. Finally, we did not include behavioral measures (e.g., motor skills,

muscle strength, etc.), which may limit the explanatory power of our results. Further studies quantitatively evaluating gymnastic skills should be conducted to draw more definitive general conclusions about how training and expertise related to functional connectivity within and between RSNs.

In conclusion, this study revealed that long-term intensive gymnastic training is associated with reorganization of intrinsic brain functional connectivity both within RSNs and between RSNs. The generally weaker intra- and inter-network functional connectivities of WCGs imply that higher degrees of skill and training may be associated with less, rather than more, functional connectivity within neural networks. Although there are a number of mechanisms that could underlay these patterns of results, one possibility is that gymnasts may have greater efficiency within neural regions related to highly skilled and precise behaviors, which may result in lower resting-state activity and functional connectivity.

Acknowledgements This work was supported by funding from the National Natural Science Foundation of China (Grant numbers: 81371535, 81428013, 81471654, and 81271548).

Compliance with ethical standards

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

References

- Abou-Elseoud A, Starck T, Remes J, Nikkinen J, Tervonen O, Kiviniemi V (2010) The effect of model order selection in group PICA. *Hum Brain Mapp* 31:1207–1216
- Alexander GE, Crutcher MD (1990) Functional architecture of basal ganglia circuits: neural substrates of parallel processing. *Trends Neurosci* 13:266–271
- Amedi A, Malach R, Hendler T, Peled S, Zohary E (2001) Visuo-haptic object-related activation in the ventral visual pathway. *Nat Neurosci* 4:324–330
- Ashby FG, Turner BO, Horvitz JC (2010) Cortical and basal ganglia contributions to habit learning and automaticity. *Trends Cogn Sci* 14:208–215
- Astafiev SV, Stanley CM, Shulman GL, Corbetta M (2004) Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat Neurosci* 7:542–548
- Baldauf D, Desimone R (2014) Neural mechanisms of object-based attention. *Science* 344:424–427
- Beauchamp MS, LaConte S, Yasar N (2009) Distributed representation of single touches in somatosensory and visual cortex. *Hum Brain Mapp* 30:3163–3171
- Beckmann CF, DeLuca M, Devlin JT, Smith SM (2005) Investigations into resting-state connectivity using independent component analysis. *Philos Trans R Soc Lond B Biol Sci* 360:1001–1013
- Bell AJ, Sejnowski TJ (1995) An information-maximization approach to blind separation and blind deconvolution. *Neural Comput* 7:1129–1159
- Bernardi G, Ricciardi E, Sani L, Gaglianese A, Papisogli A, Ceccarelli R, Franzoni F, Galetta F, Santoro G, Goebel R, Pietrini P (2013) How skill expertise shapes the brain functional architecture: an fMRI study of visuo-spatial and motor processing in professional racing-car and naive drivers. *PLoS One* 8(10):e77764
- Braunlich K, Seger C (2013) The basal ganglia. *Wiley Interdiscip Rev Cogn Sci* 4:135–148
- Bray S, Arnold AEGF, Levy RM, Iaria G (2015) Spatial and temporal functional connectivity changes between resting and attentive states. *Hum Brain Mapp* 36:549–565
- Burgess PW, Dumontheil I, Gilbert SJ (2007) The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends Cogn Sci* 11:290–298
- Calhoun V, Adali T, Pearlson G, Pekar J (2001) A method for making group inferences from functional MRI data using independent component analysis. *Hum Brain Mapp* 14:140–151
- Callan DE, Naito E (2014) Neural processes distinguishing elite from expert and novice athletes. *Cogn Behav Neurol* 27:183–188
- Calvert GA, Thesen T (2004) Multisensory integration: methodological approaches and emerging principles in the human brain. *J Physiol Paris* 98:191–205
- Calvo-Merino B, Glaser DE, Grezes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills: an FMRI study with expert dancers. *Cereb Cortex* 15:1243–1249
- Cha J, Ide JS, Bowman FD, Simpson HB, Posner J, Steinglass JE (2016) Abnormal reward circuitry in anorexia nervosa: a longitudinal, multimodal MRI study. *Hum Brain Mapp* 37:3835–3846
- Chadick JZ, Gazzaley A (2011) Differential coupling of visual cortex with default or frontal-parietal network based on goals. *Nat Neurosci* 14:830–832
- Chang Y et al (2011) Neural correlates of motor imagery for elite archers. *NMR Biomed* 24:366–372
- Chao-Gan Y, Yu-Feng Z (2010) DPARSF: a MATLAB toolbox for “pipeline” data analysis of resting-state fMRI. *Front Syst Neurosci* 4:13
- Chein JM, Schneider W (2005) Neuroimaging studies of practice-related change: fMRI and meta-analytic evidence of a domain-general control network for learning. *Cogn Brain Res* 25:607–623
- Chen G, Chen G, Xie C, Li S-J (2011) Negative functional connectivity and its dependence on the shortest path length of positive network in the resting-state human brain. *Brain Connect* 1:195–206
- Cole MW, Reynolds JR, Power JD, Repovs G, Anticevic A, Braver TS (2013) Multi-task connectivity reveals flexible hubs for adaptive task control. *Nat Neurosci* 16:1348–1355
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215
- Cropley VL, Scarr E, Fornito A, Klauser P, Bousman CA, Scott R, Cairns MJ, Tooney PA, Pantelis C, Dean B (2015) The effect of a muscarinic receptor 1 gene variant on grey matter volume in schizophrenia. *Psychiatry Res Neuroimaging* 234:182–187
- Damoiseaux J, Rombouts S, Barkhof F, Scheltens P, Stam C, Smith SM, Beckmann C (2006) Consistent resting-state networks across healthy subjects. *Proc Natl Acad Sci USA* 103:13848–13853
- Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72:443–454
- De Bondt T, Smeets D, Pullens P, Van Hecke W, Jacquemyn Y, Parizel PM (2015) Stability of resting state networks in the female brain during hormonal changes and their relation to premenstrual symptoms. *Brain Res* 1624:275–285
- De Luca M, Beckmann CF, De Stefano N, Matthews PM, Smith SM (2006) fMRI resting state networks define distinct modes of

- long-distance interactions in the human brain. *Neuroimage* 29:1359–1367
- DeBarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: how physical and mental training shape the brain. *Front Hum Neurosci* 8:280
- DeCarlo LT (1998) Signal detection theory and generalized linear models. *Psychol Methods* 3:186
- Deco G, Jirsa V, McIntosh AR, Sporns O, Kötter R (2009) Key role of coupling, delay, and noise in resting brain fluctuations. *Proc Natl Acad Sci USA* 106:10302–10307
- Di X, Zhu S, Jin H, Wang P, Ye Z, Zhou K, Zhuo Y, Rao H (2012) Altered resting brain function and structure in professional badminton players. *Brain Connect* 2:225–233
- Douw L, Wakeman DG, Tanaka N, Liu HS, Stufflebeam SM (2016) State-dependent variability of dynamic functional connectivity between frontoparietal and default networks relates to cognitive flexibility. *Neuroscience* 339:12–21
- Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. *Curr Opin Neurobiol* 15:161–167
- Doyon J, Bellec P, Amsel R, Penhune V, Monchi O, Carrier J, LeHéricy S, Benali H (2009) Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behav Brain Res* 199:61–75
- Egolf EA, Calhoun VD, Kiehl KA (2004) Group ICA of fMRI Toolbox (GIFT). *Biol Psychiatry* 55:842–849
- Feinberg DA, Yacoub E (2012) The rapid development of high speed, resolution and precision in fMRI. *Neuroimage* 62:720–725
- Felger JC, Li Z, Haroon E, Woolwine BJ, Jung MY, Hu X, Miller AH (2016) Inflammation is associated with decreased functional connectivity within corticostriatal reward circuitry in depression. *Mol Psychiatry* 21:1358–1365
- Filippi M, Valsasina P, Misci P, Falini A, Comi G, Rocca MA (2013) The organization of intrinsic brain activity differs between genders: a resting-state fMRI study in a large cohort of young healthy subjects. *Hum Brain Mapp* 34:1330–1343
- Fornito A, Zalesky A, Bullmore ET (2010) Network scaling effects in graph analytic studies of human resting-state FMRI data. *Front Syst Neurosci* 4:22
- Fornito A, Harrison BJ, Zalesky A, Simons JS (2012) Competitive and cooperative dynamics of large-scale brain functional networks supporting recollection. *Proc Natl Acad Sci USA* 109:12788–12793
- Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc Natl Acad Sci USA* 102:9673–9678
- Giacosa C, Karpati FJ, Foster NEV, Penhune VB, Hyde KL (2016) Dance and music training have different effects on white matter diffusivity in sensorimotor pathways. *Neuroimage* 135:273–286
- Greicius MD, Flores BH, Menon V, Glover GH, Solvason HB, Kenna H, Reiss AL, Schatzberg AF (2007) Resting-state functional connectivity in major depression: abnormally increased contributions from subgenual cingulate cortex and thalamus. *Biol Psychiatry* 62:429–437
- Gusnard DA, Raichle ME (2001) Searching for a baseline: functional imaging and the resting human brain. *Nat Rev Neurosci* 2:685–694
- Hänggi J, Koeneke S, Bezzola L, Jancke L (2010) Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. *Hum Brain Mapp* 31:1196–1206
- Hardwick RM, Rottschy C, Miall RC, Eickhoff SB (2013) A quantitative meta-analysis and review of motor learning in the human brain. *Neuroimage* 67:283–297
- Haslinger B, Erhard P, Altenmüller E, Hennenlotter A, Schwaiger M, Gräfin von Einsiedel H, Rummeny E, Conrad B, Ceballos-Baumann AO (2004) Reduced recruitment of motor association areas during bimanual coordination in concert pianists. *Hum Brain Mapp* 22:206–215
- Hearne L, Cocchi L, Zalesky A, Mattingley JB (2015) Interactions between default mode and control networks as a function of increasing cognitive reasoning complexity. *Hum Brain Mapp* 36:2719–2731
- Heydrich L, Blanke O (2013) Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain* 136:790–803
- Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. *Curr Opin Neurobiol* 12:217–222
- Himberg J, Hyvärinen A, Esposito F (2004) Validating the independent components of neuroimaging time series via clustering and visualization. *Neuroimage* 22:1214–1222
- Hjelmervik H, Hausmann M, Osnes B, Westerhausen R, Specht K (2014) Resting states are resting traits—an fMRI study of sex differences and menstrual cycle effects in resting state cognitive control networks. *PLoS One* 9:e103492
- Huang R, Lu M, Song Z, Wang J (2015) Long-term intensive training induced brain structural changes in world class gymnasts. *Brain Struct Funct* 220:625–644
- Huang H, Ding Z, Mao D, Yuan J, Zhu F, Chen S, Xu Y, Lou L, Feng X, Qi L, Qiu W, Zhang H, Zang YF (2016) PreSurgMapp: a MATLAB toolbox for presurgical mapping of eloquent functional areas based on task-related and resting-state functional MRI. *Neuroinformatics* 14:421–438
- Jafri MJ, Pearlson GD, Stevens M, Calhoun VD (2008) A method for functional network connectivity among spatially independent resting-state components in schizophrenia. *Neuroimage* 39:1666–1681
- Jäncke L, Koeneke S, Hoppe A, Rominger C, Hänggi J (2009) The architecture of the golfer’s brain. *PLoS One* 4:e4785
- Kastner S, De Weerd P, Desimone R, Ungerleider LC (1998) Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science* 282:108–111
- Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22:751–761
- Kim J, Lee HM, Kim WJ, Park HJ, Kim SW, Moon DH, Woo M, Tennant LK (2008) Neural correlates of pre-performance routines in expert and novice archers. *Neurosci Lett* 445:236–241
- Kim W, Chang Y, Kim J, Seo J, Ryu K, Lee E, Woo M, Janelle CM (2014) An fMRI study of differences in brain activity among elite, expert, and novice archers at the moment of optimal aiming. *Cogn Behav Neurol* 27:173–182
- Kiviniemi V, Starck T, Remes J, Long X, Nikkinen J, Haapea M, Veijola J, Moilanen I, Isohanni M, Zang YF, Tervonen O (2009) Functional segmentation of the brain cortex using high model order group PICA. *Hum Brain Mapp* 30:3865–3886
- Koechlin E, Hyafil A (2007) Anterior prefrontal function and the limits of human decision-making. *Science* 318:594–598
- Kong F, Hu SY, Wang X, Song YY, Liu J (2015) Neural correlates of the happy life: the amplitude of spontaneous low frequency fluctuations predicts subjective well-being. *Neuroimage* 107:136–145
- Leech R, Kamourieh S, Beckmann CF, Sharp DJ (2011) Fractionating the default mode network: distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *J Neurosci* 31:3217–3224
- Lewis CM, Baldassarre A, Committeri G, Romani GL, Corbetta M (2009) Learning sculpts the spontaneous activity of the resting human brain. *Proc Natl Acad Sci USA* 106:17558–17563
- Li YO, Adali T, Calhoun VD (2007) Estimating the number of independent components for functional magnetic resonance imaging data. *Hum Brain Mapp* 28:1251–1266

- Liang X, Wang J, Yan C, Shu N, Xu K, Gong G, He Y (2012) Effects of different correlation metrics and preprocessing factors on small-world brain functional networks: a resting-state functional MRI study. *PLoS One* 7:e32766
- Mason MF, Norton MI, Van Horn JD, Wegner DM, Grafton ST, Macrae CN (2007) Wandering minds: the default network and stimulus-independent thought. *Science* 315:393–395
- McKeown MJ, Makeig S, Brown GG, Jung TP, Kindermann SS, Bell AJ, Sejnowski TJ (1998) Analysis of fMRI data by blind separation into independent spatial components. *Hum Brain Mapp* 6:160–188
- Naito E, Hirose S (2014) Efficient foot motor control by Neymar's brain. *Front Hum Neurosci* 8:594
- Nakano K (2000) Neural circuits and topographic organization of the basal ganglia and related regions. *Brain Dev* 22:5–16
- Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: evidence from neurophysiology and neuroimaging. *Brain Res Rev* 62:197–211
- Nielsen JB, Cohen LG (2008) The Olympic brain. Does corticospinal plasticity play a role in acquisition of skills required for high-performance sports? *J Physiol* 586:65–70
- Orlov T, Makin TR, Zohary E (2010) Topographic representation of the human body in the occipitotemporal cortex. *Neuron* 68:586–600
- Paola M, Caltagirone C, Petrosini L (2013) Prolonged rock climbing activity induces structural changes in cerebellum and parietal lobe. *Hum Brain Mapp* 34:2707–2714
- Park IS, Lee KJ, Han JW, Lee NJ, Lee WT, Park KA, Rhyu IJ (2009) Experience-dependent plasticity of cerebellar vermis in basketball players. *Cerebellum* 8:334
- Park IS, Lee YN, Kwon S, Lee NJ, Rhyu IJ (2015) White matter plasticity in the cerebellum of elite basketball athletes. *Anat Cell Biol* 48:262–267
- Patel R, Spreng RN, Turner GR (2013) Functional brain changes following cognitive and motor skills training: a quantitative meta-analysis. *Neurorehabil Neural Repair* 27:187–199
- Piccoli T, Valente G, Linden DEJ, Re M, Esposito F, Sack AT, Di Salle F (2015) The default mode network and the working memory network are not anti-correlated during all phases of a working memory task. *PLoS One* 10(4):e0123354
- Raichlen DA, Bharadwaj PK, Fitzhugh MC, Haws KA, Torre G-A, Trouard TP, Alexander GE (2016) Differences in resting state functional connectivity between young adult endurance athletes and healthy controls. *Front Hum Neurosci* 10:610
- Rice K, Moraczewski D, Redcay E (2016) Perceived live interaction modulates the developing social brain. *Soc Cogn Affect Neurosci* 11:1354–1362
- Rizzolatti G, Luppino G (2001) The cortical motor system. *Neuron* 31:889–901
- Seeley WW, Crawford RK, Zhou J, Miller BL, Greicius MD (2009) Neurodegenerative diseases target large-scale human brain networks. *Neuron* 62:42–52
- Shirer W, Ryali S, Rykhlevskaia E, Menon V, Greicius M (2012) Decoding subject-driven cognitive states with whole-brain connectivity patterns. *Cereb Cortex* 22:158–165
- Smith SM, Fox PT, Miller KL, Glahn DC, Fox PM, Mackay CE, Filippini N, Watkins KE, Toro R, Laird AR, Beckmann CF (2009) Correspondence of the brain's functional architecture during activation and rest. *Proc Natl Acad Sci USA* 106:13040–13045
- Smith SM, Miller KL, Salimi-Khorshidi G, Webster M, Beckmann CF, Nichols TE, Ramsey JD, Woolrich MW (2011) Network modelling methods for FMRI. *Neuroimage* 54:875–891
- Sridharan D, Levitin DJ, Menon V (2008) A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proc Natl Acad Sci USA* 105:12569–12574
- Stein BE, Stanford TR (2008) Multisensory integration: current issues from the perspective of the single neuron. *Nat Rev Neurosci* 9:255–266
- Svoboda E, McKinnon MC, Levine B (2006) The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia* 44:2189–2208
- Taubert M, Lohmann G, Margulies DS, Villringer A, Ragert P (2011) Long-term effects of motor training on resting-state networks and underlying brain structure. *Neuroimage* 57:1492–1498
- Walz A, Doppl K, Kaza E, Roschka S, Platz T, Lotze M (2015) Changes in cortical, cerebellar and basal ganglia representation after comprehensive long term unilateral hand motor training. *Behav Brain Res* 278:393–403
- Wang J, Wang L, Zang Y, Yang H, Tang H, Gong Q, Chen Z, Zhu C, He Y (2009) Parcellation-dependent small-world brain functional networks: a resting-state fMRI study. *Hum Brain Mapp* 30:1511–1523
- Wang J-H, Zuo X-N, Gohel S, Milham MP, Biswal BB, He Y (2011) Graph theoretical analysis of functional brain networks: test-retest evaluation on short- and long-term resting-state functional MRI data. *PLoS One* 6:e21976
- Wang B, Fan Y, Lu M, Li S, Song Z, Peng X, Zhang R, Lin Q, He Y, Wang J (2013a) Brain anatomical networks in world class gymnasts: a DTI tractography study. *Neuroimage* 65:476–487
- Wang JH, Zuo XN, Dai ZJ, Xia MR, Zhao ZL, Zhao XL, Jia JP, Han Y, He Y (2013b) Disrupted functional brain connectome in individuals at risk for Alzheimer's disease. *Biol Psychiatry* 73:472–481
- Wang L, Liu Q, Shen H, Li H, Hu D (2015) Large-scale functional brain network changes in taxi drivers: evidence from resting-state fMRI. *Hum Brain Mapp* 36:862–871
- Wang J, Lu M, Fan Y, Wen X, Zhang R, Wang B, Ma Q, Song Z, He Y, Wang J, Huang R (2016) Exploring brain functional plasticity in world class gymnasts: a network analysis. *Brain Struct Funct* 221:3503–3519
- Weiner KS, Grill-Spector K (2013) Neural representations of faces and limbs neighbor in human high-level visual cortex: evidence for a new organization principle. *Psychol Res* 77:74–97
- Woldorff MG, Fox PT, Matzke M, Lancaster JL, Veeraswamy S, Zamarripa F, Seabolt M, Glass T, Gao JH, Martin CC, Jerabek P (1997) Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. *Hum Brain Mapp* 5:280–286
- Wu T, Kansaku K, Hallett M (2004) How self-initiated memorized movements become automatic: a functional MRI study. *J Neurophysiol* 91:1690–1698
- Zanto TP, Gazzaley A (2013) Fronto-parietal network: flexible hub of cognitive control. *Trends Cogn Sci* 17:602–603
- Zhang H, Jia W, Liao W, Zang Y (2013) Automatic component identification method based on normalized sensitivity/specificity measurement. In: Annual meeting of Organization of Hum Brain Mapping (OHBM), Seattle
- Zuo X-N, Xing X-X (2014) Test-retest reliabilities of resting-state FMRI measurements in human brain functional connectomics: a systems neuroscience perspective. *Neurosci Biobehav Rev* 45:100–118
- Zuo X-N, Kelly C, Adelstein JS, Klein DF, Castellanos FX, Milham MP (2010) Reliable intrinsic connectivity networks: test-retest evaluation using ICA and dual regression approach. *Neuroimage* 49:2163–2177
- Zuo XN et al (2014) An open science resource for establishing reliability and reproducibility in functional connectomics. *Sci Data* 1:140049