



Dissociable plasticity of visual-motor system in functional specialization and flexibility in expert table tennis players

Dazhi Yin¹ · Xuefei Wang² · Xiaoyou Zhang³ · Qiurong Yu² · Yu Wei² · Qing Cai¹ · Mingxia Fan² · Lin Li³

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Abstract

Specialization and flexibility are two basic attributes of functional brain organization, enabling efficient cognition and behavior. However, it is largely unknown what plastic changes in specialization and flexibility in visual-motor areas occur in support of extraordinary motor skills in expert athletes and how the selective adaptability of the visual-motor system affects general perceptual or cognitive domains. Here, we used a dynamic network framework to investigate intrinsic functional specialization and flexibility of visual-motor system in expert table tennis players (TTP). Our results showed that sensorimotor areas increased intrinsic functional flexibility, whereas visual areas increased intrinsic functional specialization in expert TTP compared to nonathletes. Moreover, the flexibility of the left putamen was positively correlated with skill level, and that of the left lingual gyrus was positively correlated with behavioral accuracy of a sport-unrelated attention task. This study has uncovered dissociable plasticity of the visual-motor system and their predictions of individual differences in skill level and general attention processing. Furthermore, our time-resolved analytic approach is applicable across other professional athletes for understanding their brain plasticity and superior behavior.

Keywords Brain plasticity · Expert athletes · Functional flexibility · Functional MRI · Functional specialization · Visual-motor system

Introduction

An important question in cognitive neuroscience is how the functional organization of the human brain gives rise to adaptive behavior (Dehaene et al. 1998; Miller and

Cohen 2001). One influential assumption is that the brain is optimally organized with two fundamental principles: functional specialization (segregation) and integration (flexibility) (Friston et al. 1993; Tononi et al. 1994). Brain regions that respond selectively to specific kinds of information content are described as functionally specialized (e.g., visual cortex (Kanwisher et al. 1997)), whereas those that respond to a broad range of task demands are considered functionally diverse (Anderson et al. 2013) or flexible (Yeo et al. 2015) (e.g., association cortex). From a network perspective, the attributes of segregation and integration are usually represented by communities and hubs, respectively, that is, each community constituted by a set of areas acts as a specific function (e.g., sensory processing, motor control, and attention) and the hub areas link communities to one another ensure efficient information integration (Sporns 2013). However, this segregation and integration do not provide the information about how brain processes internal thoughts and external inputs dynamically. In recent years, emerging studies emphasize that the brain is a dynamic complex system, constantly reconfigured in response to changing internal thoughts and

✉ Dazhi Yin
dzyin@psy.ecnu.edu.cn

✉ Mingxia Fan
mxfan@phy.ecnu.edu.cn

✉ Lin Li
lilin.xtt@163.com

- ¹ Key Laboratory of Brain Functional Genomics (Ministry of Education and Shanghai), School of Psychology and Cognitive Science, East China Normal University, Shanghai 200062, China
- ² Shanghai Key Laboratory of Magnetic Resonance, School of Physics and Electronic Science, East China Normal University, Shanghai 200062, China
- ³ Key Laboratory of Adolescent Health Assessment and Exercise Intervention of Ministry of Education, College of Physical Education and Health, East China Normal University, Shanghai 200062, China

external environments (Calhoun et al. 2014; Shine et al. 2019; Deco et al. 2013; Vidaurre et al. 2017). Accordingly, several studies have demonstrated that functional specialization and flexibility of brain regions are embodied by their dynamic connectivity patterns in both task-driven (Cole et al. 2013; Braun et al. 2015) and resting (intrinsic) states (Yin et al. 2016, 2019; Zhang et al. 2016; Chen et al. 2016; Pedersen et al. 2018). Hence, exploring the plasticity of functional specialization and flexibility from a dynamic framework may offer new insights into brain-behavior relationships.

Human skill learning is a complex phenomenon that can reshape functional brain organization to adopt a new behavior (Ajemian et al. 2013; Bassett and Mattar 2017). In laboratory studies with simple motor tasks (e.g., finger sequence learning), extensive neuroimaging research has demonstrated that multiple brain areas participate in motor skill learning, including sensory, motor and association areas (Doyon et al. 2009; Hardwick et al. 2013). However, the recruitment of specific neuronal circuits is dependent on the stage of motor learning: usually experience moves from slow and challenging to fast and automatic. The early phase needs to recruit widely distributed association cortices such as frontal and parietal areas. In contrast, the later phase predominantly activates primary sensorimotor and subcortical areas (e.g., putamen) (Floyer-Lea and Matthews 2005; Dayan and Cohen 2011). Beyond the changing local activation pattern, brain connectivity modulated by motor learning has also been reported (Sun et al. 2007; Tzvi et al. 2015; Coynel et al. 2010). From a dynamic network framework, recent studies have revealed that network flexibility (Bassett et al. 2011), network switching (Telesford et al. 2017) and state flexibility (Reddy et al. 2018) enable predicting the performance during motor learning. Particularly, a decrease in integration between motor and visual modules has been observed over the course of training, suggesting learning-induced autonomy of sensorimotor systems (Bassett et al. 2015). These studies have greatly advanced understanding of functional reconfiguration in response to task performance over the course of skill acquisition. Based on resting-state fMRI (functional magnetic resonance imaging), an influential study has demonstrated that motor learning can modulate subsequent resting brain activity (Albert et al. 2009), which is recognized to play a vital contribution to the offline processing of motor skills and consolidation of memories (Miall and Robertson 2006; Ma et al. 2011). However, to what extent the neural substrates supporting the simple, laboratory-based skills can explain organizational properties of long-term, training-induced, real-world, complex skills is far from clear. Moreover, for the laboratory-based simple motor learning, few studies focus on the effects of learning-induced brain plasticity on general cognitive domains such as attention.

Alternative studies have focused on extraordinary motor skills in expert athletes. The athlete's brain offers a good model for studying neuroplasticity because athletes participate in long-term training and practice, often starting very early in childhood (Nakata et al. 2010). Through this long-term intensive training, they acquire excellent abilities in quick stimulus discrimination, decision making, and specific attention. Considering that the investigation of complex, whole-body motor performance (such as playing table tennis) in the functional imaging scanners is impossible so far, researchers prefer to explore the long-term training induced neuroplasticity in expert athletes by resting-state fMRI, which has been widely used to examine intrinsic functional organization. Specifically, a number of studies have found plastic changes of resting-state functional connectivity patterns in many kinds of professional athletes, including golfers (Kim et al. 2015), basketball players (Tan et al. 2016), badminton players (Di et al. 2012), and gymnasts (Huang et al. 2018). In addition to exploring the plasticity of resting-state functional networks, some studies have examined the effects of long-term sport training on task-related brain activation (Yang 2015). For example, distinct brain activation has been observed between expert and novice archers at the moment of optimal aiming (Kim et al. 2014), between skilled golfers and novices during motor planning (Milton et al. 2007), between divers and novices during professional skill imagery (Wei and Luo 2010), and between expert athletes and nonexperts during sport-related anticipation such as badminton (Wright et al. 2010), tennis (Balser et al. 2014) and table tennis (Wang et al. 2019). Though the differences in activation patterns are task-dependent, the consistent finding is that experts have less whole-brain activity but greater activity in those areas needed for specialized processing. The convergent evidence suggests that the adaptive enhancement of sport-specific processing underpins superior performance in elite athletes. However, the influence of long-term, domain-specific training on general perceptual or cognitive domains is mixed (Yarrow et al. 2009; Overney et al. 2008; Voss et al. 2010). Moreover, although resting-state fMRI has been used to examine the neuroplasticity for different kinds of expert athletes, previous studies mainly focus on static brain connectivity or network. Few studies have investigated the neuroplasticity of professional athletes from the view of dynamical functional organization.

In considering a highly reactive sport such as table tennis, experts show extremely high visuomotor efficiency characterized by automaticity, speed, and accuracy (Wolf et al. 2014). This behavioral efficiency is achieved by long-term training and attributed to highly developed strategies in visual attention and motor domains (Hung et al. 2004). For example, through estimation of eye movements, previous study has demonstrated that the table tennis experts show more selective attention to some interest areas (e.g.,

hand-racket area) compared to novices (Piras et al. 2019). This behavioral evidence emphasizes experts' skill to extract information from the kinematics of relevant body areas and equipment during the action observation of opponents (Smith 2016). The neural substrate of the ability in understanding the intentions and to predict future movements of opponents in the interceptive sports, is largely amenable to the mirror neuron theory (Wang et al. 2019), which is an influential instantiation of embodied cognition (Caramazza et al. 2014). In essence, the anticipation of action effects in experts reflects a more fine-tuned motor representation acquired and improved during years of training (Balser et al. 2014). Accordingly, accumulating evidence indicates that the plasticity of sensory and motor systems plays a fundamental role in reaching excellent spatiotemporal information processing during motor learning (Ostry and Gribble 2016). Therefore, we mainly focus on two questions in the current study: (1) what plastic changes in dynamics of intrinsic functional interaction between visual-motor areas and other brain regions occur in expert table tennis players (TTP) due to long-term skill training, and (2) how the selective adaptability of the visual-motor system affects general attention processing.

To address these issues, we employ both resting-state and task-based fMRI to probe intrinsic and stimulus-evoked brain activity in TTP and nonathletes. Previous modelling studies using complexity measures have suggested that the brain is a dynamic system in terms of a balance between functional segregation and integration even without extrinsic inputs (Tononi et al. 1994; Zamora-Lopez et al. 2011). Accordingly, we adopt our recently established method (Yin et al. 2016, 2019) to describe plastic changes of intrinsic functional specialization and flexibility in the visual-motor areas of TTP. This novel approach is beneficial in that it shows regional specialization and flexibility using dynamical, resting-state functional connectivity. Briefly, if a region shows heterogeneous connectivity with other regions over time, it is thought to be functionally flexible, and vice versa. To quantify this flexibility, a complexity measure (Shannon entropy) is used to assess the heterogeneity of time-varying connectivity patterns of a region. Entropy, most commonly describing a state of disorder or uncertainty, herein characterizes the heterogeneity of dynamic connectivity patterns. Thus, a region with high entropy is indicative of functionally flexible. Conversely, a region with low entropy means functionally specialized.

Furthermore, a classic attention task, i.e., Flanker paradigm (Eriksen and Eriksen 1974), is performed while subjects undergo fMRI scanning. The Flanker task involves both selective attention and attentional inhibition (or conflict processes). Attention processes not only play a crucial role in supporting highly rapid response for TTP, but also are basis of many other cognitive control processes. Although another

well-known attention task, Posner's cued attention paradigm (1980), has been selected to assess the ability of spatial stimulus detection for TTP (Hung et al. 2004), the paradigm contains essential elements of highly reactive sports, such as fast responses to miscues and uncertainty about spatial location. In contrast, the Flanker paradigm, not involving core elements of sports, might be more suitable for exploring the effects of long-term sport training induced neuroplasticity on general attention processes. We hypothesize that expert TTP exhibit plastic changes of intrinsic functional specialization and flexibility in the visual-motor system compared with nonathletes. Moreover, the selective adaptability of the visual-motor system, particularly visual areas, may affect the general attention processing in TTP.

Materials and methods

Participants

We recruited 19 high-level TTP (age = 19.8 ± 1.2 years; 17 males; right-hand players) and 19 nonathletes as the controls who had no professional training in any sports (age = 19.8 ± 1.4 years; 12 males; right handedness). All subjects were college students. The TTP are all national level 1 or 2 (level 1 is the highest) and have long-term training (10.5 ± 2.6 years). The national skill level is evaluated based on their results in official competitions. Table 1 lists the detailed demographics for TTP. All participants had normal or corrected-to-normal vision. None of the participants had a history of neurological or psychiatric disorders or brain injury or substance abuse. No statistical methods were used to predetermine sample sizes, but our sample sizes were similar to those reported in previous publications on expert athletes (Kim et al. 2015; Di et al. 2012; Huang et al. 2018; Balser et al. 2014; Wang et al. 2019). The study was approved by the ethics committee of East China Normal University. Informed consent was obtained from all subjects.

Experimental paradigm

During the resting-state fMRI scans, participants were instructed to stay awake but relaxed, with their eyes closed, remain motionless, and allowed their thoughts to flow freely but not to think about anything in particular. For the task-based fMRI scans, participants were instructed to perform an attention task with an event-related design. To examine general attention, we used a classic Flanker paradigm (Eriksen and Eriksen 1974), which involves both selective attention and conflict inhibition. In this paradigm, congruent and incongruent flankers were presented on either side of a target (central) stimulus (i.e., < < < < < and > > > > > are congruent stimuli; < < >

Table 1 Demographic information for the expert table tennis players (TTP)

ID	Age	Sex	Available fMRI data	Years of training	Grade
TTP001	18	M	r-fMRI; t-fMRI	10	2
TTP002	20	M	r-fMRI; t-fMRI	10	2
TTP003	22	F	r-fMRI; t-fMRI	8	2
TTP004	19	M	r-fMRI	5	2
TTP005	18	M	r-fMRI; t-fMRI	12	1
TTP006	19	M	r-fMRI; t-fMRI	4	2
TTP007	22	F	r-fMRI; t-fMRI	12	1
TTP008	21	M	r-fMRI; t-fMRI	9	2
TTP009	20	M	r-fMRI; t-fMRI	12	2
TTP010	19	M	r-fMRI; t-fMRI	10	2
TTP011	19	M	r-fMRI; t-fMRI	14	2
TTP012	21	M	r-fMRI; t-fMRI	12	2
TTP013	21	M	r-fMRI; t-fMRI	13	2
TTP014	19	M	r-fMRI; t-fMRI	10	2
TTP015	19	M	r-fMRI	11	1
TTP016	20	M	r-fMRI; t-fMRI	13	2
TTP017	19	M	r-fMRI	11	2
TTP018	22	M	r-fMRI; t-fMRI	12	1
TTP019	19	M	r-fMRI; t-fMRI	12	1

Grade 1 is the national highest level

M male, *F* female, *fMRI* functional magnetic resonance imaging, *r* resting-state, *t* task-based

< < and > > < > > are incongruent stimuli). For each trial, participants were presented with a 300-ms fixation cross, which was followed by an 800-ms stimulus. Then, subjects were asked to respond to the orientation of the central arrow by pressing a button with their right index finger if the arrow pointed to the left and with their right middle finger if the arrow pointed to the right. The ISIs (i.e., 2900, 4900, 6900, 8900, and 10,900 ms) were set in a pseudorandom manner. A total of 60 trials were used with each stimulus category (four categories in total) appearing 15 times. The average time for each trial is 8 s, and thus the entire session lasts for 480 s. The presentation of visual stimuli and the recording of behavioral data (i.e., performance accuracy and reaction time) were performed with E-prime software (Psychology Software Tools, Inc. Pittsburgh, PA, USA).

To ensure a sufficiently large number of correct trials, participants (three TTP and one control subjects) with poor task performance (correct rate < 70% for congruent and/or incongruent trials) were excluded from subsequent imaging analysis (Yin et al. 2017). In addition, four control subjects failed to complete the task-based fMRI experiment. Thus, while 19 TTP and 19 nonathletes have available resting-state fMRI data, 16 TTP and 14 nonathletes were included in the final task-based fMRI analysis.

MRI data acquisition and scanning protocol

All the imaging data were collected on a Siemens Trio 3.0 Tesla MRI scanner (Siemens, Erlangen, Germany) at the Shanghai Key Laboratory of Magnetic Resonance, East China Normal University. Resting-state fMRI scans of the whole brain were acquired using a T2*-weighted echo planar imaging (EPI) sequence: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, 32 axial slices, slice thickness = 3.5 mm, gap = 0.8 mm, flip angle = 90°, field of view (FOV) = 192 × 192 mm², voxel size = 3.0 × 3.0 × 3.5 mm³, and 240 volumes. Task-based fMRI scans were also acquired using a T2*-weighted EPI sequence: TR = 2000 ms, TE = 30 ms, 32 axial slices, slice thickness = 3.5 mm, gap = 0.8 mm, flip angle = 90°, FOV = 192 × 192 mm², voxel size = 3.0 × 3.0 × 3.5 mm³, and 240 volumes (8 min in total, match with the time duration of task paradigm). High-resolution T1-weighted images were obtained in a sagittal orientation employing a MPRAGE (magnetization prepared rapid gradient echo) sequence: TR = 2530 ms, TE = 2.34 ms, 192 slices, slice thickness = 3.5 mm, flip angle = 7°, inversion time = 1100 ms, FOV = 256 × 224 mm², and voxel size = 1.0 × 1.0 × 1.0 mm³.

Resting-state fMRI data preprocessing

We performed preprocessing of the resting-state fMRI data using Statistical Parametric Mapping 8 (SPM8; <http://www.fil.ion.ucl.ac.uk/spm>) and Data Processing Assistant for Resting-State fMRI (DPARSF) (Chao-Gan and Yu-Feng 2010) implemented in Matlab (Math Works, Natick, MA, USA). The first 10 volumes were discarded for signal equilibrium and to allow participants to adapt to the scanning environment, leaving 230 volumes for further analysis. The remaining data were corrected for the acquisition time differences between slices, followed by correction of head movement between scans. The corrected functional scans were further normalized to a standard Montreal Neurological Institute (MNI) space and resampled to 3-mm isotropic voxels. Then, spatial smoothing was conducted using an isotropic Gaussian kernel of 6 mm full width at half-maximum. Subsequently, the blood oxygenation level dependent (BOLD) signal of each voxel was detrended to remove linear trends and then passed through a bandpass filter (0.01–0.08 Hz) to reduce low-frequency drift and high-frequency physiological noise (Biswal et al. 1995; Lowe et al. 1998). Finally, several nuisance covariates were regressed out, including head-motion parameters, cerebrospinal signal, white matter signal, and global mean signal (Zhang et al. 2016; Liao et al. 2017). The resulting time courses were extracted for each brain region by averaging the signals of all voxels within that region.

Notably, the criteria for excessive head motion used in this study were translation > 2 mm or rotation $> 2^\circ$ in any direction (Huang et al. 2018). However, no subjects exceeded these criteria, and none were excluded. To further consider the possible contaminating effects of micro head motion on intrinsic functional connectivity networks (Power et al. 2012; Dijk et al. 2012; Yan et al. 2013), the mean head motion was calculated separately for each participant as the averaged root mean square of the three translations and three rotations and treated as a covariate in the following statistical analysis (Yin et al. 2016; Hutchison and Morton 2015). In addition, no consensus has been reached with respect to the removal of the global signal when calculating functional connectivity. Global signal removal has been shown to reduce physiological noise and movement-related effects (Yan et al. 2013; Fox et al. 2009; Birn et al. 2006), but it may also increase the number of negative correlations (Saad et al. 2012). Recently, Zhang and colleagues demonstrated that variability in dynamic functional connectivity profiles is highly correlated whether or not the global signal was removed (2016). Therefore, we consequently adopted the strategy of removing the global signal following the recent studies on dynamic functional connectivity analysis (Zhang et al. 2016; Liao et al. 2017) and validated our main findings without removal of the global signal.

Construction of dynamic functional networks

We employed a widely used sliding window approach to construct dynamic functional networks (Hutchison et al. 2013; Keilholz et al. 2017). Briefly, we first divided the human brain into 90 sections according to the frequently used Automated Anatomical Labeling (AAL) template (Tzourio-Mazoyer et al. 2002). The definition and abbreviation of each area are listed in Supplementary Table 1. Though the consistency has been demonstrated using different brain atlases (both functional and structural) in our prior methodological work (Yin et al. 2016, 2019), we also replicated our main results using another Harvard–Oxford atlas (HOA) with 112 regions, which has been used in some previous studies related to motor skill learning (Bassett et al. 2011, 2015; Reddy et al. 2018). Notably, because of the limited FOV size in the z -dimension, cerebellar regions had to be partially omitted to ensure sufficient coverage of the cerebrum, and, therefore, were not included in the analysis. Then, we used a tapered window created by convolving a rectangle (width = 22 TRs = 44 s) with a Gaussian curve ($\sigma = 3$ TRs) and slid in steps of 1 TR (Yin et al. 2016; Allen et al. 2014), resulting in $W = 208$ windows in total. However, so far, there is no universally accepted criterion for window selection. Therefore, a larger window length (i.e., 100 s) (Liao et al. 2017) was also applied for validation of our main findings. For each time window, Pearson's correlation

coefficients between the mean time courses of any pair of regions were calculated, and a symmetric connectivity matrix (90×90 for AAL atlas or 112×112 for HOA) was generated. Finally, Fisher's Z -transformation was applied to the connectivity matrix so that their distributions could better satisfy normality.

$$Z = \frac{1}{2} \log \left(\frac{1+r}{1-r} \right)$$

Here, r is the Pearson's correlation coefficient. Thus, dynamic functional connectivity matrices were obtained for each participant.

Mapping intrinsic functional flexibility of the brain

Based on the dynamic functional connectivity matrices of each subject, we computed the normalized probability distribution $P_i(j)$ for a given brain region i as follows:

$$P_i = \frac{n(c_{ij})}{k \times w}, j = 1, 2, \dots, N, \text{ and } j \neq i$$

where $n(c_{ij})$ denotes how many times the connection between i and j emerged across temporal windows, k is a predefined threshold indicating the number of the strongest connections reserved for region i at each time window, and w denotes the number of temporal windows. $P_i(j)$ denotes the probability of occurrence for the connection between regions i and j across all temporal windows. The greater the value of $P_i(j)$, the more frequent the interaction between region i and j across the temporal windows and vice versa. Regarding the k threshold, we have justified the choice of $k = 3$ for both human and monkey datasets in our previous studies (Yin et al. 2016, 2019). We, therefore, used the same threshold $k = 3$ for the current study.

Subsequently, a complexity measure H_i (i.e., Shannon entropy) was applied to the probability distribution of each brain region i :

$$H_i = - \sum_{j=1}^N P_i(j) \times \log_2 P_i(j)$$

Here, H_i was used to quantify functional flexibility, which characterizes heterogeneous connectivity between region i and others over time. A high value of H_i indicates functionally flexible, and a low H_i indicates functionally specialized (Fig. 1). To further confirm the reliability of the method, we calculated the mean brain maps of intrinsic functional flexibility for both TTP and controls as a general comparison with our previous findings (Yin et al. 2016, 2019) and a result from the temporal variability method (Zhang et al. 2016).

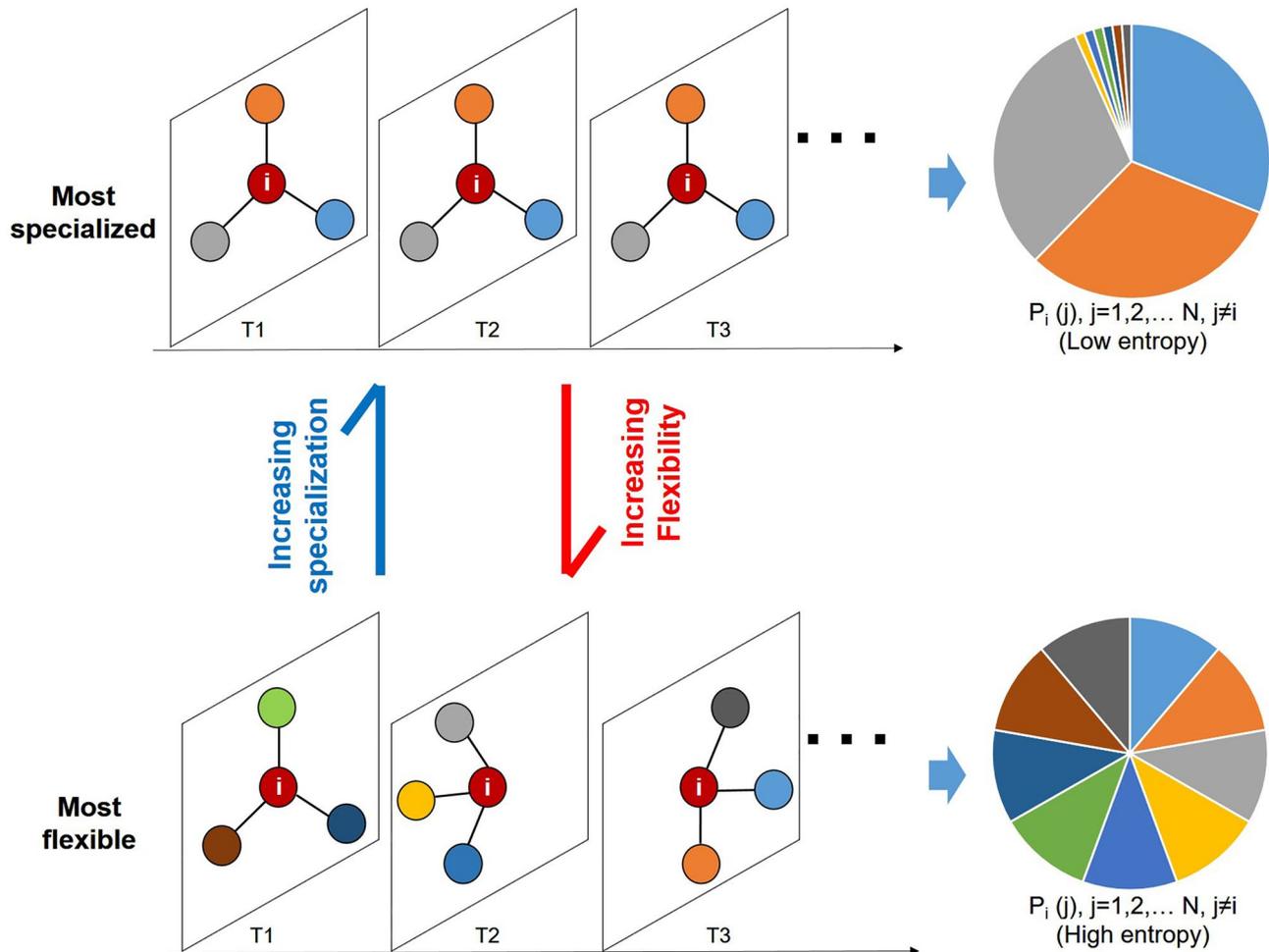


Fig. 1 Illustration of specialization and flexibility based on a dynamic network framework. In this framework, the functional role of each region i is embodied by its dynamic reconfiguration of functional connectivity over time T . This spatiotemporal connectivity pattern of region i can be represented as a probability distribution $P_i(j)$, $j=1, 2, \dots, N$, $j \neq i$. A region showing a heterogeneous probability distribu-

tion of connectivity (high entropy) was defined as functionally flexible, and the opposite was considered functionally specialized (low entropy). A region having an increase in entropy indicates increasing flexibility, and a region having a decrease in entropy indicates increasing specialization

Between-group analysis of entropy in the visual-motor system

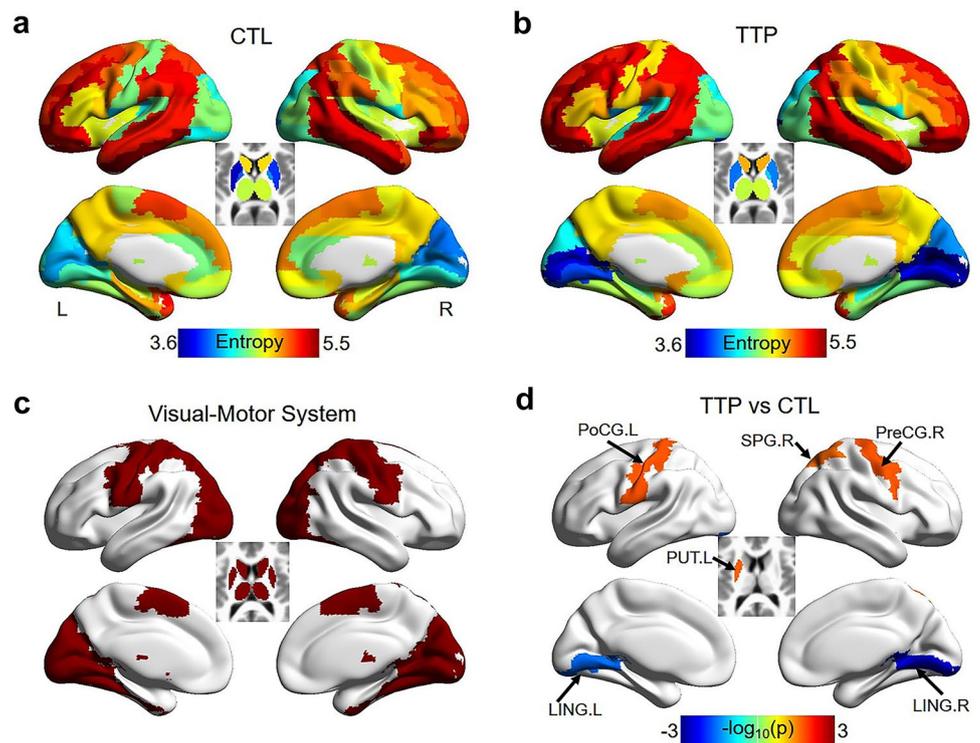
To investigate the plasticity of the intrinsic functional flexibility of visual-motor areas in TTP, we mainly focused on 30 ROIs, including 14 visual areas, eight sensorimotor areas, and eight subcortical regions (Fig. 2c and Supplementary Table 2). For each ROI, a nonparametric permutation test was used to detect between-group differences in entropy. Briefly, we first calculated the differences in mean entropy values between TTP and control groups. A null distribution of the difference was then obtained by randomly reallocating all of the entropy values into two groups and recomputing the mean differences between the two randomized groups (10,000 permutations). The 95th percentile points of the null distribution were used as critical values for a one-tailed test

of the null hypothesis with a probability of type I error of 0.05 (Wang et al. 2013). Of note, before the permutation tests, multiple linear regressions were applied to remove the effects of age, sex, and the age-sex interaction (Wang et al. 2016a). Finally, considering multiple comparisons (i.e., $n=30$ ROIs), we used an adjusted $p < (1/n) = 0.033$ as statistically significant following previous studies (Lynall et al. 2010; Reinwald et al. 2018), which is equivalent to saying that we expect less than one false-positive regional result at this threshold. Simultaneously, we assessed the effect size of between-group differences using Cohen's d .

Specificity of the dynamic measure

To test the specificity of our dynamic measure (i.e., entropy of a region's spatiotemporal connectivity pattern), we

Fig. 2 Plastic changes of intrinsic functional flexibility in the visual-motor system of expert table tennis players (TTP). **a** and **b** show brain maps of intrinsic functional flexibility for control subjects (CTL) and TTP, respectively. The insert panel shows subcortical regions. The color bar denotes entropy values. **c** indicates regions of interest in the visual-motor system. **d** shows regions with significant (adjusted $p < 0.033$, Cohen's $d > 0.6$) changes in intrinsic functional flexibility in TTP. Warm colors denote increasing flexibility, and cold colors denote increasing specialization. *PoCG* postcentral gyrus, *PreCG* Precentral gyrus, *SPG* superior parietal gyrus, *PUT* putamen, *LING* lingual gyrus, *L* left, and *R* right



additionally performed a static measure, functional connectivity strength (FCS), frequently used for identifying functional hubs (Yin et al. 2016; Liang et al. 2013). The FCS refers to average functional connectivity between one region and all other regions. Here, the functional connectivity was assessed by Pearson's correlations between the mean time courses of any pair of regions across the entire resting-state scan. We conducted the same statistical analysis as for the dynamic measure.

Task fMRI data preprocessing

Preprocessing of task fMRI data was performed using the SPM8 toolbox as follows: the functional images were first corrected for delay in slice acquisition and rigid-body head movement. Here, the criteria for excessive head motion were defined the same as that in resting-state fMRI preprocessing (i.e., translation > 2 mm or rotation $> 2^\circ$ in any direction), and no subjects were excluded according to these criteria. The corrected images were subsequently spatially normalized to the MNI space using an EPI template and then resampled to 3-mm isotropic voxels. Finally, spatial smoothing was conducted using an isotropic Gaussian filter at a full width at half maximum of 6 mm.

Univariate brain activation analysis

Individual activation maps were created using standard procedures in the SPM8 toolbox. Briefly, we modeled

each category of events (i.e., congruent and incongruent trials) with delta functions at the onset of events convolved with a canonical hemodynamic response function. Each category of events was defined as one condition in the general linear model (GLM) model, with error trials and six parameters of head movement specified as regressors of no interest (Yin et al. 2017). The contrast maps of congruent/incongruent versus baseline were obtained based on beta values estimated from the GLM model and then subjected to group-wise activation analysis.

For within-group activation analysis, we performed a two-tailed, one sample t test. The clustered regions that were robustly activated were determined by AlphaSim-corrected $p < 0.05$, i.e., a voxel-wise $p < 0.001$ incorporating a whole-brain image mask, and the minimum spatial cluster extent was determined by 1000 Monte Carlo simulations using the AlphaSim program as implemented in the REST toolbox (Song et al. 2011). For between-group analysis, we conducted a two-tailed, two sample t test, with age, sex, and the age-sex interaction as covariates. We also considered $p < 0.05$, AlphaSim-corrected (i.e., voxel-wise $p < 0.001$, and the minimum cluster size determined by 1000 Monte Carlo simulations), as statistically significant. Notably, the two sample t test was performed within the mask that represented the addition of significant within-group activation patterns (Yin et al. 2017).

Correlation analysis

We further tested the relationship between intrinsic functional flexibility and behavioral scores in TTP. For the visual-motor areas showing significant between-group differences in entropy, Pearson correlation analyses were carried out between entropy and skill levels, years of training, and behavioral accuracy and reaction time. Notably, considering that skill levels are noncontinuous variables, nonparametric Spearman correlations were used. We considered $p < 0.05$ as statistically significant and also performed a strict Bonferroni correction for the correlations (here, six regions showing significant between-group differences were enrolled for the correlation analysis). Thus, the corrected threshold is $p < 0.05/6 = 0.0083$.

For the regions showing significant between-group differences in attention-related neural responses, correlation analyses were conducted between the magnitude of brain activity and the behavioral accuracy and reaction time in TTP. Moreover, to link the intrinsic and stimulus-driven brain function, we also performed correlation analyses between attentional ability and brain activation strength in the regions whose intrinsic functional flexibility could predict the individual differences in attention. We used the threshold of $p < 0.005$ as statistically significant for the voxel-level correlations.

The visualization of functional results was performed using BrainNet Viewer (Xia et al. 2013), bspmview (www.bobspunt.com/software/bspmview/), and Mango (<http://ric.uthscsa.edu/mango/mango.html>).

Results

Brain maps of intrinsic functional flexibility in TTP and controls

In this study, no significant differences were observed between TTP and controls in age ($p = 0.99$, $t = 0.01$) and sex ($p = 0.16$, chi-squared value = 2.0). To replicate previous studies, we first conduct whole-brain mapping of intrinsic functional flexibility. In general, we found that the higher-order association cortices, such as the lateral prefrontal cortex, parietal cortex and temporal lobe, showed high flexibility, whereas primary sensory areas showed low flexibility (or high specialization) for both TTP and control groups (Fig. 2a, b). This result is consistent with previous findings (Yin et al. 2016, 2019; Zhang et al. 2016; Chen et al. 2016).

Plastic changes in intrinsic functional flexibility in the visual-motor system of TTP

Subsequently, we mainly focused on plastic changes of the visual-motor system in TTP. Through between-group

analysis, we found that motor-related regions, including the left postcentral gyrus, left putamen, right precentral gyrus and right superior parietal gyrus, showed a significant increase in entropy (i.e., increase in flexibility) in TTP (adjusted $p < 0.033$, all Cohen's $d > 0.6$). In contrast, visual areas, such as the bilateral lingual gyri, showed a significant decrease in entropy (i.e., increase in specialization) in TTP (adjusted $p < 0.033$, all Cohen's $d > 0.6$) (Fig. 2c, d and Table 2). Our finding indicates a dissociable change in intrinsic functional specialization and flexibility in the visual-motor system of TTP.

To further parse the connectivity reconfiguration of the visual-motor regions, we computed the differences in the mean probability distribution of connectivity between TTP and control groups. We found that the bilateral lingual gyri in TTP showed a decreased probability of connectivity with widely distributed regions, such as frontal, parietal, and higher-order visual cortices, and an increased probability of connectivity with primary visual area V1 (Fig. 3a). In contrast, sensorimotor areas in TTP showed an increased probability of connectivity with widely distributed regions and a decreased probability of connectivity with a small concentration of brain areas. For example, the left putamen showed increased probability of connectivity with widely distributed frontal, motor and visual areas, and a decreased probability of connectivity with the pallidum (Fig. 3b). This result provides an intuitive understanding to how the connectivity patterns of visual-motor areas reconfigured.

Intrinsic functional flexibility of sensorimotor areas associated with skill level and years of training

Through association analysis, we found a positive correlation between entropy in the left putamen and skill level in TTP ($\rho = 0.59$, $p = 0.008$, Bonferroni corrected). This finding indicates that the higher the skill level in table tennis, the higher the flexibility in the left putamen. In addition, the entropy of the left postcentral gyrus ($r = -0.49$, $p = 0.035$,

Table 2 Significant differences in nodal entropy between expert table tennis players (TTP) and nonathletes

Brain region	Abbreviation	p value	Cohen's d
Right lingual gyrus	LING.R	0.0035	- 0.93
Left postcentral gyrus	PoCG.L	0.017	0.70
Right precentral gyrus	PreCG.R	0.018	0.71
Left lingual gyrus	LING.L	0.024	- 0.66
Right superior parietal gyrus	SPG.R	0.024	0.67
Left putamen	PUT.L	0.028	0.65

The positive Cohen's d indicates that entropy of the region in TTP is greater than that in nonathletes, while a negative Cohen's d represents a decrease of entropy in TTP compared with nonathletes. All the p values are adjusted

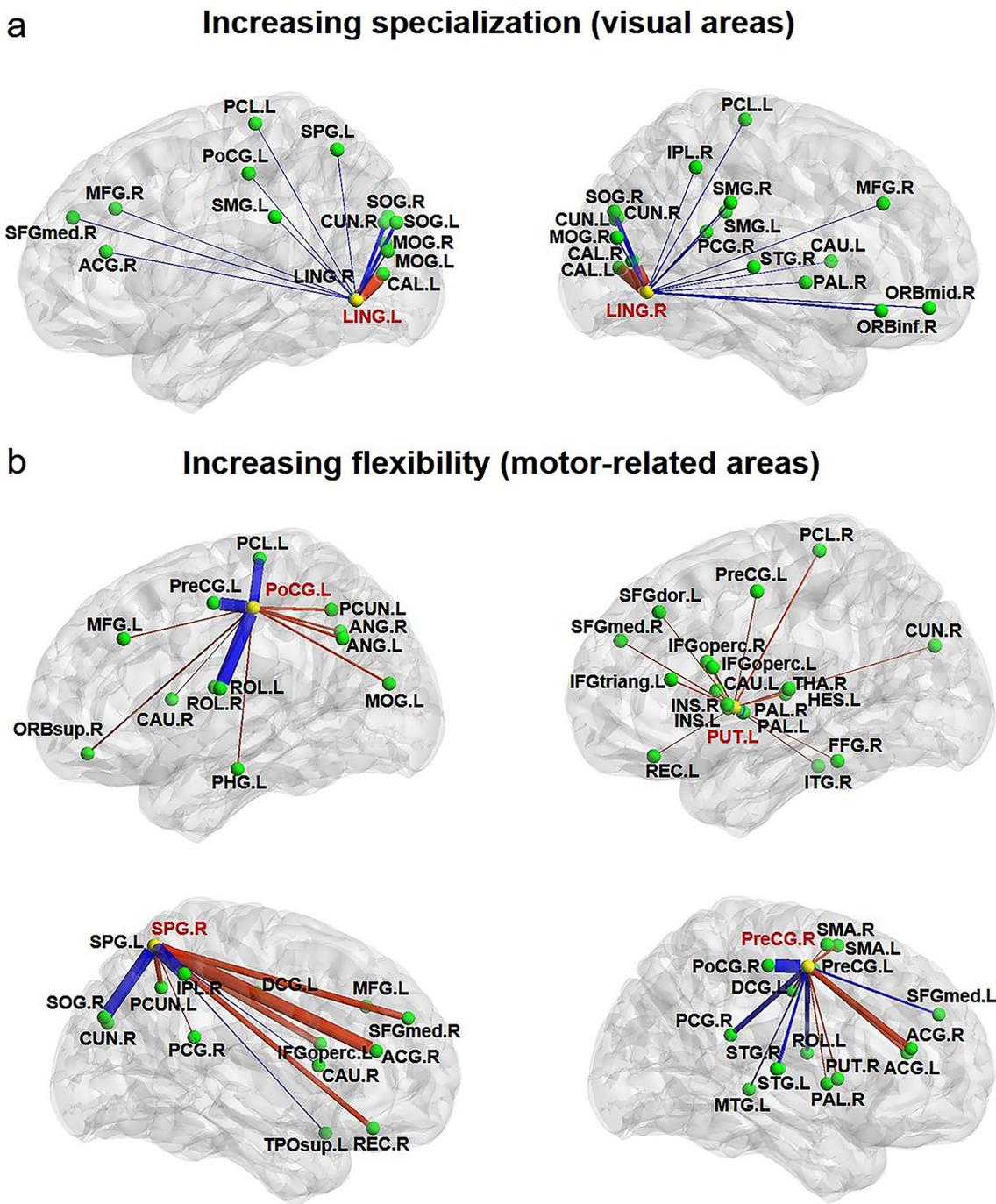


Fig. 3 The differences in mean connectivity probability between expert table tennis players (TTP) and controls. The yellow balls indicate regions with significant between-group differences in entropy. Bilateral lingual gyri in TTP show a decreased probability (blue lines) of connectivity with widely distributed regions, such as frontal and parietal cortices, and an increased probability (red lines) of connectivity with early visual area V1. This finding suggests increasing functional specialization of visual areas. In contrast, motor-related areas (i.e., left postcentral gyrus, left putamen, right precentral gyrus,

and right superior parietal gyrus) in TTP show an increased probability (red lines) of connectivity with widely distributed regions, and a decreased probability (blue lines) of connectivity with a small concentration of brain areas. This finding suggests increasing functional flexibility in motor-related areas. The thickness of lines reflects the magnitude of changes in connectivity probability. The total thickness of red and blue lines are equivalent. All abbreviations are listed in Supplementary Table 1

uncorrected) and right precentral gyrus ($r = -0.50$, $p = 0.031$, uncorrected) showed negative correlations with years of training in TTP (Fig. 4). This finding indicates that the flexibility in primary sensorimotor areas declines as years of training increases in high-level TTP, but overall flexibility is higher than in controls. No correlations were observed between the entropy in visual areas and skill level and years of training.

Intrinsic functional flexibility of the visual cortex predicted individual differences in general attention performance

To investigate the general attention processing, subjects were instructed to perform a classic Flanker task (Fig. 5a). In TTP group, we found that reaction time equal to: 437 ± 45 ms for congruent condition, 494 ± 40 ms for incongruent condition; and behavioral accuracy equal to: $96.7\% \pm 4.5\%$ for congruent condition, $90.9\% \pm 6.6\%$ for incongruent condition. In control group, we found that reaction time equal to: 419 ± 55 ms for congruent condition, 470 ± 57 ms for incongruent condition; and behavioral accuracy equal to: $98.4\% \pm 3.2\%$ for congruent condition, $96.2\% \pm 5.7\%$ for incongruent condition. Through between-group analysis, we found a significant decrease in behavioral accuracy ($p = 0.026$) in TTP for the incongruent condition, but no significant differences in the congruent condition. No significant differences in reaction time were observed in congruent and incongruent conditions (Fig. 5b). Moreover, we found that intrinsic functional flexibility of bilateral lingual gyri positively correlated with behavioral accuracy in the incongruent condition in TTP ($r = 0.56$, $p = 0.023$ for the left lingual gyrus; $r = 0.44$, $p = 0.086$, marginally significant for the right lingual gyrus) (Fig. 5c). These findings indicate that intrinsic functional flexibility in the visual cortex predict individual differences in behavioral accuracy during general attention processing, and the enhanced functional specialization (i.e., decreased functional flexibility) in the visual

cortex induced by long-term training domain-specific may have an adverse effect on other domains of attention.

Brain activation response to the Flanker attention task in TTP and controls

To detect attention-evoked brain activity, we adopted the commonly used GLM model to obtain brain activation maps in response to congruent and incongruent stimuli for all subjects. Through within-group analysis, we found in the control subjects that brain activation in response to congruent stimuli mainly included bilateral visual areas, bilateral superior parietal gyri, left sensorimotor areas and left insula, whereas the bilateral dorsal anterior cingulate cortices were additionally activated during incongruent stimuli ($p < 0.001$, cluster size > 119 voxels for congruent condition; $p < 0.001$, cluster size > 120 voxels for incongruent condition; both thresholds were AlphaSim-corrected) (Supplementary Fig. 1a and Fig. 6a). In contrast, the activation patterns in response to congruent and incongruent stimuli processing were similar in TTP, and primarily involved in bilateral visual areas, bilateral superior parietal gyri, left sensorimotor areas, bilateral insula, bilateral dorsal anterior cingulate cortex, and right middle frontal gyrus ($p < 0.001$, cluster size > 146 voxels for congruent condition; $p < 0.001$, cluster size > 150 voxels for incongruent condition; both thresholds were AlphaSim-corrected) (Supplementary Fig. 1b and Fig. 6b). In accordance with behavioral results, we did not find significant between-group differences in brain activation in response to congruent stimuli. In contrast, we found significantly increased activation in the left superior parietal gyrus in response to incongruent stimuli in TTP ($p < 0.001$, cluster size > 23 voxels, AlphaSim-corrected) (Fig. 6c).

Though increased activation of the left superior parietal gyrus in response to incongruent stimuli was observed in TTP, we did not find any correlation between activation strength and behavioral accuracy or reaction time. We further conducted a voxel-wise correlation analysis in bilateral

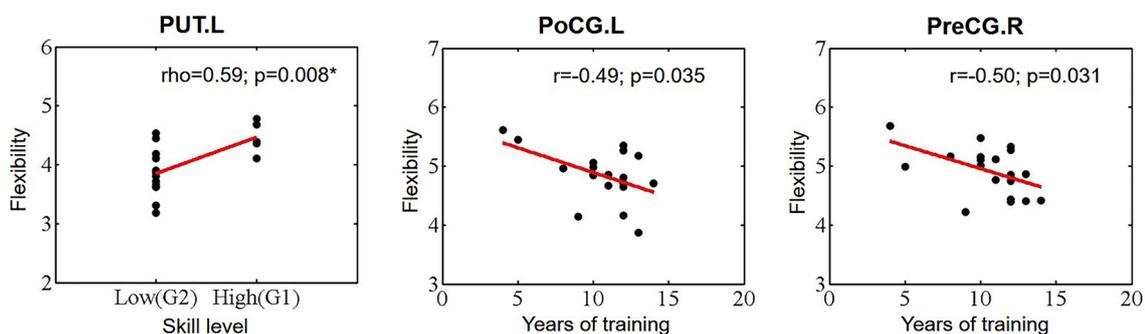
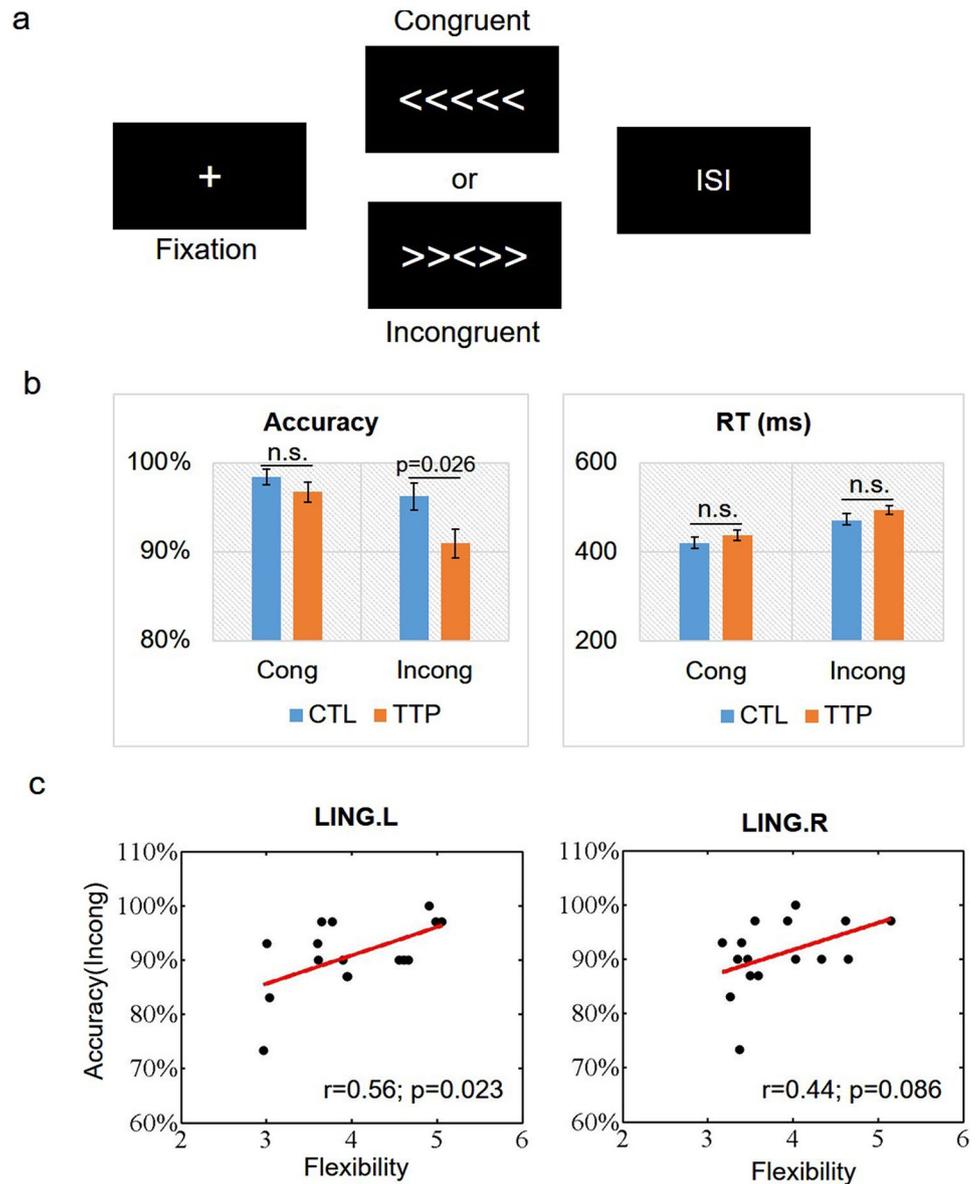


Fig. 4 Correlations between the flexibility of motor-related regions and skill level and years of training for expert table tennis players. *PUT* putamen, *PoCG* postcentral gyrus, *PreCG* precentral gyrus, *L*

left, *R* right, *G1* national grade 1, and *G2* national grade 2. The correlations with skill level (noncontinuous variable) were performed using nonparametric Spearman rho. * indicates Bonferroni corrected

Fig. 5 Intrinsic functional flexibility of the visual cortex predicts individual differences in general attention performance. **a** shows one single trial of the classic Flanker task used in the event-related fMRI experiment. Participants were presented with a 300-ms fixation cross, which was followed by an 800-ms stimulus. The stimulus is an array of five arrows, and participants were asked to respond to the orientation of the central arrow by pressing a button with their right index finger if the arrow pointed to the left, and with their right middle finger if the arrow pointed to the right. The interstimulus intervals (ISIs) (i.e., 2900, 4900, 6900, 8900, and 10,900 ms) were set in a pseudorandom manner. **b** shows behavioral accuracy and reaction time (RT) during congruent (Cong) and incongruent (Incong) stimuli for table tennis players (TTP) and controls (CTL). n.s. denotes nonsignificant. **c** shows positive correlations between intrinsic functional flexibility of bilateral lingual gyri (LING) and behavioral accuracy for incongruent stimuli in TTP. The correlation for the right lingual gyrus is marginally significant. *fMRI* functional magnetic resonance imaging, *L* left, and *R* right



lingual gyri for behavioral accuracy and brain activity in response to incongruent stimuli. We found behavioral accuracy was negatively correlated with brain activity in the right lingual gyrus ($p < 0.005$, uncorrected) in TTP (Fig. 6d). This finding suggests that the strength of stimulus-evoked brain activity in the right lingual gyrus also predicts individual differences in behavioral accuracy with incongruent stimuli, in addition to the intrinsic functional flexibility.

Validation analysis

To test the effects of global signal regression in data preprocessing, we replicated our main results without removing the global signal. We found high correlations between brain-wide entropy with and without global signal regression

for both controls ($r = 0.90$, $p < 0.0001$) and TTP ($r = 0.89$, $p < 0.0001$) (Supplementary Fig. 2). The significant between-group differences in entropy of visual-motor areas were consistently observed except for the right superior parietal gyrus (Supplementary Table 3). Moreover, we consistently found significant correlations ($p < 0.05$) between the flexibility of visual-motor areas and behavioral scores except for a marginal significance for the correlations between the left postcentral gyrus ($r = -0.44$, $p = 0.059$) and years of training, and between the left lingual gyrus and behavioral accuracy ($r = 0.47$, $p = 0.068$) (Supplementary Fig. 3). These findings suggest that our main results are robust to global signal regression choice.

To test the effects of brain parcellation, we replicated our main results using a HOA parcellation with 112 regions.

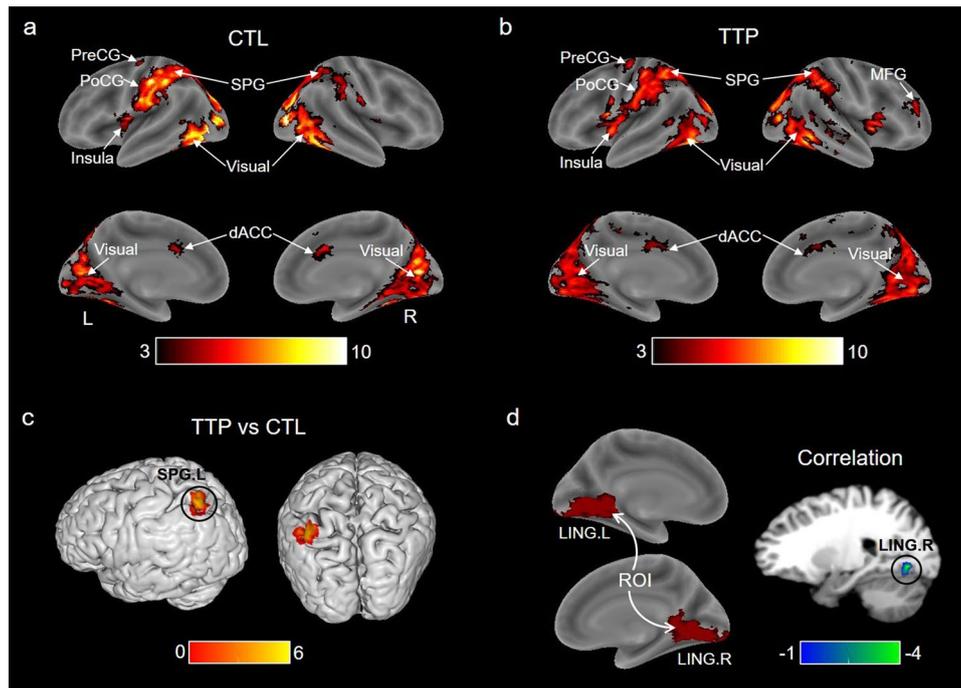


Fig. 6 Brain activation in the Flanker attention task. **a** and **b** present the within-group activation patterns in response to incongruent stimuli for controls (CTL) and expert table tennis players (TTP), respectively ($p < 0.001$, cluster size > 120 voxels for CTL; $p < 0.001$, cluster size > 150 voxels for TTP; both thresholds are AlphaSim-corrected). The color bar denotes t values. **c** shows increased activation of the left SPG in response to incongruent stimuli in TTP compared with CTL ($p < 0.001$, cluster size > 23 voxels, AlphaSim-corrected). **d** Considering that intrinsic functional flexibility in the bilateral lingual

gyri predicts individual differences in behavioral accuracy, a voxel-wise correlation analysis was further conducted between behavioral accuracy and brain activity in bilateral lingual gyri induced by incongruent flankers in TTP. As a result, behavioral accuracy negatively correlated with brain activity in the right lingual gyrus ($p < 0.005$, uncorrected). *PoCG* postcentral gyrus, *PreCG* precentral gyrus, *SPG* superior parietal gyrus, *dACC* dorsal anterior cingulate cortex, *MFG* middle frontal gyrus, *LING* lingual gyrus, *ROI* regions of interest, *L* left, and *R* right

We consistently found that the higher-order association cortices, such as the lateral prefrontal cortex, parietal cortex, and temporal lobe, showed high flexibility, whereas primary sensory areas showed low flexibility (or high specialization) for both TTP and control groups (Supplementary Fig. 4a, b). Through between-group analysis, a dissociable plastic change in intrinsic functional specialization and flexibility in the visual-motor system was also observed (Supplementary Fig. 4c and Supplementary Table 4). Though the flexibility of the left putamen was not significantly different between groups using HOA, it significantly correlated with skill level in TTP ($\rho = 0.63$, $p = 0.004$). Moreover, the flexibility of the left lingual gyrus consistently predicted individual differences in behavioral accuracy ($r = 0.59$, $p = 0.016$), but not for the right lingual gyrus ($r = 0.38$, $p = 0.143$) (Supplementary Fig. 5). Although some differences exist, our main results are conserved even with a different brain atlas.

To test the effects of window length, we replicated our main results using a larger window length (i.e., 100 s). We found high correlations between brain-wide entropy with a window length of 44 and 100 s for both controls ($r = 0.85$, $p < 0.0001$) and TTP ($r = 0.87$, $p < 0.0001$) (Supplementary

Fig. 6). Significant between-group differences in entropy in visual-motor areas were consistently observed except for a marginally significant difference for the left putamen ($p = 0.058$) (Supplementary Table 5). Moreover, we consistently found significant correlation between the flexibility of the left putamen ($\rho = 0.63$, $p = 0.004$) and skill level, but a marginal significance for the correlation between the left postcentral gyrus and years of training ($r = -0.45$, $p = 0.051$) and no significant correlations for the right precentral gyrus and the bilateral lingual gyri ($p > 0.1$) (Supplementary Fig. 7). Although some main results are conserved, some correlations are not significant. It is possible that the use of large window length may not capture the dynamic information of brain activity very well.

To test the specificity of our dynamic measure (i.e., entropy of a region's spatiotemporal connectivity pattern), we additionally used a frequently used static measure (i.e., FCS). We found that the sensorimotor, visual, dorsolateral prefrontal, dorsal anterior cingulate and insular cortices had higher intrinsic FCS (Supplementary Fig. 8a, b). This result is consistent with previous findings identifying brain hubs (Liang et al. 2013). Using the same procedures for

between-group analysis as for the dynamic measure, TTP showed decreased intrinsic FCS in the bilateral superior parietal gyri and right supplementary motor area (Supplementary Fig. 8c and Supplementary Table 6). No increased intrinsic FCS were observed in TTP. Moreover, no correlations were found between intrinsic FCS in regions showing significant between-group differences and any behavioral data (i.e., skill levels, years of training, reaction time, and behavioral accuracy in the Flanker task). These findings indicate that our dynamic measure could provide unique information for understanding functional brain organization in contrast with the traditional static measure.

Discussion

In this study, we combined both resting-state and task-based fMRI to investigate neuroplastic mechanisms underlying expert levels of performance in TTP. Extensive studies have suggested that dynamical organization of spontaneous/intrinsic brain activity is endowed with meaningful spatiotemporal structure, enabling the expression of a rich, flexible repertoire of functional configurations (Deco et al. 2011, 2013; Park and Friston 2013; Barttfeld et al. 2015). However, understanding the functional specificity of intrinsic brain activity is somewhat hard and usually requires a link to specific behaviors. In contrast, task-based fMRI has advantages for studying behavior-driven brain activity. Hence, the integration of resting-state and task-based fMRI may offer more comprehensive information for brain-behavior relationships.

Based on the dynamic network framework, we found that motor-related regions, including the left postcentral gyrus, left putamen, right precentral gyrus and right superior parietal gyrus, showed a significant increase in intrinsic functional flexibility in TTP. Moreover, a positive correlation was observed between intrinsic functional flexibility of the left putamen and skill level, whereas intrinsic functional flexibility of the left postcentral gyrus and right precentral gyrus showed negative correlations with years of training. The putamen, a subcortical region, is a main component of corticostriatal circuits (Alexander et al. 1986). Different corticostriatal circuits are relevant for distinct functions, such as motor, executive and affective functions (Lawrence et al. 1998; Yin et al. 2018). The putamen is mainly involved in the motor loop (i.e., sensorimotor cortex–putamen–globus pallidus–thalamus–sensorimotor cortex) and plays a crucial role in motor control as evidenced in both basal ganglia dysfunction and motor learning (Doyon et al. 2009; Seger 2006). A previous study indicated that later stages of motor skill learning increase activity in subcortical motor regions, including the putamen, suggesting a contribution to automatic performance (Floyer-Lea and Matthews

2004). Particularly, Lehericy and colleagues have revealed that motor skill (i.e., sequence learning) is stored in the sensorimotor territory of the putamen, supporting speedy performance (2005). We, therefore, speculate that intrinsic functional flexibility of the putamen is indicative of movement automaticity, a key feature of skill level in TTP.

In addition, previous work has shown that long-term learning increases activity in the primary somatosensory and motor cortex, suggesting plastic development of new representations for both motor output and somatosensory afferent information (Floyer-Lea and Matthews 2005). Consistently, we found plastic increases in intrinsic functional flexibility of the left postcentral gyrus and right precentral gyrus in TTP. Both regions showed decreased probability of connectivity with ipsilateral primary somatosensory or motor areas, whereas they showed an increased probability of connectivity with widely distributed regions, such as frontal, parietal, and subcortical motor control regions. In particular, the right precentral gyrus, not directly responsible for right-hand players, probably works as a “compensator” in the brain of TTP. This increasing flexibility of spatiotemporal connectivity in the primary somatosensory and motor areas is likely a result of adaptation to support extraordinary motor performance in elite TTP. However, our correlation analyses indicate that the flexibility of primary sensorimotor areas declines as years of training increases in high-level TTP, but overall flexibility is higher than that in controls.

In contrast with sensorimotor areas, we found the visual cortex (i.e., bilateral lingual gyri) showed decreased intrinsic functional flexibility (or increased intrinsic functional specialization) in TTP. In other words, bilateral lingual gyri in TTP showed a decreased probability of connectivity with widely distributed regions, such as the frontal, parietal and higher-order visual cortices, but an increased probability of connectivity with primary visual area V1. Previous behavioral studies have suggested that the ability to “read” the opponent’s movement pattern is directly related to the experts’ perceptual advantage in superior pick-up of essential information, particularly for fast ball sports (Abernethy et al. 2001; Abernethy and Russell 1987; Zhao et al. 2018). For table tennis, Piras and colleagues demonstrated that experts fixated more on the hand-racket during forehands and on the trunk during backhand drive techniques compared to novices when they were instructed to predict the direction of the ball after the opponent’s throw (2019). Extensive practice with this selective attention may lead to modifications of the perceptual visual system (Schoups et al. 2001; Green and Bavelier 2003). Therefore, the increased intrinsic functional specialization of the primary visual cortex in TTP is probably associated with the ability of selective attention on limited interest features crucial for action prediction, although the degree of specialization of the visual cortex is not indicative of skill level.

Through further examining general attention processing, we found no significant between-group differences in reaction time for either congruent or incongruent flankers. Although impressive attention performance has been observed in expert athletes, generalization to new tasks is still inconclusive. Using Posner's cued attention task (1980), previous studies have reported that reactive-sport athletes, such as volleyball players (Castiello and Umiltà 1992) and TTP (Hung et al. 2004), exhibited greater attentional flexibility in spatial stimulus detection, i.e., a reduction in attention cost (reaction time to invalid cues), along with a similar or reduced level of attention benefit (reaction time to valid cues). However, some studies found the effects of athlete experience were small and not significantly superior to novices in an attentional cuing paradigm (Voss et al. 2010; Wang et al. 2016b). Furthermore, Overney and colleagues argued for enhanced temporal but not attentional processing in expert tennis players compared to nonathletes (2008). A possible reason for the inconsistency may be primarily due to different experimental paradigms. Actually, even though experts show superior response to Posner's cued attention task, it is largely due to the paradigm containing essential elements of sports, such as fast responses to miscues and uncertainty about spatial location. In contrast, our currently used Flanker task is not involving core elements of sports, and the findings, therefore, support similar performance for generalized attention processing between TTP and nonathletes.

Interestingly, we observed a slight decrease in behavioral accuracy in response to incongruent flanking stimuli in TTP compared to controls, but both groups showed high accuracy (>90%). Moreover, the intrinsic functional flexibility of bilateral lingual gyri showed positive correlations with behavioral accuracy in TTP. That is, the greater the specialization of the visual cortex, the lower the behavioral accuracy. This result suggests that long-term table tennis training can enhance functional specialization of the primary visual cortex, which may result in an adverse effect on other domains of attention. Through the task-based fMRI, we found a negative correlation between activation strength of the right lingual gyrus and behavioral accuracy in TTP. This finding implies that the greater the involvement of the lingual gyrus, the relatively worse the performance. Previous evidence has indicated that skilled athletes may have unique motor preparation and visual attention strategies to achieve their extraordinary behavior (Nougier et al. 1991). A visual search strategy characterized by fewer fixations of longer duration has been reported in TTP, which means that talented athletes may put their gaze close to the relevant interest areas and allocate covert attention during fixations through microsaccades (Piras et al. 2016, 2019). This visual attention strategy may help them to capture information from surrounding objects of the fixation during playing

table tennis, but probably plays a counterproductive role in processing incongruent flankers. In addition, we found significantly increased activation strength in the left superior parietal gyrus in the TTP response to incongruent flankers, but it was not correlated with behavior. The superior parietal gyrus, belonging to the posterior parietal cortex, is mainly dedicated to sensory-motor integration (Andersen and Buneo 2002) and concerned with visuospatial attention (Rushworth et al. 2003; Casey et al. 2000). It is possible that overactivation of the superior parietal gyrus in TTP may serve a compensatory role in visual attention.

It should be noted that unlike intrapersonal self-paced sports, table tennis as an interpersonal interactive sport, requires players to continuously predict the actions of opponents. This capability of action anticipation achieved by expert athletes after years of training is thought to rely, at least in part, on a set of brain areas known as the mirror neuron system or action observation network (Smith 2016). Although there remains some inconsistency in the described composition of this network in the human brain, the mirror neuron system presumably involves the inferior frontal gyrus, the premotor cortex, the inferior parietal lobe, the supplementary motor area, the sensorimotor areas, and the cerebellum (Caramazza et al. 2014; Kilner and Lemon 2013). Balsler and colleagues have reported that some of these regions show stronger neural activation in expert tennis players compared with novices when they predict the outcomes of the opponents' actions (2014). This finding might suggest that the expert athletes have acquired fine-tuned motor representations mediated by mirror neuron mechanism. According to the mirror neuron theory or embodied cognition (Caramazza et al. 2014), the mapping of visual inputs onto corresponding representations of actions within the motor system is largely automatic, which may underpin the rapid motor response for skilled athletes. Moreover, recent study has found that the action anticipation of expert TTP engages both sensorimotor and semantic areas (Wang et al. 2019). Beyond the classic mirror neuron theory, the observed result implies that the skilled action understanding is likely dependent on the brain systems extending to higher-level conceptual (e.g., language-like structure) representations. From a probabilistic and dynamic network framework, our result consistently reveals that sensorimotor areas of expert TTP exhibit an increased probability of connectivity with widely distributed frontal and parietal regions in the absence of any task inputs. In the future, it is very important to further explore how the plastic changes of intrinsic functional organization in expert athletes affect the brain activation in response to sport-specific action anticipation, which may enrich the understanding to mirror neuron theory or embodied cognition framework.

There are also several methodological considerations pertinent to the present study. First, all the fMRI data that we

study here were collected using a traditional EPI sequence with 2 s TR. The resulting limited FOV size in the z direction could not cover the entire cerebellum for all subjects. We, therefore, excluded the cerebellum during constructing functional networks following previous studies (Bassett et al. 2011; Reddy et al. 2018). Though the cerebellum is involved in motor skill acquisition, previous studies have suggested that the activity of cerebellum decreases during later stages of motor learning (Dayan and Cohen 2011). It would be interesting to test plastic reorganization of cerebellar regions in the future with multiband EPI acquisitions, which allow many more slices to be acquired in a shorter time. Thus, high temporal resolution could provide enhanced sensitivity to brain activity dynamics. Second, although increasing attention has been paid to dynamic functional organization, the specificity of the statistical measure should be kept in mind. Previous studies on simple motor skill learning have mainly examined network-level dynamics of functional organization based on community detection (Telesford et al. 2017; Bassett et al. 2015) or clustering (Reddy et al. 2018) techniques. In contrast, our approach is focused on dynamics of node-level connectivity patterns. Interestingly, Bassett and colleagues found a dissociation of visual and motor systems as learning progressed (2015). Consistently, we observed dissociable changes in intrinsic specialization and flexibility in visual and motor areas in expert TTP. These results indicate that different statistical approaches could provide unique information on dynamic brain organization. Additionally, we did not find correlations among the static measure (i.e., FCS) with any behavioral scores, but between-group differences in FCS were observed. This finding further suggests the specificity of our dynamic measure. Third, the same as many previous studies (Debarnot et al. 2014), the cross-sectional design was adopted to reveal differences in brain organization between expert athletes and nonathletes. The main issue with this approach is that between-group differences in brain organization before training and differences in experiences during long-term training may confound our findings. Though longitudinal design is a solution to this problem, it is extremely difficult if the training occurs over long periods, such as ten years. Fourth, due to the rarity of national, top-level athletes, the sample size is relatively small, which may potentially affect statistical significance and the replicability of our findings. We, therefore, calculated both effect size using Cohen's d and p values to ensure the reliability of our findings, and a relatively loose false-positive correction method was used following previous studies (Lynall et al. 2010; Reinwald et al. 2018). Moreover, we performed a number of validation analyses in relation to methodology. Our main results are robust to different parameters or analytic strategies. Finally, in contrast with the years of training, the hours of training and the consistency of training over years may give more accurate and detailed evaluation for

the skill training. However, it is hard to precisely count the hours of training over ~10 years and keep the consistency of training across athletes. Therefore, we used the number of years as a measure of training duration following previous studies on professional athletes such as golfers (Kim et al. 2015), badminton players (Di et al. 2012), gymnasts (Huang et al. 2018) and TTP (Wang et al. 2019).

In conclusion, from the view of the dynamic network framework, we have uncovered dissociable changes of intrinsic functional specialization and flexibility in the visual-motor system in TTP compared to nonathletes. Moreover, intrinsic functional flexibility in sensorimotor areas was associated with skill level or years of training. In contrast, intrinsic functional flexibility in the visual cortex predicted individual differences in behavioral accuracy during general attention processing. This study provides new insights into the plasticity of the visual-motor system in supporting extraordinary motor performance, and our time-resolved analytic approach is applicable across other professional athletes for understanding their brain plasticity and superior behavior.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00429-021-02304-w>.

Author contributions DZY, LL, MXF, and QC designed the research. XFW, XYZ, QRY, and YW collected experimental data. DZY analysed data and wrote the draft manuscript. All authors provided feedback on the manuscript.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability Codes used in this study are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare no competing interests.

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