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RESEARCH ARTICLE

Nonlinear neuroplasticity corresponding to sports experience: A voxel-based morphometry and resting-state functional connectivity study

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Abstract

We aimed to investigate the structural neuroplasticity associated with different levels of sports experience and its effect on the corresponding resting-state functional circuitry. We recruited 18 skilled baseball batters (SB), 19 intermediate baseball batters (IB), and 17 healthy controls (HC), and used magnetic resonance imaging methods to compare their regional gray-matter volume (GMV) and seed-based resting-state functional connectivity (rsFC). Our results revealed that a quadratic function could better depict intergroup differences in regional GMV than a linear function. In particular, the IB showed lower or higher regional GMV than the other two groups. The difference in GMV in the supplementary motor area and areas belonging to the ventral stream, including the middle temporal gyrus and middle temporal pole, might be possibly related to baseball-specific motor and perceptual experience, such as inhibitory action control and pitch identification. On the other hand, the stronger rsFC seeded from the right middle temporal pole to the default mode network, particularly in the precuneus, in the SB and IB relative to that in the HC might be possibly associated with the theory of mind, such as deciding whether to swing or not against the pitcher by detecting the spatial information of pitches. In conclusion, our three-group design enabled the capture of the unique and transient changes that occur during the intermediate phase of expertise development. Our findings indicated that structural and functional brain changes do not necessarily linearly increase as a function of experience as previously suggested by the literature.

KEYWORDS

baseball players, gray-matter volume, neuroplasticity, resting-state functional connectivity, sports, voxel-based morphometry

1 | INTRODUCTION

Recent neuroimaging and neurophysiological studies have shown that in addition to developmental processes, motor-skill learning, and experience can induce neuroplasticity, which is defined as brain structural and functional reorganization (review see Dayan & Cohen, 2011; Hebb, 1949; May, 2011; Zatorre, Fields, & Johansen-Berg, 2012). Experience-induced neuroplasticity has been found in professional golfers (Jäncke, Koeneke, Hoppe, Rominger, & Hänggi, 2009), ballet dancers (Hänggi, Koeneke, Bezzola, & Jäncke, 2010), judo wrestlers (Jacini et al., 2009), and jugglers (Gerber et al., 2014). Previous studies have attributed expertise-related regional changes in gray-matter volume (GMV) to the development of sport-specific skills by players of different types of sports (Meier, Topka, & Hänggi, 2016; Schlaffke et al., 2014; Wenzel, Taubert, Ragert, Krug, & Villringer, 2014).

The majority of studies have shown that regional GMV increases as a function of training experience (review see Hänggi et al., 2015; Huang, Lu, Song, & Wang, 2015), whereas some studies have provided contrary findings (Gondoh et al., 2009; Hänggi et al., 2010; Hüfner et al., 2011; Wei, Luo, & Li, 2009). For example, as compared

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with healthy controls, judo wrestlers (Jacini et al., 2009), martial artists, and endurance athletes (Schlaffke et al., 2014) exhibit increased GMV in their supplementary motor area (SMA), whereas ballet dancers (Hänggi et al., 2010) exhibit decreased GMV in the same area. This discrepancy might be attributed to the specificity of motor-task training. In open-skill sports, for example, judo or martial arts, skills are predominantly perceptual and externally paced; whereas in closed-skill sports, such as ballet dance, skills tend to be self-paced without being affected by the environment (Knapp, 1963). SMA has been functionally associated with the control of postural stability, the coordination of the temporal sequences of actions, bimanual coordination, and the initiation of internally generated movement (as opposed to stimulus-driven movement) (Nachev, Kennard, & Husain, 2008; Tanji, 1994, 1996). Counter intuitively, ballet dancers who are frequently engaged in the initiation of internally generated movement exhibit decreased SMA, whereas judo wrestlers and martial artists who are more frequently engaged in the initiation of movements driven by external stimulus exhibit increased SMA.

Similar to years of sport practice, a short period of motor training triggers changes in regional GMV (Bezzola, Mérillat, Gaser, & Jäncke, 2011; Boyke, Driemeyer, Gaser, Büchel, & May, 2008; Draganski et al., 2004; Driemeyer, Boyke, Gaser, Büchel, & May, 2008; Erickson et al., 2011; Taubert, Lohmann, Margulies, Villringer, & Ragert, 2011). For example, over 3 months of learning three-ball juggling, learners demonstrated an expansion of the regional GMV in their mid-temporal area (hMT/V5) and left intraparietal sulcus (IPS), which are both involved in motion perception and visuomotor processing (Draganski et al., 2004). The same results were observed after 7 days of learning the same task (Driemeyer et al., 2008). Interestingly, these regional GMV changes decreased to the baseline when learners stopped training (Draganski et al., 2004; Driemeyer et al., 2008). These results reinforce the concept that the human brain adapts to external stimuli with extremely highly flexibility even during the very early phase of motor skill acquisition.

Most of the aforementioned studies recruited two groups of participants, including one group of experts (or learners) and one group of healthy controls (or nonlearners). This kind of design provides insight into the linear relationship between regional GMV and expertise-related (or learning) experience. Following this linearity hypothesis, some studies first located the brain areas that changed over the duration of practice and then compared regional changes in the GMV of experts and nonexperts (Groussard et al., 2014). However, linear models might be limited because they cannot capture the unique and transient effects that occur during a certain period of expertise development, such as those during the intermediate phase. The differences in GMV between experts and intermediates and between experts and healthy controls might also explain the discrepancy regarding the increase or decrease in regional GMV reported by different studies. For example, years of sports experience are often associated with increased regional GMV in the SMA, whereas 17–30 weeks of aerobic training are associated with decreased regional GMV in the right SMA and frontal middle orbital gyrus (Gondoh et al., 2009).

Jäncke et al. (2009) compared GMV changes across four groups with different levels of golf-playing experience. These groups included professional golfers, amateur golfers (with a handicap of 1–14), intermediate golfers (with a handicap of 15–36), and nongolfers. They found that GMV did not significantly differ between the two expert groups (professional and amateur golfers) and between the two non-expert groups (intermediate and non-golfers) but differed between the two expert groups and the two nonexpert groups. Specifically, the expert groups showed greater GMV changes in the bilateral premotor cortex (PMC) and the left IPS than the nonexpert groups. The authors thus concluded that GMV changes in a stepwise, not a linear, manner as a function of golf-playing experience. This finding is important because it showed that structural neuroplasticity follows a pattern other than a linear one. To the best of our knowledge, this is the only study that recruited more than two groups of participants and found that GMV changes in a stepwise manner as a function of expertise-related experience in sports (Jäncke et al., 2009).

Given the above information, we were motivated to investigate the structural changes corresponding to different levels of sports experience in athletes' brains. We recruited skilled and intermediate baseball batters (hereafter refer to SB and IB, respectively), and compared their regional GMV at the whole-brain level with that of individuals without any baseball-playing experience (i.e., healthy controls [HC]). Given that baseball batters are required to make rapid decisions to swing or not swing at the upcoming pitch in a split second, we expected that the regional GMV of motor areas, such as the primary motor cortex, PMC, and SMA, would be altered in batters but not in controls. Applying a three-group design would allow us to examine whether the regional GMV changes induced by sports experience could be better depicted by a linear or a nonlinear trend. However, evidence remains as of yet insufficient for us to formulate a particular hypothesis. A linear trend would suggest that structural changes corresponding to sports experience predominantly depend on the quantity of practice, as suggested by the majority of previous studies that applied a two-group design. On the other hand, a nonlinear trend would suggest that the intermediate phase of motor skill acquisition might be a unique and transitional phase.

Furthermore, regional GMV changes are associated with the intrinsically connecting functional network architecture, called resting-state functional connectivity (rsFC; Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995; Fox et al., 2005), in athletes (Di et al., 2012; Tan et al., 2017), musicians (Fauvel et al., 2014), chess experts (Duan et al., 2012; Jung et al., 2013), and patients (Seeley, Crawford, Zhou, Miller, & Greicius, 2009). In these studies, the areas showing significant regional GMV changes between experts and nonexperts (or between patients and normal controls) were selected as seed regions of interest (ROI) for the further investigation of the influence of structural changes on functional circuitry. For example, Duan et al. (2012) reported that compared with controls, chess experts showed decreased GMV in their bilateral caudate nuclei but strengthened rsFC with posterior cingulate cortex and bilateral angular gyrus, which are both important nodes of the default mode network (DMN; Raichle et al., 2001). The authors speculated that the reduction in GMV may be attributed to the effect of neural pruning (Sowell, Thompson, & Toga, 2004), which removes unused or redundant synapses, enhances local computational capacity, and eventually improves local neuronal connections, as well as integration with other widely distributed areas (Hagmann et al., 2010; Luna & Sweeney, 2004; Luo & O'Leary, 2005).

On the other hand, rsFC is altered by the prior history of network activation (Buckner & Vincent, 2007; Dosenbach et al., 2007; Lewis, Baldassarre, Committeri, Romani, & Corbetta, 2009; Miall & Robertson, 2006). In chess experts, the connection between the caudate nuclei and DMN is strengthened, indicating the extensive engagement of DMN, which is associated with goal-directed cognitive performance and theory of mind (Fox et al., 2005; Raichle et al., 2001), in chess problem-solving (Duan et al., 2012). Similarly, compared with novices, basketball players also showed increased expertise-related regional GMV in distributed areas and strengthened connecting rsFC within DMN, salience network, and executive control network (Tan et al., 2017). Given these findings, we thus expected to find that batters exhibit functional reorganization in the rsFC within DMN as compared with HC participants. We also examined the trend of seed-based rsFC among the three groups. As in the regional GMV studies, there was also not enough related evidence regarding the trend of differences in the seed-based rsFC corresponding to different levels of experience. We thus speculated linear and nonlinear patterns across the three groups as speculated for the regional GMV data.

To summarize, we examined regional GMV changes and rsFC connections between SB, IB, and HC to investigate the structural and functional neuroplasticity corresponding to different levels of sports experience. Our potential contribution is our applied three-group design, which enabled us to investigate the effect of motor training experience and to examine the pattern of neuroplasticity changes. We expected to find regional GMV changes in motor areas (e.g., primary motor cortex, PMC, and SMA) and their connecting rsFC within DMN in SB and IB participants. Given the lack of related evidence in the literature, we did not formulate a specific hypothesis regarding the pattern of differences in regional GMV and rsFC connections across the three groups. Instead, we speculated that neuroplasticity exhibits linear and nonlinear patterns.

2 | METHODS

2.1 | Participants

Fifty-four male collegiate participants were recruited for the study, including 18 SB, 19 IB, and 17 HC participants. The demographic characteristics of the three groups are summarized in Table 1. SB participants were from highly ranked Taiwanese university baseball teams, with an average of 9.3 years of baseball-playing experience by the time of this experiment. Most of them have participated in international competitions. IB participants were recruited from baseball teams of different university departments, with an average of 4.2 years of baseball-playing experience. They had little experience in participating formal competitions, at most twice in a year in departmental competitions within their own university. HC participants did not have any experience in playing baseball, and did not have a regular exercise habit. All of the participants did not have specific experience in other sports except that one IB participant played football but merely for recreational purposes. All participants were classified as right-handers in accordance with the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had any history of a neurological or psychiatric disorder. This study was approved by the Research Ethics Committee of National Taiwan University. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

2.2 | Data acquisition

Magnetic resonance imaging (MRI) scans were performed on a 3T Siemens Magnetom Skyra scanner (Siemens Medical Solutions, Erlangen, Germany) with a 64-channel head coil. To reduce head motion, the participant's head was placed on a cushion during scanning.

2.2.1 | Structural images

T1-weighted, high-resolution, and three-dimensional images were obtained using a magnetization-prepared rapid gradient-echo sequence. The following acquisition parameters were used: echo time (TE) = 3.3 ms; repetition time (TR) = 2,530 ms; flip angle = 7°; number of slices = 192; slice thickness = 1 mm; image matrix = 256 × 256 voxels; field of view (FOV) = 256 × 256 mm.

2.2.2 | Resting-state functional images

Images were obtained using an echo-planar imaging (EPI) sequence with the following parameters: TE = 25 ms; TR = 2,000 ms; flip angle = 90°; number of slices = 180; FOV = 216 × 216 mm; image matrix = 64 × 64 voxels. During 6 min of the resting scan, participants were asked to keep their eyes open by viewing a white cross with a black background and to relax their mind without thinking about anything in particular.

2.3 | Data analysis and statistical analysis

2.3.1 | Voxel-based morphometry

The raw data of T1 images acquired from scanner were in the format of Digital Imaging and Communications in Medicine (DICOM) and then converted to the format of Neuroimaging Informatics Technology Initiative (NIfTI) using MRIcron (Chris Rorden, Columbia, SC) software. The NIfTI files were then analyzed through voxel-based morphometry (VBM; Ashburner & Friston, 2000) for the computational analysis of differences in local GMV using the VBM8 toolbox in Statistical Parametric Mapping 8 (SPM) (Wellcome Trust Centre for Neuroimaging, London, UK) software package in MATLAB R2016b (MathWorks, Natick, MA).

VBM analysis was conducted as follows: (a) very light bias regularization (0.0001) and Gaussian kernel of 60 mm cutoff at a bias half maximum (FWHM) with International Consortium for Brain Mapping (ICBM) East Asian brains used as a template for structural images. (b) DARTEL algorithm was used to normalize all structural images into Montreal Neurological Institute (MNI) space. (c) Normalized GM, white matter (WM), and cerebrospinal (CFS) images were segmented with the thorough cleanup of any partitions. (d) GM images were subjected to nonlinear modulated normalization. (e) Segmented GM images were smoothed with a Gaussian kernel of 8 mm full-width at a half-maximum (FWHM). (f) Modulated GM images of the three groups were subjected to statistical analysis. To avoid the edge effect around the border, the threshold of all voxels was set with an intensity value of 0.02. A one-way ANOVA was performed with age and BMI entered as covariates of no interest in the statistical model to assess structural differences across three different groups. The threshold of the statistical parametric map was at a voxel-wise intensity of $p < .001$ and a spatial extent threshold of $p < .01$ based on Monte Carlo simulations (i.e., 43 voxels).

Then, we used the Masbar tool (http://marsbar.sourceorge.net/) to extract the regional GMV of each resultant significant cluster as ROI for each participant. Then, we calculated the average of the three groups and fitted the data to the average years of baseball-playing experience of the three groups with both a linear regression and a second-order quadratic polynomial (Gardner, Aglinskas, & Cross, 2017; Mattavelli, Andrews, Asghar, Towler, & Young, 2012). These ROI analyses were used to test whether a linear or a nonlinear trend could better depict the pattern of differences among the three groups. Finally, we reported the R^2 value of each fitted equation for each ROI. The significant clusters also served as seed ROIs for subsequent rsFC analysis.

2.3.2 | Resting-state functional connectivity

Image preprocessing and statistical analysis were performed using Data Processing Assistant for rs-fMRI (DPARSF) (Yan & Zang, 2010) with Data Processing and Analysis for Brain Imaging (DPABI) toolbox (Yan, Wang, Zuo, & Zang, 2016) in SPM8. The preprocessing procedure was as followed: (a) EPI and T1 DICOM images were transformed into NIfTI images. (b) The first 10 volumes of each participant were discarded. (c) Slice timing was performed. (d) Head motion was corrected using a rigid body 6. (e) Multiple regression analysis was performed to remove head motion signal under the criterion of head movement exceeding 2.0 mm or 2.0° of head rotation. (f) A probability threshold of 0.99 on tissue segmentation maps with WM and CSF was set in nuisance covariate analysis and a global signal with auto mask defaulted in DPARSF. (g) Individual structural images were coregistered to functional data. (h) Spatial normalization to MNI space was performed. (i) Spatial smoothing with a Gaussian kernel of 4 mm FWHM was performed. (j) Filtering (0.01–0.1 Hz) was performed to reduce the effects of low-frequency drifts and high-frequency aliasing (Biswal et al., 1995; Lowe, Mock, & Sorenson, 1998).

The significant whole clusters obtained from VBM analysis were defined as seeds. For each participant, the mean time course of each seed was correlated with the time courses of each voxel in the 90% coverage group mask using Pearson correlation. The r-map of each participant was converted into z-map using Fisher's z-transform analysis to acquire optimum normality. Then, the z-map of each group was compared with zero using one-sample *t* test and with age, BMI, and global GMV as covariates of no interest to determine the significant correlations of each seed across the whole brain. The significance level for each group was set at $p < .05$ using AlphaSim correction (with combination of voxelwise threshold of $p < .01$ and a minimum cluster size of 201, 201, and 172 voxels for SB, IB, and HC groups, respectively). The z-maps of the three groups were calculated into a positive mask for each seed through Image Calculator in DPABI by setting the value of mask to a value greater than zero. Finally, group difference was tested using one-way ANOVA with an AlphaSim correction threshold of $p < .001$ (with combination of voxel-wise threshold of $p < .05$ and a minimum cluster size of 92 voxels) with the aforementioned positive mask. To further examine the trend of the differences of seed-based rsFC among the three groups, we also performed a ROI analysis by extracting the correlation from the seed of the significant cluster (ROI) for each participant and fitting the average data of the three groups to the average years of baseball-playing experience of the three groups with a linear and a second-order quadratic polynomial, respectively.

3 | RESULTS

3.1 | Demographic characteristics

As shown in Table 1, the three groups were significantly different in their ages, with SB participants being younger than IB and HC participants ($p < .05$ in post hoc comparisons with Bonferroni correction).

TABLE 1 Demographic characteristics and global brain measurements of the skilled batters (SB), intermediate batters (IB), and healthy controls (HC)

	SB (*n* = 18)		IB (*n* = 19)		HC (*n* = 17)		
Variable	Mean	*SD*	Mean	*SD*	Mean	*SD*	*p*
Age (years)	20.5	1.6	22.9	1.5	23.1	1.9	.00**
Height (cm)	177.7	6	174.8	6.2	174.9	6.5	.30
Weight (kg)	77.4	6.2	69.3	12.7	72.7	13.7	.10
BMI (kg/m^2)	24.6	1.9	22.6	3.6	23.6	3.5	.18
Commencement age (years)	9.6	1.7	11.5	3.3			.03*
Baseball experience (years)	9.3	2.2	4.4	2.6			.00**
Weekly training (hr)	20.2	5.1	5.8	2.5			.00**
Total GMV (cm^3)	731.4	53.2	752.2	31.3	731.5	57.9	.33
Total WMV (cm^3)	563.1	34	581.4	40.9	576.3	56.1	.44

BMI = body mass index; GMV = gray-matter volume; WMV = white-matter volume; *SD* = standard deviation. ** $p < .01$; * $p < .05$, ANOVA or independent *t* test.

Though the three groups were not significantly different in their body mass index (BMI; $p = .18$), BMI has been proven to influence the regional GMV (Pannacciulli et al., 2006), particularly in men (Taki et al., 2008). Thus, both age and BMI were entered as covariates of no interest in the VBM and rsFC statistical models to regress out their potential effects. Moreover, SB participants began to play baseball earlier than IB participants ($p < .05$) and had more baseball experience in terms of years ($p < .01$) and weekly training hours ($p < .01$).

3.2 | Voxel-based morphometry

Total GMV ($p = .329$) and white-matter volume (WMV, $p = .439$) did not significantly differ across groups (Table 1). As shown in Figure 1, ANOVA detected a group effect in five clusters. These clusters included the right SMA, two clusters in the right middle temporal pole extending upwards to the superior temporal pole, the left middle temporal gyrus (MTG) connecting with superior temporal gyrus (STG), and the left rectus connected with the orbital part of the superior frontal gyrus (SFG) (see Table 2 for details). In general, the differences across three groups in the reported areas exhibited a U-shaped pattern, with SB and HC participants showing greater GMV than IB participants. This pattern, however, exhibited a reverse U-shape in the left rectus. Moreover, the GMV of SB and HC participants were significantly

TABLE 2 Brain regions and peak locations with group differences identified through one-way ANOVA

Region	Cluster size (in voxels)	MNI x	MNI y	MNI z	F score
R. SMA	396	3	22.5	49.5	13.85
L. MTG/STG	76	−45	−13.5	−13.5	13.22
L. Rectus/SFG (orb)	64	−7.5	42	−28.5	11.74
R. Middle/superior temporal pole	91	45	4.5	−31.5	10.71
R. Middle temporal pole	162	31.5	9	−36	10.49

Each cluster was determined using a voxel-wise intensity of $p < .001$ (uncorrected) with a cluster size greater than 43 voxels. R = right hemisphere; L = left hemisphere; SMA = supplementary motor area; SFG (orb) = superior frontal gyrus (orbital part); MNI = Montreal Neurological Institute.

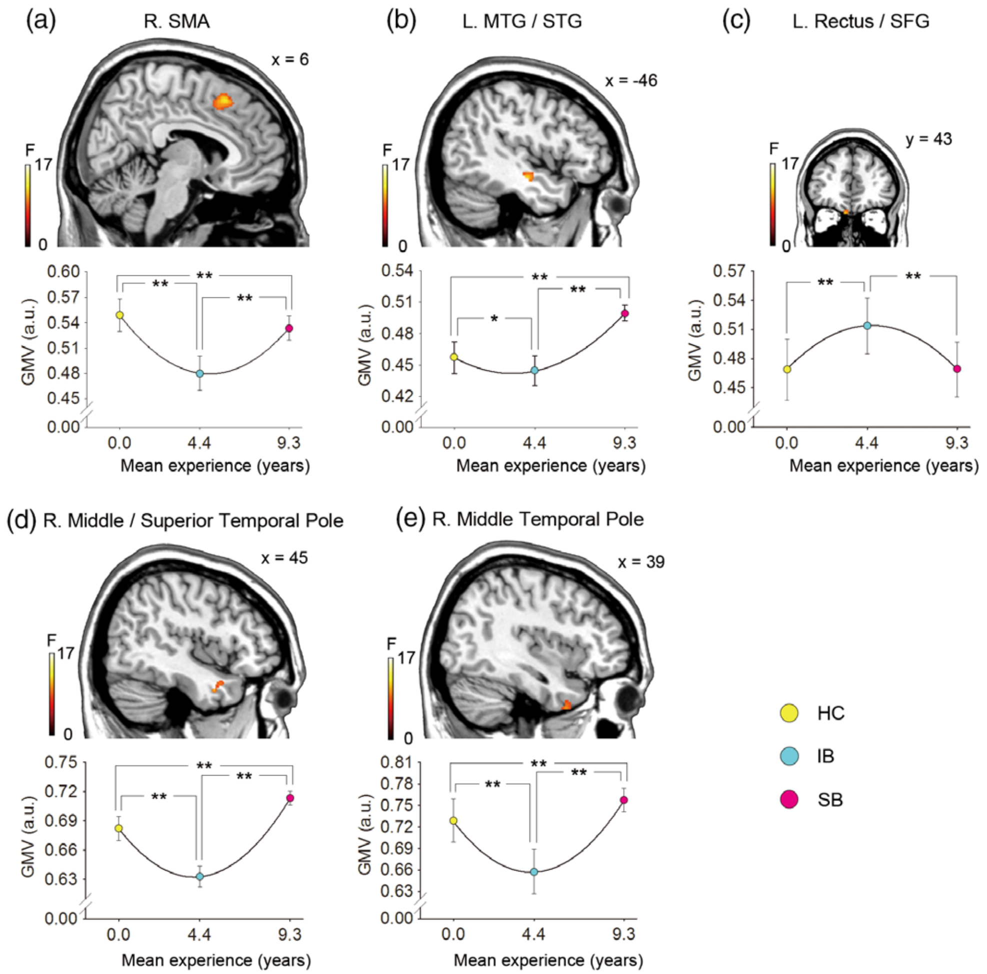

FIGURE 1 Brain regions showing group differences identified through one-way ANOVA ($p < .001$ uncorrected with cluster size greater than 43 voxels), each with the average regional gray-matter volume for the three groups fitted to the average years of baseball-playing experience for the three groups with a quadratic polynomial. Panel a: Right supplementary motor area (SMA); panel b: Left middle/superior temporal gyrus (MTG/STG); panel c: Left rectus/superior frontal gyrus (SFG); panel d: Right middle/superior temporal pole; panel e: Right middle temporal pole (SB = skilled batters; IB = intermediate batters; HC = healthy controls; * $p < .05$; ** $p < .01$; error bars indicate *SD*)

TABLE 3 R^2 values of the quadratic and linear regressions fitting the average regional gray-matter volume and resting-state functional connectivity of the three groups to the average years of baseball-playing experience of the three groups

Region	Regression	R^2	Equation
VBM			
R. SMA	Quadratic	1	$y = 0.549 - 0.028x + 0.003x^2$
	Linear	0.033	$y = 0.528 - 0.001x$
L. MTG/STG	Quadratic	1	$y = 0.457 - 0.01x + 0.002x^2$
	Linear	0.568	$y = 0.446 + 0.005x$
L. Rectus/SFG (orb)	Quadratic	1	$y = 0.469 + 0.019x - 0.002x^2$
	Linear	0.001	$y = 0.485 - 0.0002x$
R. Middle/superior temporal pole	Quadratic	1	$y = 0.682 - 0.024x + 0.003x^2$
	Linear	0.167	$y = 0.660 + 0.004x$
R. Middle temporal pole	Quadratic	1	$y = 0.728 - 0.033x + 0.004x^2$
	Linear	0.099	$y = 0.698 + 0.004x$
rsFC			
R. Middle temporal pole to precuneus	Quadratic	1	$y = (-0.007) + 0.075x - 0.006x^2$
	Linear	0.673	$y = 0.037 + 0.022x$

VBM = voxel-based morphometry; rsFC = resting-state functional connectivity; R = right hemisphere; L = left hemisphere; SMA = supplementary motor area; MTG = middle temporal gyrus; STG = superior temporal gyrus; SFG (orb) = superior frontal gyrus (orbital part)

different, with SB showing greater GMV than HC, except that the GMV in the right SMA of SB was lower than that in the right SMA of HC.

We further extracted the regional GMV of each significant cluster as ROI for each participant and fitted the average data of the three groups to the average years of baseball-playing experience of the three groups (i.e., mean values of 9.3, 4.4, and 0 for SB, IB, and HC participants, respectively), for each ROI. As shown in Table 3, for all ROIs, the data could be perfectly fitted by the quadratic polynomial with R^2 values equal to 1. Whereas the fittings by the linear regression were generally poor and at most moderate (R^2 values from 0.001 to 0.568).

3.3 | Resting-state functional connectivity

As shown in panel a of Figure 2 (top rows), when the right middle temporal pole was used as a seed, adjacent clusters in the right MTG extending to inferior temporal gyrus (ITG) and parahippocampal gyrus in the three groups were significantly and positively correlated. Activity in the left MTG connected with the middle temporal pole and ITG, as well as in the medial SFG, was also significantly and positively correlated with the right middle temporal pole in all of the groups. In addition, activity in the precuneus was positively correlated in the SB and IB participants. As shown in panel a (lowest row) and panel b of Figure 2, ANOVA further detected the group effect in the precuneus (peak at −6, −57, 39; 322 voxels), with SB and IB participants showing greater correlations than those in HC participants. Moreover, the pattern of differences among the three groups corresponding to baseball-playing experience for the three groups could be better depicted by a quadratic polynomial than a linear regression (R^2 values of 1 and 0.673, respectively; details see Table 3). No group difference for rsFC existed between the other seed ROIs and any other brain voxels.

4 | DISCUSSION

To expand our knowledge of neuroplasticity associated with sports experience, we designed this study with three groups of participants with limited to intermediate and extensive baseball-playing experience. Such a design not only allowed us to subtly look into the neuroplasticity corresponding to different levels of sports experience but also provided the possibility to examine the trend of neuroplasticity changes, to the best of our knowledge, has not been investigated yet.

We identified nonlinear pattern of differences in the regional GMV and connecting rsFC among the three groups. Differences in the regional GMV in the right SMA and areas belonging to the ventral stream, such as the left MTG and right middle temporal pole, of the three groups exhibited a U shape. IB participants showed the lowest GMV among the three groups. In contrast, for the left rectus/SFG (orbital part), the pattern was in a reverse U shape with IB showing greater GMV than the other two groups. Using areas that showed group effect in GMV as seed ROIs to investigate the effect of structural neuroplasticity on functional circuitry, we further found that the rsFC between the right middle temporal pole and precuneus was stronger in the SB and IB groups than in the HC groups. In a similar vein, the differences among the three groups could be depicted in a nonlinear trend. These findings demonstrated that the intermediate phase of expertise development is a unique period and exhibits transitional change, which has been overlooked in the literature. Our results suggested that neuroplasticity may not only linearly change as a function of external experience. This interpretation agrees with that of Jäncke et al. (2009), who showed that regional GMV in the bilateral PMC and left IPS changes in a stepwise pattern in individuals with different levels of golf-playing. Therefore, future studies aiming to detect brain areas sensitive to experience should avoid being limited to linear models (Groussard et al., 2014).

An increasing number of functional neuroimaging studies have shown that activation induced by observing an action in the so-called

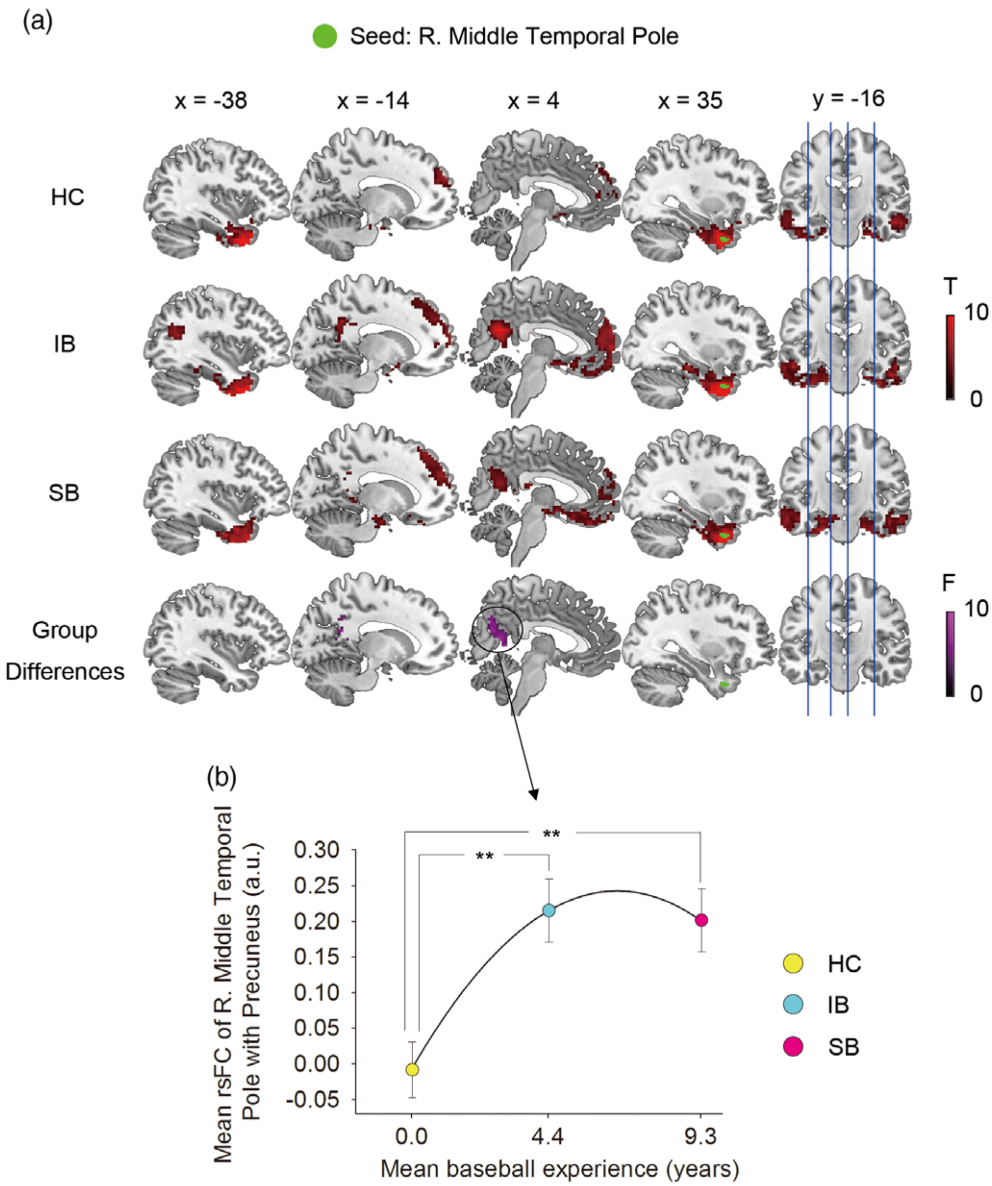

FIGURE 2 Panel a: Pattern of resting-state functional connectivity (rsFC) seeded from the right middle temporal pole in skilled batters (SB), intermediate batters (IB), and healthy controls (HC) ($p < .05$ using AlphaSim correction with combination of voxelwise threshold of $p < .01$ and a minimum cluster size of 201, 201, and 172 voxels for SB, IB, and HC groups, respectively), as well as in intergroup differences as identified through one-way ANOVA ($p < .001$ using AlphaSim correction with combination of voxelwise threshold of $p < .05$ and a minimum cluster size of 92 voxels); panel b: The mean rsFC of the right middle temporal pole with precuneus for the three groups fitted to the average years of baseball-playing experience for the three groups with a quadratic polynomial (**$p < .01$ for pairwise comparison; error bars indicate *SD*)

action observation network (AON) does not necessarily linearly increase as a function of familiarity with the observed action; specifically, observing an unfamiliar action induces an equivalent or higher activation compared with observing a familiar action (Cross et al., 2012; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Liew, Sheng, Margetis, & Aziz-Zadeh, 2013; Tipper, Signorini, & Grafton, 2015). A quadratic, or U-shaped, function was thus proposed to describe the relationship between AON activation and familiarity (Cross et al., 2012; Gardner et al., 2017; Liew et al., 2013). Given that structural neuroplasticity reflects the changes in functional activation or connectivity, finding the nonlinear trend of regional GMV differences associated with the development of sports expertise as in the current study is reasonable.

Our result for the right SMA implied that the type of sports (open- vs. closed-skills sport) does not have a crucial role in determining whether the regional GMV would increase or decrease in response to sports experience (Hänggi et al., 2010; Jacini et al., 2009; Schlaffke et al., 2014). Nevertheless, the phase that exerts the most intense effect on neuroplasticity during expertise development remains unknown. We considered the regional GMV of SMA in individuals without any baseball-playing experience as the baseline. Our results indicated that 4 years of sports experience is associated with significantly low GMV in the regional GMV of SMA. The continuous accumulation of experience over approximately 10 years significantly increased the GMV in this area, which, however, remained lower than that in participants without any baseball-playing experience. This finding emphasized the contribution of our three-group design. Suppose we only recruited two groups of participants and applied two different designs: batters with high and intermediate levels (i.e., SB vs. IB) and high-level batters versus controls (SB vs. HC). Given our present results, these two designs could have provided opposing findings even under the same question: what is the effect of baseball-playing experience on structural neuroplasticity? In other words, comparing SB with IB would reveal a positive effect because the SMA volume of SB is higher than that of IB. In contrast, comparing SB with HC would reveal a negative effect because the SMA volume of SB is lower than that of HC. Interestingly, in other areas, such as left MTG and right middle temporal pole, the two different designs (i.e., SB vs. IB, SB vs. HC) would not provide different results because SB had the highest regional GMV among the three groups. One thus could always interpret that greater baseball-playing experience is associated with the increased GMV in these areas. The difference between the right SMA and the areas belonging to the ventral stream might show that the change in GMV in the right SMA is slower or less sensitive than other areas in participants with an intermediate level of experience.

These differences may be attributed to functional differences. SMA is associated with motor planning and motor control and has a particularly critical role in inhibition (review see Nachev et al., 2008; Tanji, 1994, 1996). A recent electroencephalography study revealed that baseball batters demonstrated better performance in correctly inhibiting their action in a GO/No-Go task that was tailored to reflect a real scenario experienced by a baseball batter (Muraskin et al., 2016). Notably, the better behavioral performance of batters than that of novices could be mapped to differential activity in the SMA. Therefore, the altered SMA volume found in the SB participants might be possibly related to the participants' enhanced inhibitory control abilities. However, at this moment, we are still unable to account for the decrease in SMA volume relative to the baseline SMA volume following intermediate-intensity training. Future studies on functional and structural domains should apply a three-group design to continue investigating this issue. Examining structural neuroplasticity on the cellular or even molecular levels might be also helpful in understanding the underlying biological mechanisms of neuroplasticity.

The left MTG, right middle temporal poles, and even left rectus/SFG could be considered as areas that belong to the ventral stream, an occipitotemporal network that is primarily involved in the processing of the features or perceptual dimensions of objects and is known as the “what” pathway (Goodale, 2008; Goodale et al., 1994; Goodale & Milner, 1992; Milner & Goodale, 2008; Milner, Goodale, & Vingrys, 1995). The ventral stream is crucial in object identification and recognition, such as observing a target or identifying an opponent, and thus plays an important role in sports. Indeed, bilateral MTG has been associated with action observation (review see Caspers, Zilles, Laird, & Eickhoff, 2010), and its GMV is altered due to sports experience, as found in diving (Wei et al., 2009), judo (Jacini et al., 2009), and juggling (Draganski et al., 2004; Gerber et al., 2014). Moreover, previous studies in the sports domain have shown that skilled players could better anticipate the action of their opponent than less-skilled players because they have a better visual search strategy, that is, a better ability to detect the important kinematic action cues (for a review see Müller & Abernethy, 2012; Williams, Davids, & Williams, 1999). Therefore, the greater regional GMV in the left MTG and the right temporal pole in SB participants than in HC participants might be possibly related to the extensive experience of high-level batters in identifying pitches and observing the action performed by the pitcher. We speculated that the lower GMV of IB than HC may be attributed to the following: during the intermediate phase of baseball expertise development, the decrease of these areas might be compensated by the increase of left rectus/SFG. In contrast, the bilateral rectus in internationally competitive judo wrestlers increases, as reported by Jacini et al. (2009). Our speculation, however, has to be validated by future studies with a three-group design.

Finally, using the right middle temporal pole as the seed ROI, we found that the connecting rsFC for SB and IB are very similar, with most areas within the DMN, including the bilateral MTG, ITG, precuneus, and mSFG. By comparing the three groups, we found that the connecting rsFC with precuneus were stronger in SB and IB (with no difference between them) than in HC. Such findings were consistent with previous studies in which experts showed higher seeded-based (defined as structural differences in regional GMV) rsFC with DMN (Di et al., 2012; Duan et al., 2012; Fauvel et al., 2014; Jung et al., 2013; Tan et al., 2017) than controls. DMN is associated with goal-directed cognitive performance and theory of mind (Fox et al., 2005; Raichle et al., 2001). Moreover, the precuneus has been associated with the processing of spatial information during motor preparation and execution (Cavanna & Trimble, 2006; Kawashima, Roland, & O'Sullivan, 1995; Wenderoth, Debaere, Sunaert, & Swinnen, 2005). Therefore, we speculated that high rsFC within the DMN, particularly in the precuneus, in the batters might be possibly associated with the theory of mind, such as deciding whether to swing at the pitch thrown by the pitcher or not by detecting the spatial information of the pitches.

Previous rsFC studies have shown that after learning a motor skill, such as using chopsticks with the nondominant hand (Yoo, Sohn, & Jeong, 2013) or finger tapping (Ma, Narayana, Robin, Fox, & Xiong, 2011), the rsFC of related motor areas increased during the beginning of learning and remained unchanged or decreased after the skill stabilized. These results were inconsistent with our findings, which showed that the rsFCs of SB and IB were higher than that of HC. Moreover, the rsFC of SB and IB were not different from each other because these groups are far from the initial learning phase.

5 | CONCLUSIONS

This study applied a three-group design and recruited participants with different levels of baseball-playing experience. The three-group design enabled the identification of the unique and transient changes that occur during the intermediate phase of expertise development. Regional GMV and rsFC exhibited nonlinear trends that could be illustrated as parabolic shapes. Regional GMV changes in the SMA and areas belonging to the ventral stream may be possibly associated with baseball-specific motor and perceptual experience, such as inhibitory action control and pitch identification. In contrast, the stronger rsFC seeded from the right middle temporal pole to the DMN, particularly in the precuneus, in SB and IB participants than that in the HC participants might be possibly associated with the theory of mind, such as deciding whether to swing or not against the pitcher by detecting the spatial information of pitches. Our experimental design and corresponding findings expanded the current understanding of neuroplasticity by showing that structural or functional brain changes do not necessarily linearly increase as a function of sports experience as suggested by the literature.

6 | LIMITATIONS

Given that this study is a cross-sectional study, we could not rule out the possibility that the neuroplastic changes that we identified here are not induced by different levels of baseball-playing experience but are simply due to different structural and functional predispositions for learning (López-Barroso et al., 2013; Wong, Skoe, Russo, Dees, & Kraus, 2007; Zatorre et al., 2012). A longitudinal study is needed to confirm our findings and speculations. MRI could detect regional GMV only at a macroscopic scale, and various microscopic changes at the synaptic level or larger scales, such as the rapid intracortical dendritic spine and axonal terminal remodeling, glial hypertrophy, and synaptogenesis, may contribute to sports-induced neuroplasticity (Dayan & Cohen, 2011; Grutzendler, Kasthuri, & Gan, 2002; Ilg et al., 2008; Kempermann, Kuhn, & Gage, 1997; Sagi et al., 2012; Trachtenberg et al., 2002; Zatorre et al., 2012). Future studies are needed to investigate the biological mechanisms that underlie this form of plasticity. Finally, though VBM8 toolbox has been widely used in brain morphological studies, it is relatively old. Future studies might confirm our results with a more recent toolbox.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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