

Effect of different motor skills training on motor control network in the frontal lobe and basal ganglia

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ABSTRACT: During human motor control, the three pathways of motor control coordinate to complete human response and inhibition control, so whether different types of motor skills training will affect the three pathways of motor control is the main question in this study. Magnetic resonance imaging was combined with behavioural evaluation to analyse the effects of different special training sessions on the motor control network of the frontal lobe and basal ganglia and to explore the role of the central nervous system in the regulation of motor behaviour. A Stop-signal paradigm was used to measure reaction and inhibition capacity, functional magnetic resonance imaging was used for whole brain scanning, and resting state data were collected. Compared to the control group, the competitive aerobics athletes had better reflexes while the soccer players had both better reflexes and inhibitory control. Furthermore, we found that training in the two sets of skills resulted in significant differences in different resting state brain function parameters compared with the control group. Additionally, there were significant differences among the three groups in the direct and indirect pathways of motor control in terms of functional connectivity. Open skill training may improve reaction ability while closed skill training improve both reaction and inhibition ability. These results suggest that the strength of the functional connectivity between the right inferior frontal gyrus and the left putamen may be a key to improving the inhibitory, and the left supplementary motor area- bilateral thalamic loop may play an inhibitory role in motor control.

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INTRODUCTION

Motor control is the regulation of movement in organisms that possess a nervous system and includes reflexes as well as directed movement [1]. Successful motor control is crucial to interacting with the world to carry out goals as well as to regulate balance and stability. Therefore, the motor control processes in the frontal lobe and subcortical basal ganglia (BG) participate in regulation through three pathways of motor control, including the direct pathway—cortex-striatum-internal globus pallidus (GPi)/substantia nigra pars reticulata (SNr)-thalamus-cortex, the indirect pathway—cortex-striatum-external globus pallidus (GPe)-GPi/SNr-thalamus-cortex, and the hyperdirect pathway—cortex-subthalamic nucleus -GPi/SNr-thalamus-cortex. Among them, the direct pathway mainly initiates the motor response, and the hyperdirect pathway regulates response inhibition; when the selected motor response is achieved or needs to be cancelled, the indirect pathway performs response inhibition through the multistage neural projection of the frontal cortical-striatum pathway [2, 3]. In the early stage of task-based functional magnetic resonance imaging (fMRI) in our laboratory, it has been indicated

that the projection of the frontal-BG network plays an important role in motor control [4].

Response inhibition is the process of suppressing unnecessary, inappropriate or potentially dangerous actions in the process of motor control [5]. In sports, response inhibition is of great significance in controlling and regulating athletes' movement accuracy, direction and speed [6, 7]. For example, in a basketball game, when an offensive player is moving, our usual reaction is to immediately follow the movement of the attacking player. However, when an offensive player misleads with a feint, we need to stop the start of the movement action immediately and turn to the true movement of the attacker in a clear example of response inhibition. As an important part of human executive function, the level of response inhibition and its internal mechanism have attracted the attention of many researchers. In recent years, the Stop-signal paradigm, derived from stop signs, has become a classic paradigm used in the field of cognitive neuroscience to study response inhibition. It can measure and explore the response time and inhibition process of response inhibition or be

combined with brain imaging technology to deduce the neural pathways of response inhibition and form a corresponding model [8, 9].

In general, sports may be categorized into open skill and closed skill sports. Open skill sports are defined as those in which players are required to react in a dynamically changing, unpredictable and externally paced environment (e.g., soccer, basketball) [10]. By contrast, closed skill sports are defined as those in which the sporting environment is relatively highly consistent, predictable, and self-paced by the players (e.g., competitive aerobics, gymnastics, running, swimming) [10–12]. However, response inhibition in different kinds of motor training is very important in competition, and how different kinds of motor training influence the response and inhibition ability through the network connection between the frontal lobe and BG is the problem that will be addressed in this study.

Based on this, our study intends to adopt the stop-signal response inhibition paradigm and use fMRI technology to explore the behavioural differences between open skills and closed skills. From the perspective of central nervous system neural inhibition loops, the possible reasons for the difference in brain activation and the neural mechanism underlying motor control in individuals with different exercise training levels were discussed.

MATERIALS AND METHODS

Participants

In this study, thirty-five (35) female athletes were recruited from Beijing Normal University's interuniversity teams at a single institution: twenty (20) soccer athletes (soccer group, SG) and fifteen (15) competitive aerobics athletes (competitive aerobics group, CAG). Fifteen (15) individually matched controls that lacked any specific sports training were also recruited (control group, CG). All athletes are Chinese national level 1 athletes and above. All subjects underwent a comprehensive verbal screening procedure to ensure that they did not violate any of the exclusive criteria for the fMRI experiment: (1) history of neurological or cardiovascular disease; (2) medications; (3) cochlear implants or any metallic objects in the body; (4) cardiac or neural pacemakers and (5) history of musculoskeletal

injury in the limbs. All participants were compensated and signed an informed consent form prior to participation in the study. All research procedures were performed in accordance with relevant guidelines and regulations as approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning (Beijing Normal University, China). The research was conducted in compliance with Declaration of Helsinki.

Experimental session

The Stop-signal paradigm was used to evaluate the behaviour of response inhibition. The Stop-signal paradigm consists of Go and Stop tasks, and in each trial, a computer screen displays either a red solid circle or a blue solid circle stimulus. In the Go task (66.7%), the subjects are required to press the button quickly; in the Stop task (33.3%), a blue Stop signal appears randomly with a determined stop signal delay (SSD) after presentation of a blue solid circle stimulus. When the blue stop signal appears, the subjects are asked to stop the ongoing or upcoming reaction. For every three trials, there are two Go tasks and one Stop task, with the same number of red and blue solid circle stimuli. The value of the SSD in the Stop task changes dynamically. Starting from 250 ms, it increases by 50 ms for every successful inhibition and decreases by 50 ms for every failed inhibition [13] (Fig. 1). The experimental program was presented in E-prime 2.0 (<https://www.pstnet.com>).

Functional magnetic resonance imaging

MRI Data Acquisition

A Siemens MAGNETOM trio 3.0T magnetic resonance imaging system (Brain Imaging Center, Beijing Normal University) was used for image acquisition. The subject's head was fixed in place, and the subject was required to keep still, stay awake and keep their eyes closed. The resting state response was scanned by fMRI: TR = 2000.0 ms, TE = 30.0 ms, angle of rotation = 90°, number of layers 33, matrix = 64×64, FOV = 218×218 mm², and scanning time = 486 s. Structural image scanning: T1-MPRAGE was used for three-dimensional whole brain scanning, with 176 layers, 1.0 mm thickness, TR = 1900 ms, TE = 3.44 ms, angle of rotation = 9°, and FOV = 256×256 mm².

Functional MRI Data Analysis

All the functional data were preprocessed using SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>) and DPABI [14]. The following main step preformed: 1) after removing the first 10 volumes in time, and the head move was corrected; 2) slice-timing correction, motion correction, spatial realignment; 3) normalization, resampling as 3 mm³ cube voxels. The DARTEL tool was used to compute the transformations from the individual native space to the MNI space and vice-versa. No participant had head motion with more than 2.0 mm maximum displacement in any direction or 2.0 mm of any angular motion throughout the course of the scan. RESTplus was then used for linear trend removal and temporal bandpass filtering

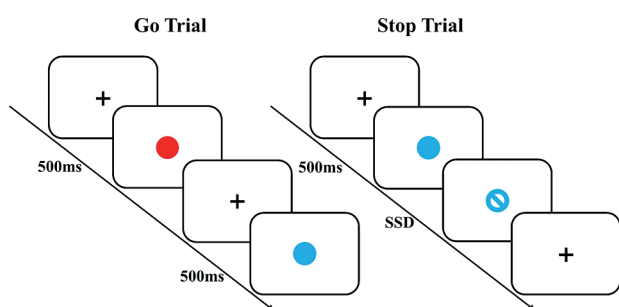


FIG. 1. Experimental process of stop-signal behavioral task. Note: SSD: Stop signal delay.

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(0.01–0.08 Hz) [15]. Degree centrality (DC) and voxel-mirrored homotopic connectivity (VMHC) were calculated. Then, the data were spatially smoothed (FWHM = 8 mm) by SPM12 before the amplitude of low-frequency fluctuation (ALFF) was calculated [16]. Finally, according to the previous research in our laboratory and the results of ALFF, DC and VMHC in this experiment, we ex-

tracted a number of spheres with a radius of 3 mm as seed points for functional connectivity (FC) analysis, and the data for FC analysis was not smoothed. Our extracted spheres include the supplementary motor area (SMA), inferior frontal gyrus (IFG), caudate, putamen, GPi, GPe and thalamus. BrainNet Viewer was used for visual presentation of results [4, 17].

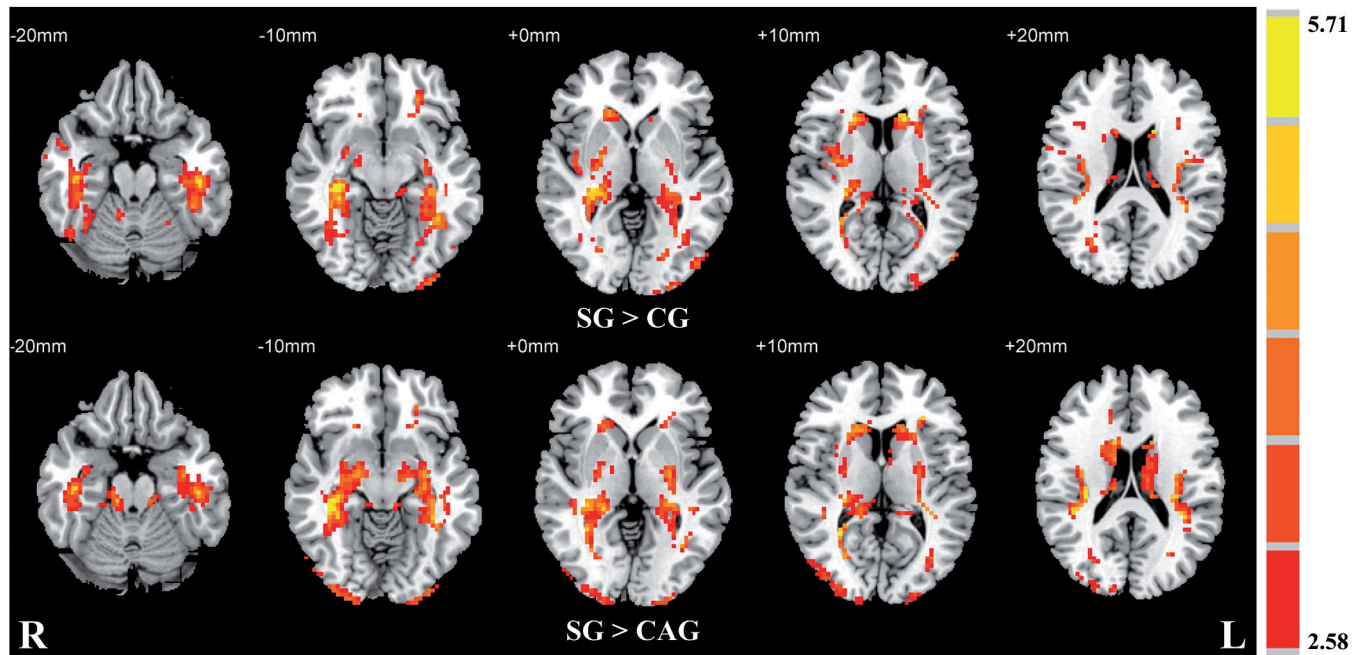


FIG. 2. Effects of different specialized training on brain ALFF.

Note: Yellow and red indicate brain regions that showed significant ($p < 0.05$ GRF corrected). CG: control group; SG: soccer group; CAG: competitive aerobics group; Side L: left hemisphere; Side R: right hemisphere.

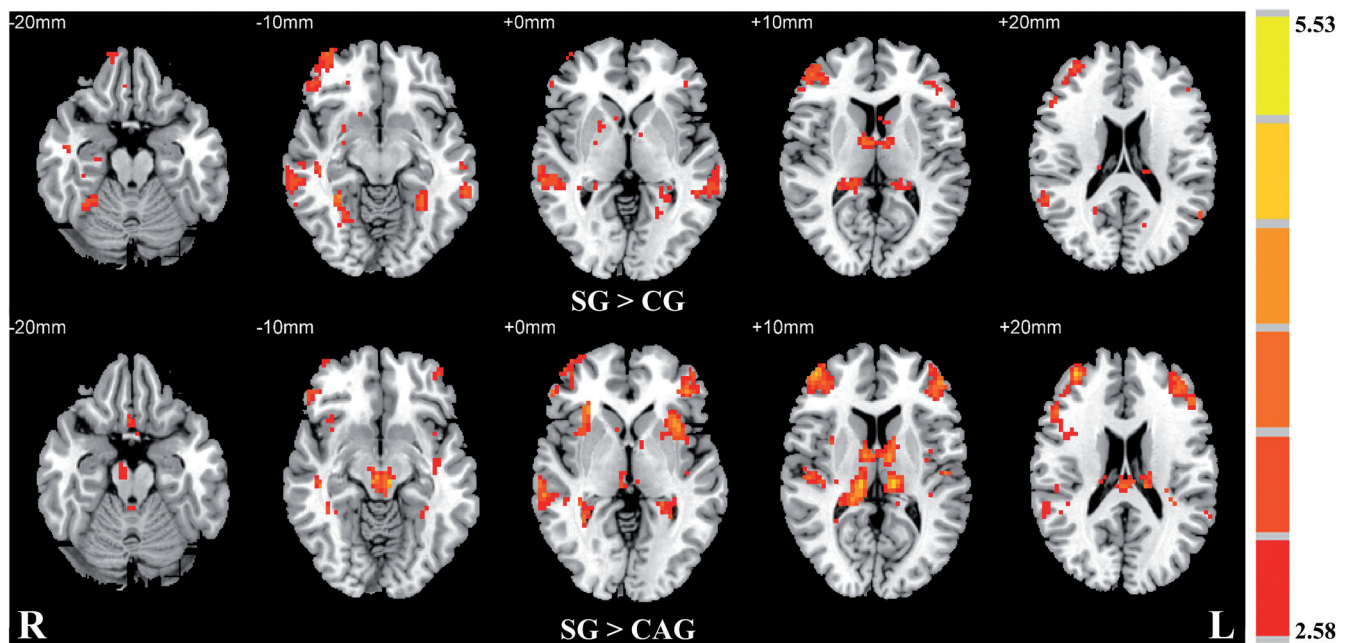


FIG. 3. Open vs. closed skill training effect on brain degree centrality.

Note: Yellow and red indicate brain regions that showed significant ($p < 0.05$ GRF corrected). CG: control group; SG: soccer group; CAG: competitive aerobics group; Side L: left hemisphere; Side R: right hemisphere.

Statistical analysis

RESTplus was used to perform statistical analysis on the preprocessed data and one-way ANOVA at the whole brain level with the ALFF, DC and VMHC. Pairwise two-sample t tests were then performed at the whole brain level. Additionally, to avoid demographic differences, age, BMI and years of training were included in the statistical analysis. The results of one-way ANOVA and two sample t tests were corrected by Gaussian random field (GRF) theory (voxel level $p < 0.01$, cluster level $p < 0.05$, corrected results showed significant difference); GRETNA was used to conduct two-sample t tests on the FCs from the three groups ($p < 0.05$ was considered statistically significant [18]).

Behavioural data were analysed by SPSS 20.0 for CG, CAG and SG data by one-way ANOVA ($p < 0.05$ was considered statistically significant). The Z-values from all seeds as the FC strength and SSRT were analysed via Pearson correlation test. Stop signal reaction time (SSRT) was calculated by the average reaction time (RT) minus the average SSD [19].

RESULTS

Sample characteristics.

There were significant differences in body mass index (BMI) and years of training among the three groups (Table 1).

Open vs. closed skill training effect on response inhibition

The behavioural test results on the response and inhibition ability were statistically analysed and are displayed in Table 2. The means and standard deviations show that there are behavioural differences among the three groups. Table 2 shows that the RT in the CAG was significantly lower than that in the CG ($p < 0.05$), and the RT in the SG was significantly lower than that in the CG

($p < 0.05$); the SSRT in the SG was significantly lower than that in both the CG and the CAG ($p < 0.05$). The SSD setting in the Stop-signal task maintained the inhibition accuracy of each subject at approximately 50%, but the subjects were not informed of the task characteristics in advance. Therefore, after seeing the blue solid circle stimulus, the subjects tried to slow down the executive response process to ensure successful inhibition. Consequently, the Red Go RT was used to measure reaction ability, and the SSRT was used to measure inhibition control.

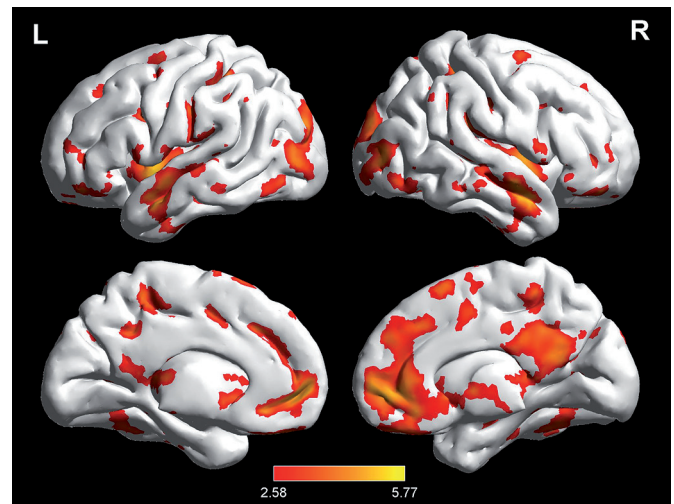


FIG. 4. Open skill training effect on brain voxel-mirrored homotopic connectivity.

Note: Yellow and red indicate brain regions that showed significant ($p < 0.05$ GRF corrected). Side L: left hemisphere; Side R: right hemisphere.

TABLE 1. Characteristics of the training and control groups.

Variables	CG	CAG	SG	F	P
N	15	15	20	—	—
Age (years)	18.87 ± 0.99	20.07 ± 1.58	19.30 ± 1.38	3.08	0.055
BMI (kg/m ²)	20.04 ± 1.49	19.63 ± 0.92	21.56 ± 2.20	6.42	0.003*
Years of training (years)	—	10.73 ± 3.35	10.80 ± 2.07	86.94	0.000*

Note: * denotes significant difference.

TABLE 2. Behavioral differences of reaction and inhibition ability between athletes of different sports and non-athletes

Group	Red Go RT (ms)	Go accuracy (%)	Success rate of inhibition (%)	SSRT (ms)
CG	522 ± 60.4	98.7 ± 1.2	55.1 ± 4	193.3 ± 43.9
CAG	476.2 ± 38.1 [#]	98.9 ± 1.5	55.7 ± 5.4	180.3 ± 36.8
SG	465.6 ± 40.2*	98.2 ± 1.6	55.2 ± 4.6	99.8 ± 29.8 ^Δ *

Note: [#] denotes significant difference from CG ($p < 0.05$). *denotes significant difference CG ($p < 0.05$). ^Δdenotes significant difference from CAG ($p < 0.05$). Red Go RT: Red Go Reaction time. SSRT: Stop signal reaction time.

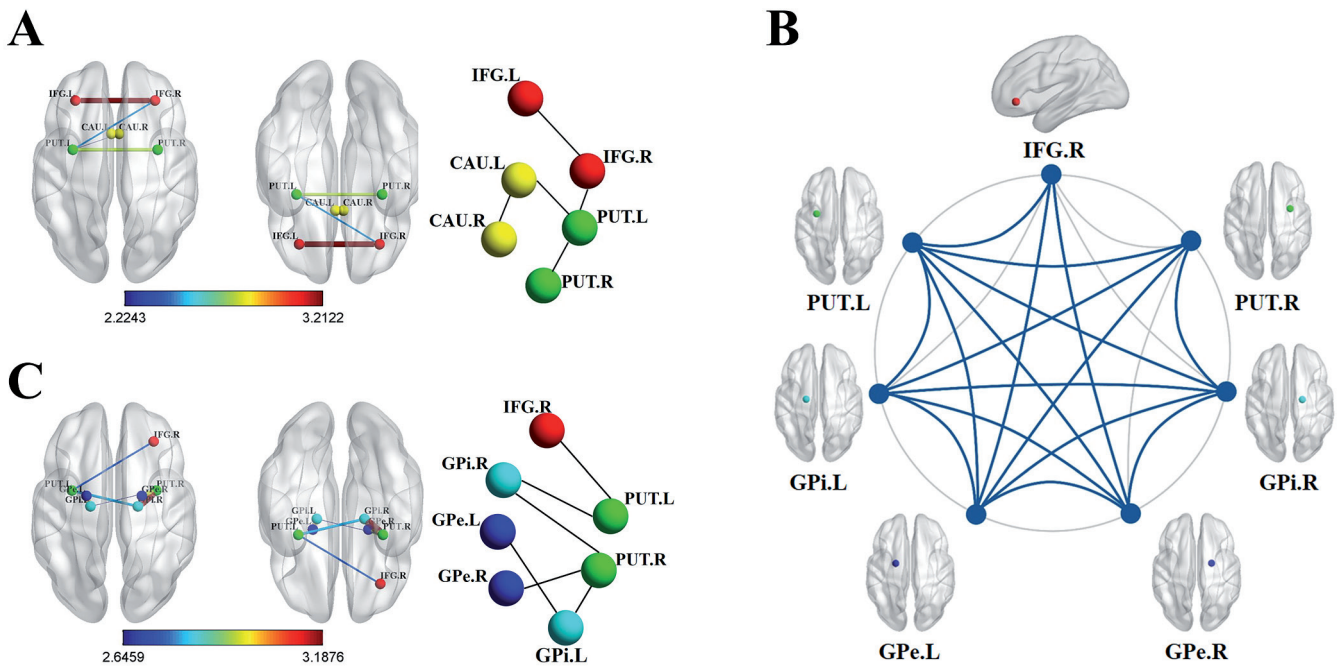


FIG. 5. Open vs. closed skill training effect on brain FC.

A) The difference of brain function network connection between long-term closed skill training and control group. The line segment represents the significantly enhanced functional connection between long-term closed skill training and the control group ($p < 0.05$). The color of the line segment indicates the degree of significant difference. The warmer the color, the more significant the difference. B) The curves show the functional connection between the long-term open skill training and the control group ($p < 0.01$). The dark blue curves show the connection with significant difference. The light gray curves show the connection with no significant difference. C) The difference of brain function network connection between long-term open skill training and closed skill training. The line segment represents the significantly enhanced functional connection between long-term open skill training and closed skill training ($p < 0.01$). The color of the line segment indicates the degree of significant difference. The warmer the color, the more significant the difference. L: left hemisphere; R: right hemisphere; IFG: inferior frontal gyrus; CAU: caudate; PUT: putamen; GPi: internal globus pallidus; GPe: external globus pallidus.

Open vs. closed skill training effect on brain ALFF

Compared with the CG, the ALFF values of the left SMA, bilateral caudate, putamen, and thalamus in the SG were significantly enhanced; compared with the CAG, the ALFF values of the bilateral caudate, putamen, pallidus and thalamus in the SG were significantly enhanced (Fig. 2).

Open vs. closed skill training effect on brain functional network connectivity

Open vs. closed skill training effect on brain DC

Compared with the CG, the DC values of the left medial frontal gyrus, SMA, pallidum, bilateral middle frontal gyrus, caudate, putamen, and thalamus in the SG were significantly enhanced; compared with the CAG, the DC values of the left IFG, bilateral middle frontal gyrus, caudate, putamen, and thalamus in the SG were significantly enhanced (Fig. 3).

Open vs. closed skill training effect on brain VMHC

Compared with the CG, the VMHC values of the bilateral medial superior frontal gyrus, IFG, SMA, caudate, putamen, pallidum, GPi, and thalamus in the SG were significantly enhanced (Fig. 4).

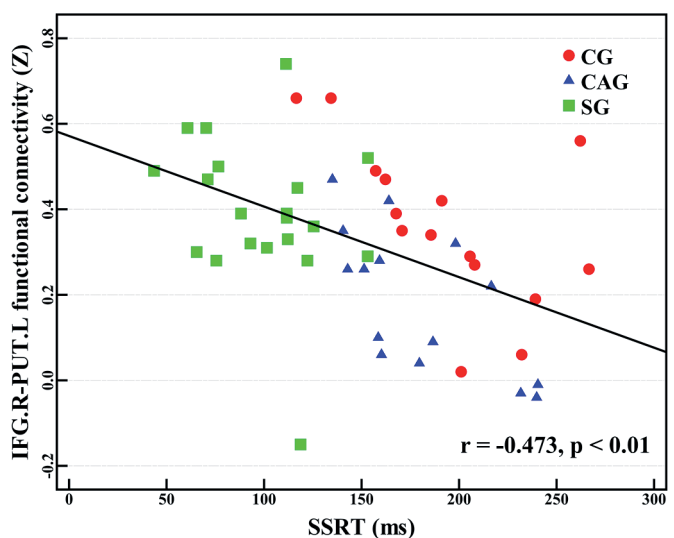


FIG. 6. Correlation between brain functional connectivity strength and the inhibitory control.

Open vs. closed skill training effect on brain FC

Figure 5A shows that the CAG had stronger FC among the bilateral IFG, caudate and putamen than the CG. Figure 5B shows that the SG had stronger FC among the right IFG, bilateral putamen, GPI and GPe than the CG. Figure 5C shows that the SG had stronger FC among the right IFG, putamen, GPI and GPe than the CAG. However, there was no significant difference among the three groups in the SMA.

FC in the brain is associated with inhibitory control

The correlation analysis of the Z-values with SSRT revealed a significant negative correlation between the right IFG–left putamen FC and SSRT. The results showed a significant negative correlation between the two variables ($r = -0.473$, $P < 0.01$), indicating that the stronger the FC strength between the right IFG and the left putamen, the shorter the inhibition time and the stronger the inhibition control (Fig. 6).

DISCUSSION

This study was the first to explore the regulatory effects of direct and indirect pathways of motor control among soccer players, competitive aerobics athletes and a CG on human reaction and inhibitory control. The differences in ALFF, DC, VMHC and FC values between soccer athletes, competitive aerobics athletes and the CG may further reveal the influence of open vs. closed skill training on brain functional plasticity.

Direct pathways regulate the reaction ability by frontal lobe-BG

Response time reflects how long it takes a person to respond to external stimuli. The response ability is the required ability for an athlete to quickly execute motor responses during a competition. For example, competitive aerobics athletes need to complete a set of fixed choreography quickly when they hear music and make their actions match the beat of the music, whereas soccer players in the field of play need to pass and catch the ball quickly, as well as run according to previously practised tactics. Performance of the reaction ability requires the involvement of direct pathways in the frontal-BG circuit: the premotor cortex initiates the motor response, passes through the striatum, GPI and thalamus, and finally reaches the primary motor cortex.

Open skill training has been shown to improve response ability [12]. Whereas, seed-based FC analysis is a model-based method from which we can select several seeds or regions of interest and explore functional communication between brain regions [21, 22]. In this study, the FC of the SG and CAG was stronger than that of the CG, and both the SG and CAG had faster reaction times than the CG, and it is speculated that the FC between the bilateral IFG and the left putamen may be an important factor influencing the Go reaction time. Meanwhile, Cui et al. [20] testified that long-term exercise training has been found to promote the plasticity of the frontal lobe function and FC. The strength of the FC between the bilateral GPI and the thalamus in the SG was significantly enhanced compared

with that of the CG; furthermore, the ALFF and VMHC values in the bilateral putamen, globus pallidum and thalamus of the SG were significantly higher than those in the CG. ALFF could reflect the spontaneous neuron activity, and VMHC can measure the correlations between blood oxygen level-dependent time series and reflect the communication pattern of information between two cerebral hemispheres [23, 24]. Thus, it is suggested that in the direct path of motor control, the intensity of spontaneous activity and the strength of the FC of each nucleus may affect the reaction time. In the analysis of the FC of the SG and CAG, the FC of the SG among the right IFG, bilateral putamen and GPI was significantly enhanced, but not between each pair of the above nuclei. Except for ALFF, VMHC, DC was also considered a promising magnetic resonance technique that can reveal the connectivity of brain networks at the voxel level [25]. The definition of DC value was made by calculating the centrality of a node by adding the centrality of adjacent nodes, which can be a brain region or voxel, and the higher the score, the greater the centre or the importance of nodes in the functional network [26]. In this study, the ALFF and DC values of the SG were significantly increased in the bilateral putamen, globus pallidum and thalamus but not significantly changed in the right IFG, which may be an important reason that the SG and CAG have unremarkable differences in reaction time. In conclusion, it can be seen that long-term open vs. closed skill training can affect the direct pathways of brain motor control and improve the response ability of the direct pathways of motor control; however, soccer, as an open skill sport, may need a more rapid reaction to cope with different situations in the game than closed skill sports.

Indirect pathways regulate inhibitory control by the frontal lobe-BG

Inhibitory control is mainly regulated by indirect pathways between the frontal cortex and BG. The BG participates in a variety of control processes and plays a regulatory role in inhibitory control in motor and cognitive processes. Additionally, different regions of the BG mainly receive projections from cortical regions with different functions [27, 28]. As a part of the frontal lobe, the right IFG plays an important role in the inhibition process and may be directly involved in inhibitory control, directly or indirectly projecting information to the BG to stop ongoing motor behaviour [29, 30]. Eagle et al. [31] believe that Go/No-Go and Stop-signal tasks have similar anatomical mechanisms but different neurobiological mechanisms. Dalley et al. [32] and Guo et al [3] further found that the Stop-signal task mainly activated the right IFG, while the Go/ No-Go task activated the left IFG, which reflected the unilateral trend of IFG participation in inhibitory tasks.

In this study, the VMHC value and FC strength among the right IFG, bilateral putamen, GPI, GPe and thalamus of the SG were higher than those of the CG. The FC between the right IFG and the left putamen of the SG was stronger than that of the CAG and the CG, and the ALFF value of the right IFG and the left putamen was higher than that of the CAG and the CG. In terms of sport types, open

skill sports involve unpredictable environments, active decision making, and ongoing adaptability in which participants must alter responses to randomly occurring external stimuli, such as soccer players sometimes cancel intended actions (i.e., inhibitory control) and make new decisions (i.e., cognitive flexibility and problem solving) according to rapidly changing situations, whereas closed skill sports are performed in a relatively stable and predictable environment in which motor movements follow set patterns. [33, 34]. So when considering inhibition ability is essential in open motor skill training, such as feint training is essential in football and basketball, this results may suggest that long-term open skill training could change the FC strength of the brain motor control network and improve the inhibitory ability of players on the field. Aron et al. [29] conducted relevant studies on SSRT values and brain activation areas and showed that the IFG was negatively correlated with SSRT values. This study further analysed the correlation between SSRT and the FC between the right IFG and left putamen and found that the connectivity strength of the right IFG-left putamen was highly correlated with SSRT. The stronger the connectivity strength, the shorter the SSRT. This may prove that the right IFG-left putamen connection plays an important inhibitory role in the indirect pathway of motor control, and improving the FC strength of the right IFG-left putamen may enhance the inhibitory ability. An increase in the FC strength between the caudate and the putamen, which is related to information processing and executive function, may also improve the information processing ability of the BG. In competitive aerobics competitions, athletes are required to completely reproduce the combination of fixed movements that have been practised thousands of times in training. By contrast, in a soccer match, the players are required to combine the movements practised hundreds of times in training randomly and in a timely manner according to the random situations encountered on the field to cooperate technically and tactically with their teammates. Therefore, the difference between open skill sports and closed skill sports also leads to the difference in behavioural results in our experiment; that is, long-term open skill training can improve the reaction and inhibition ability, while long-term closed skill training can only improve the reaction ability.

The left SMA-bilateral thalamic loop is involved in motor inhibition

The SMA is located in the dorsal-medial cortex of the superior frontal gyrus and is involved in coordinated movement, bilateral coordination, postural stability, and the initiation and execution of movement [35, 36]. In addition, the SMA and thalamus together constitute the key node of the frontal-BG neural network in inhibitory control mechanisms [37, 38]. Furthermore, the SMA-thalamic circuit is associated with response selection and inhibition during motor control [39, 40]. In the early stage, our laboratory conducted whole-brain analysis on voluntary movement control by using task-state fMRI technology and found that the primary motor cortex, SMA and thalamus were activated during voluntary movement of the upper and lower limbs, which proved that the SMA-thalamic loop participated in exercise execution.

Electrophysiological experiments showed that exhausted exercise led to decreased electrical activity of SMA neurons in rats and inhibition of the SMA-thalamic pathway, suggesting that the SMA-thalamic pathway is related to inhibitory capacity [4, 41]. These findings highlight the importance of the SMA-thalamic circuit, which is part of the medial frontal lobe, is closely linked to the primary motor cortex and the medial cingulate cortex [42]. Furthermore, the SMA, premotor cortex and primary motor cortex all play key roles in motor control and motor skill acquisition. In particular, the transition between space and motion seems to be largely dependent on the interaction of these three regions [43].

In this study, it was found that the ALFF, DC and VMHC values of the SG in the left SMA and bilateral thalamus were significantly enhanced compared with the CG, but there was no significant change in the FC, suggesting that further analysis of the brain structure network may be required by diffusion tensor imaging technology in future studies. The increase in the ALFF value indicated that the intensity of the soccer players' spontaneous activity was increased after long-term sports training. The increase in the DC value indicates that the SMA-thalamic circuit plays an important role in the functional brain network of soccer players, which may be related to soccer players' need for the SMA to perform motion control during a competition. The increase in the VMHC suggests that soccer players' SMA-thalamic circuit plays an important role in communicating and coordinating movement between the left and right hemispheres of the brain. Chen et al. [44] studied the functional neuroplasticity of inhibitory control and found that the left SMA-bilateral thalamic loop plays an important role in inhibitory control, suggesting that the difference in the ALFF value, DC value and VMHC value may prove that long-term open skill training may improve response selection, response inhibition and cognitive control ability as a way to improve motor control ability.

CONCLUSIONS

In this study, we found that open vs. closed skill training has different effects on the direct and indirect pathways of brain motor control. Closed skill training can improve the reaction ability, while open skill training can improve the reaction and inhibition ability. The strength of the FC between the right IFG and the left putamen may be the key to improving inhibitory ability, and the SMA-thalamic loop may play an inhibitory role in motion control. Additionally, the regulation mode of inhibition control is complicated and may be regulated by indirect pathways and the left SMA-bilateral thalamic loop.

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Competing interests

The authors declare no competing interests.

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