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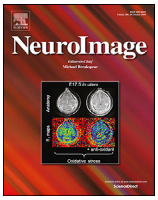

Predicting domain-specific actions in expert table tennis players activates the semantic brain network

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ABSTRACT

Motor expertise acquired during long-term training in sports enables top athletes to predict the outcomes of domain-specific actions better than nonexperts do. However, whether expert players encode actions, in addition to the concrete sensorimotor level, also at a more abstract, conceptual level, remains unclear. The present study manipulated the congruence between body kinematics and the subsequent ball trajectory in videos of an expert player performing table tennis serves. By using functional magnetic resonance imaging, the brain activity was evaluated in expert and nonexpert table tennis players during their predictions on the fate of the ball trajectory in congruent versus incongruent videos. Compared with novices, expert players showed greater activation in the sensorimotor areas (right precentral and postcentral gyri) in the comparison between incongruent vs. congruent videos. They also showed greater activation in areas related to semantic processing: the posterior inferior parietal lobe (angular gyrus), middle temporal gyrus, and ventromedial prefrontal cortex. These findings indicate that action anticipation in expert table tennis players engages both semantic and sensorimotor regions and suggests that skilled action observation in sports utilizes predictions both at motor-kinematic and conceptual levels.

1. Introduction

Action observation is common in our daily life, and we continuously process others' actions to predict their goals, intentions, and motivations. In the context of interactive sports, this processing is a core skill that enables the smooth prediction of the actions of opponents. The rich and specialized experience achieved by expert sport players after years of training contributes to their ability to anticipate the movements of other players (Beilock et al., 2008; Stapel et al., 2016; Wang et al., 2019). This ability is believed to rely, at least in part, on a network of brain areas known as the action mirror neuron system (MNS) or action-observation network (AON) (Smith, 2016; Yarrow et al., 2009). However, interpreting the reasoning of others, which in sports is linked with predicting the outcome of a stream or trajectory of ongoing movements, is likely to require also an abstract level of processing. It is unlikely that the MNS alone enables the inference of the intentions of observed actions (Kilner, 2011). Indeed, the MNS is usually thought to encode concrete representations of actions, including the kinematic information and the pattern of muscle activity. The current study aims to explore whether domain specific action anticipation activates brain areas related to abstract, conceptual processing more in expert players than in novice players.

Professional players of interceptive sports, such as table tennis, provide a useful model to explore the brain correlates of processing movements at an abstract, conceptual level. Expert players must continuously predict the opponents' different ball striking actions during matches and they differ from nonexperts in the repertoire of actions they have learned to perform. Compared with less-experienced or nonexpert players, experienced players show also superior abilities in perceptual processing of other players' actions in a variety of different sport domains (Aglioti et al., 2008; Causer et al., 2017; Ward et al., 2002; Williams et al., 2009). The forward model proposes that if we have performed a particular action, the action representations stored in the MNS can be used to simulate the outcome or subsequent actions when we observe the same action (Blakemore and Decety, 2001). Such internal simulation, presumably, makes processing actions faster and more accurate than that using only

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external feedback. This model is in line with neuroimaging studies, that indicate stronger response in some regions of MNS in expert vs. novice players when observing or anticipating sports-related actions (Balser et al., 2014; Wright et al., 2010, 2011).

The mirror neurons were originally described as visuomotor neurons that are activated during both action execution and pure action observation (di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). The human MNS has been suggested to involve at least ventral and dorsal premotor cortices, primary motor cortex, parietal cortex (Kilner and Lemon, 2013), visual cortex and cerebellum (Molenberghs et al., 2012), and to contribute especially to action understanding (Nishitani and Hari, 2000). Balser et al. (2014) found that compared with novices, tennis professionals show increased activation in the superior parietal lobe, intraparietal sulcus, inferior frontal gyrus, and cerebellum when they predict the outcomes of the opponents' actions. Similarly, many other studies have found distinct effects of motor experience (e.g., expert players vs. nonexperts) on behavioral and neural measures of action processing (Draganski et al., 2004; Jin et al., 2011; Wright et al., 2010; Xu et al., 2016).

Beyond the classic mirror neuron framework, which originally builds on sensorimotor level of processing, the ability to understand the intention of an action, and even the underlying tactic at a more abstract level, is likely to be dependent on brain networks extending to higher-level conceptual representations (Gerson et al., 2017; Vannuscorps and Caramazza, 2015). Players can acquire conceptual knowledge about actions after long-term sport training (van Elk et al., 2014), which may help in predicting actions based on the initial portion of a certain action sequence. Efficient analysis of movement sequence may thus be facilitated by segmenting and creating predictions also beyond fine-grained kinematic details. Indeed, movement sequences can be considered as language-like structures where individual movement kinematics build a coherent entity. For example in dance, movement sequences have been described to reflect regularities and "grammar"-like structure, and expert knowledge of this segmentation facilitates e.g. working memory and learning of new sequences (Opacic et al., 2009). Expert observer, compared to novice observer, may perform also the perceptual analysis of domain-specific movements by relying on a more abstract, conceptual level of processing. Our basic assumption is that processing of opponents movements in interceptive sports utilizes integration between the sensorimotor (mirror neuron) network and the semantic network to understand the intentions and to predict future movements (Kilner, 2011; Ondobaka et al., 2014; Spunt and Lieberman, 2012). Whether action processing relies on conceptual expectations at a semantic level, remains elusive.

Although the MNS and semantic regions are distinct networks in the brain, there are connections between these systems, and they could form an interlinked system (Postle et al., 2008; Pulvermuller, 2005; Rizzolatti and Luppino, 2001). Some empirical studies, for example, by Glover and Dixon (2002), have found that semantic information (e.g., written words 'large' or 'small') can modulate the planning stage of a reaching movement. In addition, researchers have found that conceptually incongruent actions (those contradicting the semantic knowledge of the observer; e.g., bringing a cup to the ear) elicit an increased response of the MNS (particularly in fronto-central-parietal regions) relative to congruent actions (e.g., bringing a cup to the mouth) (Cross et al., 2012; Stapel et al., 2010). Studies using event-related potentials also support the involvement of semantic network in action understanding. Although the N400 was initially described following the onset of incongruent verbal stimuli, it has recently been detected also for incongruent non-verbal stimuli such as actions (Balconi and Caldiroli, 2011; Lee et al., 2018; Proverbio et al., 2010). Incongruent actions, i.e. movements that mismatch to the preceding context, evoke the classic N400 effect (Amoruso et al., 2014; Reid and Striano, 2008; Sitnikova et al., 2003). Moreover, N400 response seems to be modulated by the degree of congruence and expertise (Amoruso et al., 2014). In the context of interceptive sports, however, it has not been clarified to what extent expert players create expectations of actions based on previously acquired conceptual -level knowledge, utilizing same brain areas as for semantic processing.

Therefore, the current study aimed to identify the neural basis of action processing in expert table tennis players by using functional magnetic resonance imaging while participants observed an incongruent or congruent ball striking action sequence. We hypothesized that during processing of sport action sequences conceptual knowledge dependent on the semantic regions of the brain is involved, especially in expert players. We further expected that the conceptual violation in incongruent actions would increase activation of both the semantic brain regions and the MNS in expert players compared with that in nonexperts.

2. Methods

2.1. Participants

Twenty-five expert table tennis players (20.04 ± 1.67 years of age; 10 males) and a control group of 25 college students (20.68 ± 1.57 years of age; 12 males) who had no professional training in table tennis were recruited for the study. The expert table tennis players were members of professional university teams and had more than 7 years of table tennis training (mean, 12.16 years; range, 7–18 years). Expert players and controls did not differ in age or level of education. All participants had normal or corrected-to-normal vision and had no history of psychiatric, medical, or neurological illness. All participants provided written informed consent prior to the study. The experimental protocol was approved by the ethics committee of Shanghai University of Sport.

2.2. Stimuli

Twenty videos depicting a female table tennis player serving, with an equal probability of serving to the left and right, were recorded from the perspective of her opponent (Canon 5D Mark III; resolution, 1280 × 720 pixels). The captured videos were processed using Adobe Premiere software (Adobe Systems Incorporated, San Jose, CA, USA). The player's face in the video was blurred to eliminate the influence of facial features and head motion. Each video was interrupted and exported into a file containing 30 continuous pictures (resolution, 640 × 360 pixels) around the point of racket–ball contact (the seventeenth picture), thus including the initial server's swing (body kinematics video clip, 16 pictures) and the visible ball trajectory until the ball touched the table (ball trajectory video clip, 13 pictures). Each picture was presented for 40 ms and the duration of the entire video was 1200 ms. Two conditions were created by manipulating the videos. Each body kinematics video clip was either combined with its own ball trajectory video clip (congruent video clips) or with the ball trajectory video clip of a serve in the opposite direction (incongruent video clips; Fig. 1) (Tomeo et al., 2012). This resulted in 40 modified videos including 20 congruent and 20 incongruent action videos (see online Supplementary material for examples of these two videos, S1 and S2).

Supplementary video related to this article can be found at https://doi.org/10.1016/j.neuroimage.2019.06.035

2.3. Functional magnetic resonance imaging task

Participants completed an action anticipation task using E-prime software (Psychology Software Tools, Pittsburgh, PA) during functional magnetic resonance imaging (fMRI) scanning. There were 40 trials in total presented randomly, including 20 congruent trials and 20 incongruent trials. Each trial began with the presentation of a fixation cross that lasted 2 s to alert participants to the upcoming video (Fig. 2). Then, a 1200-ms action sequence was presented. After the entire video was presented, the participants were required to report the correct direction (left or right) where the ball would travel given the preceding body kinematics, as accurately as possible and regardless of the subsequent ball trajectory. Responses were given by pressing the corresponding button on a two-button pad. Each trial contained a variable jitter interval of 0 ms, 2000 ms, 4000 ms, or 6000 ms. Participants had practiced before the scanning to familiarize with the task.

2.4. Procedure and imaging parameters

The fMRI was conducted using a 3 T scanner (GE Discovery MR750 3.0 T scanner, GE Medical Systems, Waukesha, WI). Functional images were acquired using a gradient echo-planar imaging sequence (repetition time, 2000 ms; echo time, 30 ms; 43 slices; voxel size, $3.44 \times 3.44 \times 3.2\ \text{mm}^3$; interslice gap, 0 mm; fractional anisotropy, 90°; field of view, $220 \times 220\ \text{mm}^2$). Additionally, a T1-weighted anatomical MRI was also acquired (repetition time, 8.156 ms; echo time, 3.18 ms; 176 slices; voxel size, $1 \times 1 \times 1\ \text{mm}^3$; fractional anisotropy, 8°; field of view, $256 \times 256\ \text{mm}^2$).

2.5. Data analysis

2.5.1. Behavioral data analysis

We calculated the percentage of correct responses (accuracy) for each experimental condition. Trials in which participants responded earlier than 100 ms or later than 2800 ms from the end of the video presentation were discarded from the analysis (Tomeo et al., 2012). The task was practiced before the scanning session and no trials in either group needed to be discarded. Response accuracy was analyzed by repeated measures analysis of variance (ANOVA) with group (experts versus nonexperts) as a between-subjects factor and condition (congruent versus incongruent action videos) as a within-subjects factor.

Statistical analysis was performed using SPSS 20.0 (IBM SPSS, Inc., Chicago, IL, USA). The post hoc test of significant main effects was corrected using Bonferroni corrections. A simple effects test, which also used Bonferroni corrections, was conducted when the interaction was significant. All statistical analyses were conducted using a significance level of $p = 0.05$. Partial eta-squared (η^2_p) values were reported to demonstrate the effect size in the ANOVA.

2.5.2. fMRI data analysis

Functional imaging data were preprocessed and analyzed using DPARSF (http://rfmri.org/DPARSF) (Yan and Zang, 2010), including slice timing, head motion correction, normalized to individual participants' T1-segmented anatomical scans with a resolution of $3\ \text{mm} \times 3\ \text{mm} \times 3\ \text{mm}$, and smoothed with an isotropic Gaussian kernel of 6 mm full width at half maximum.

For each participant, a general linear model (GLM) analysis was performed to analyze statistically the preprocessed images with a canonical hemodynamic response function at the onset of each video using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). Head movement estimates were included in the general linear model as regressors. The data and model were high-pass filtered to a cutoff of 128 s. After model estimation, the task-related T-contrast was performed for the incongruent condition relative to the congruent condition. The resulting contrast images, which reflected the intensity of brain activation for each participant were subjected to a second-level (group-level) analysis using one-sample *t*-tests for each group and independent-sample *t*-tests (expert players vs. nonexperts) at the whole brain level. Activation maps were obtained based on permutation tests using DPARSF (1000 permutations) (Winkler et al., 2016) with threshold-free cluster enhancement (TFCE) (Chen et al., 2018; Libby et al., 2014; Smith and Nichols, 2009). The TFCE-based corrected voxelwise significance threshold was set at $p_{(FWE)} < 0.05$.

To assess more directly how action processing modulated activity across the semantic network, we used a prior anatomical hypothesis and defined regions of interest (ROIs) based on a meta-analysis of semantic processing to comprise the following seven brain regions with an established role in semantic analysis: the posterior inferior parietal lobe (angular gyrus), middle temporal gyrus, fusiform and parahippocampal gyri, dorsomedial prefrontal cortex, inferior frontal gyrus, ventromedial prefrontal cortex, and posterior cingulate gyrus (Binder et al., 2009). Using the MarsBaR toolbox (http://marsbar.sourceforge.net), the mean percentage signal changes in these seven regions were obtained. For each region, a group × condition analysis of variance (ANOVA) model was used to test for a group by stimulus interaction, which would indicate the extent to which a difference in activity in these areas when viewing incongruent and congruent action videos varied between groups.

3. Results

3.1. Behavioral results

The response accuracy was entered into a repeated measures ANOVA with group (expert vs. nonexpert players) as the between-subject factor and condition (congruent vs. incongruent action) as the within-subject factor. The analysis showed a significant main effect of condition ($F_{(1, 48)} = 116.16$, $p < 0.001$, $\eta^2_p = 0.71$); the response accuracy was higher in the congruent condition (mean ± SE, 77.10% ± 2.50%) than in the incongruent condition (29.30% ± 2.98%). The two-way interaction of group × condition was significant ($F_{(1, 48)} = 6.15$, $p = 0.017$, $\eta^2_p = 0.11$). The simple effects analysis of the interaction showed that the response accuracy of the expert table tennis players (mean ± SE; 37.00% ± 3.96%) was higher than that of the nonexperts (21.60% ± 3.96%) in the incongruent condition ($p = 0.008$) but not in the congruent condition ($p = 0.190$). Although the response accuracy was low, expert players who had more table tennis experience were better at anticipating the real ball trajectory based on the preceding body kinematics than nonexperts in the incongruent condition. The simple effects analysis also showed that both expert and nonexpert players showed higher response accuracy in the congruent condition than in incongruent condition ($p < 0.001$ for all).

3.2. fMRI results

The results of the whole-brain analysis are given in Table 1. For expert

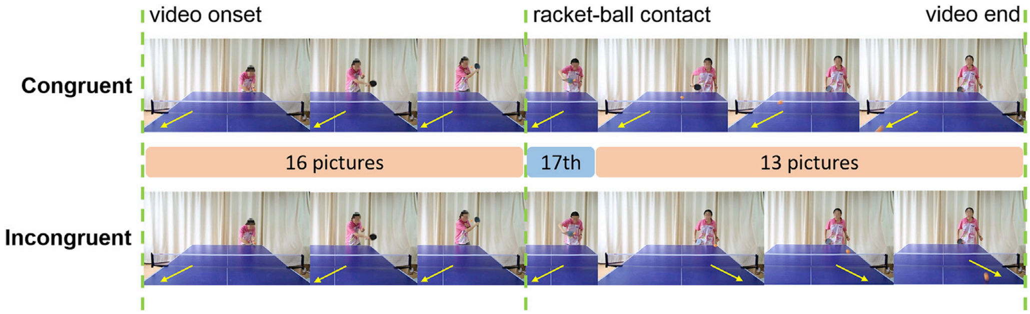

Fig. 1. Exemplar frames of congruent and incongruent videos. A single table tennis player qualified as a National Player of First Grade was serving. The difference between the congruent and incongruent videos occurred after the point of racket–ball contact, with the directions of the body kinematics and ball trajectory being either matched (top row) or mismatched (bottom row).

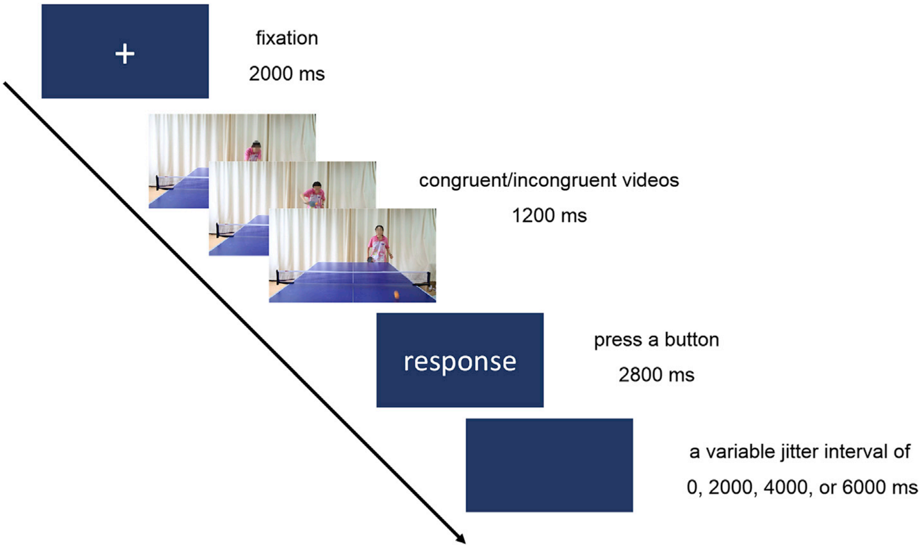

Fig. 2. Sequence of events within a single trial of the action anticipation task.

table tennis players, the incongruent condition elicited greater activations than did the congruent condition in the left fusiform gyrus, right parahippocampal gyrus, left middle temporal gyrus, left orbital inferior frontal gyrus, right precuneus, left and right caudate, left orbital superior frontal gyrus, right middle temporal gyrus, and right middle cingulate gyrus (Fig. 3). There was no brain region for which nonexperts showed higher activation in the incongruent vs. congruent comparison.

The analysis of group differences indicated stronger activation in the expert table tennis players than in the nonexperts in the right caudate, right anterior cingulate gyrus, left anterior cingulate gyrus, right middle frontal gyrus, right postcentral gyrus, and right precentral gyrus (Fig. 4).

To further explore whether action processing also involved the semantic network, we conducted an ROI analysis. The intensity of the activations for all participants in each condition was extracted from the ROIs and was entered into a 2 (group) × 2 (condition) repeated measures ANOVA. The analysis showed a significant interaction of group by condition in the posterior inferior parietal lobe (angular gyrus) ($F_{(1, 48)} = 4.844$, $p = 0.033$, $\eta^2_p = 0.092$), middle temporal gyrus ($F_{(1, 48)} = 5.437$, $p = 0.024$, $\eta^2_p = 0.102$), and ventromedial prefrontal cortex ($F_{(1, 48)} = 4.073$, $p = 0.049$, $\eta^2_p = 0.078$). The simple effects analysis showed a greater signal change for the incongruent condition than for the congruent condition in expert table tennis players ($ps \leq 0.008$) but not in nonexperts ($ps \geq 0.574$) in these three regions (Fig. 5). A significant main effect of condition was found in the dorsomedial prefrontal cortex ($F_{(1, 48)} = 10.772$, $p = 0.002$, $\eta^2_p = 0.183$) and the posterior cingulate gyrus ($F_{(1, 48)} = 4.065$, $p = 0.049$, $\eta^2_p = 0.078$); in these areas the incongruent condition showed higher activation than the congruent condition, but no main effect of group or an interaction between group and condition was founds. No significant effects were found for the other ROIs.

The activation map for the whole-brain analysis and the semantic ROIs are overlapped in Fig. 6. Areas of overlap were found in inferior frontal gyrus, middle temporal gyrus, angular gyrus, middle frontal gyrus and posterior cingulate gyrus.

4. Discussion

The present study investigated action anticipation in expert table tennis players. We used incongruent and congruent action sequences within the movement repertoire of the player's expertise and focused on the activation of the semantic network (Brass et al., 2007; Reid and Striano, 2008; Tomeo et al., 2012). Consistent with our hypothesis, we found stronger activations in experts compared with nonexperts in brain regions associated with semantic analysis during the anticipation of incongruent vs. congruent actions. We also found enhanced activation in the sensorimotor area in experts, most likely reflecting the role of motor experience in the processing of domain-specific action. Our results suggest that skilled action anticipation engages also conceptual level analysis beyond sensorimotor level.

The behavioral results showed that response accuracy was higher for expert table tennis players than for nonexperts in the incongruent but not the congruent condition. This result supports the notion that expert players are better able to use the initial body movements to predict the action outcomes within their domain of expertise (Aglioti et al., 2008; Causer et al., 2017; Tomeo et al., 2012). Similar conclusions have been reached in studies using a temporal occlusion paradigm in which skilled racquet-sport players were superior in using opponent's kinematic information prior to racket-ball contact (Cañal-Bruland, van Ginneken, van der Meer and Williams, 2011; Farrow et al., 2005). It is noteworthy, that due to task requirements the differences between expert and novice players in our study may partly reflect also experience-related differences in encoding and maintenance of the initial body kinematics, besides perceptual processes. Importantly, our behavioral findings indicated the validity of participant selection, relevant for interpreting the effects of sport experience on the activations of motor and semantic-conceptual regions.

Many studies have investigated the role of the sensorimotor area in action processing (Ferrari et al., 2009; Hickok, 2009; Pomiechowska and Csibra, 2017). The whole-brain analysis in the present study showed that activations in the right precentral gyrus and postcentral gyrus were stronger in expert table tennis players than in nonexperts for the incongruent vs. congruent comparison. The area in precentral gyrus appears to correspond to the primary motor hand representation (Graziano et al., 2002), in line with strong emphasis of hand actions in table tennis serving. However interestingly, the differences were shown in the ipsilateral (right) hemisphere. These results, together with the higher response accuracy in experts, indicate that motor simulation of body-kinematics-based representations in the sensorimotor areas could underpin the superior action anticipation.

We also found stronger activation in expert players in the right middle frontal gyrus and anterior cingulate gyrus for the incongruent vs. congruent contrast. The right middle frontal gyrus has been shown to be active when reorienting to unexpected stimuli (Doricchi et al., 2009), whereas the anterior cingulate gyrus is involved in error detection (Swick and Turken, 2002). The observed pattern of stronger neural responses in these two regions in expert table tennis players may thus be further related to the successful recruitment of the brain network needed for

Table 1
Results of the whole-brain analysis.

Region	BA	Number of Cluster	T value	MNI coordinates		
				X	*Y*	*Z*
Expert table tennis players: incongruent condition > congruent condition						
Left fusiform gyrus	37	343	4.54	−39	−45	−24
			3.77	−21	−69	−36
			4.34	−9	−84	−15
Right parahippocampal gyrus	30	32	4.15	21	−33	−12
Left middle temporal gyrus	37	556	4.40	−60	−57	−3
			3.72	−48	−45	12
Left orbital inferior frontal gyrus	47	577	5.75	−45	33	−3
			4.46	−33	15	36
			5.75	−45	33	−3
Right precuneus	/	1451	5.26	12	−39	42
			5.12	−15	−69	33
			4.81	−6	−45	39
Left caudate	/	115	5.19	−12	15	0
Right caudate	20	127	5.01	33	−9	−9
Left orbital superior frontal gyrus	11	868	4.62	−24	60	−3
			4.35	24	51	21
Right middle temporal gyrus	37	580	4.13	42	−66	12
			4.09	39	−54	36
			3.80	51	−42	48
Right middle cingulate gyrus	23	56	5.34	3	−6	36
Expert > nonexpert players: incongruent condition minus congruent condition						
Right caudate	25	17	4.68	9	9	−6
Right anterior cingulate gyrus	32	85	4.36	15	45	9
			3.98	9	36	−9
			3.74	24	48	21
Left anterior cingulate gyrus	25	53	3.75	−3	30	12
Right middle frontal gyrus	46	26	4.65	33	24	39
			3.78	33	30	36
Right postcentral gyrus/ right precentral gyrus	4	77	4.45	48	−21	48
			4.02	48	−9	51

Note: Clusters with $p_{(FWE)} < 0.05$ were considered statistically significant. Coordinates (XYZ) are in Montreal Neurological Institute (MNI) space. BA indicates Brodmann Area.

skilled action anticipation. Indeed, expert observer may better capture the relevant segments in movement trajectory for efficient analysis of the input. Furthermore, the observed activation in the caudate for expert players during the processing of an incongruent action also indicated enhanced action anticipation relative to that in nonexperts, given that the caudate is usually related to anticipation of outcomes (Knutson et al., 2001; Lauwereyns et al., 2002; Tricomi et al., 2004). To sum up, the group comparision in the whole-brain analysis revealed stronger activation in the sensorimotor areas, triggered by a movement trajectory anticipation task, in expert table tennis players. This difference is likely to reflect changes in brain due to experience in interactive sports.

As hypothesized, the semantic network was involved when expert table tennis players predicted the ball trajectory of table tennis serving actions. The ROI analysis showed that activations in the posterior inferior parietal lobe (angular gyrus), middle temporal gyrus, and ventromedial prefrontal cortex were greater in the incongruent condition than in the congruent condition for expert players only. Activation revealed by the whole brain analyses partially overlapped with several regions in the semantic ROIs (Fig. 6), which together suggested the involvement of semantic areas in action processing. Our results are in line with the model by Kilner (2011), which proposes two pathways underlying skilled action processing. The ability to understand actions at an abstract level is encoded in the ventral pathway, including the middle temporal gyrus, that can help predict the most probable intentions of the observed actions through a process of semantic retrieval of the action representations. Our results were consistent with the hypothesis that expert table tennis players generate conceptual expectations during action processing that support active inference of their opponents' intentions (de Lange et al., 2008; Gerson et al., 2017; Ondobaka et al., 2014; Patterson et al., 2007; Vannuscorps and Caramazza, 2015).

The semantic regions that constituted the ROIs in present study were derived from a meta-analysis (Binder et al., 2009) and are associated with the processing of the spoken or written words. Our results suggest that these regions are not limited to the processing of word stimuli but are also associated with the processing of conceptual/abstract information about actions. This interpretation is in line with some studies showing the same brain mechanisms underlying language and action processing, which could both activate semantic representations (Amoruso et al., 2013; Pulvermuller, 2005; Reid et al., 2009; Reid and Striano, 2008). In the field of sport science, Beilock et al. (2008) found that hockey training experience had an impact on language understanding related to hockey actions. Taken these findings together, we propose that the semantic regions are an integral part of the brain network supporting expert table tennis players' ability to predict the outcomes of an opponents' striking actions.

Our ROI analysis also revealed greater activation in two other semantic regions (dorsomedial prefrontal cortex and posterior cingulate

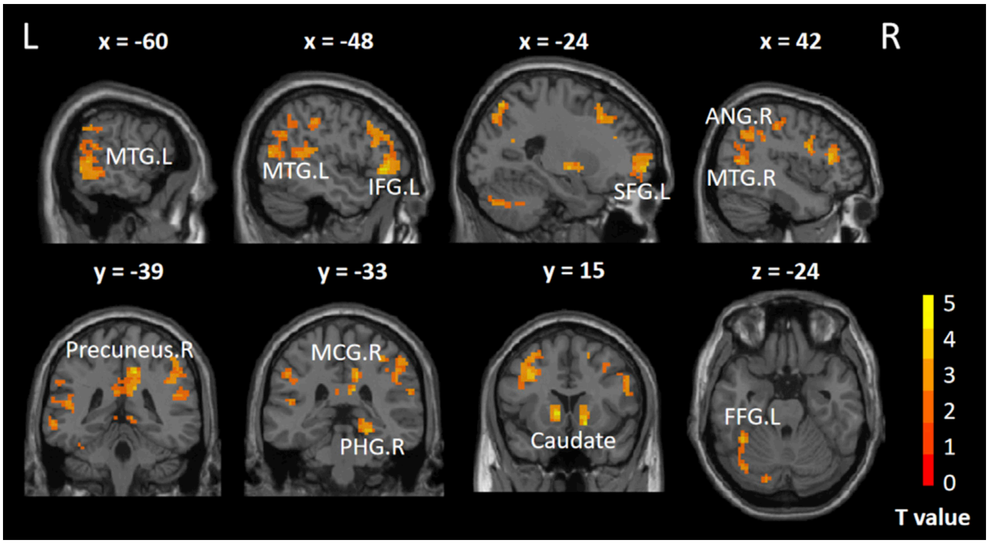

Fig. 3. Significant clusters in selected brain regions of expert table tennis players for the incongruent condition activation greater than the congruent condition activation with a corrected significance level of $p_{(FWE)} < 0.05$. MTG.L indicates left middle temporal gyrus; IFG.L, left orbital inferior frontal gyrus; SFG.L, left orbital superior frontal gyrus; ANG.R, right angular gyrus, MTG.R, right middle temporal gyrus; precuneus.R, right precuneus; MCG.R, right middle cingulate gyrus; PHG.R, right parahippocampal gyrus; and FFG.L, left fusiform gyrus. The color bar indicates *t* values; L, left; R, right.

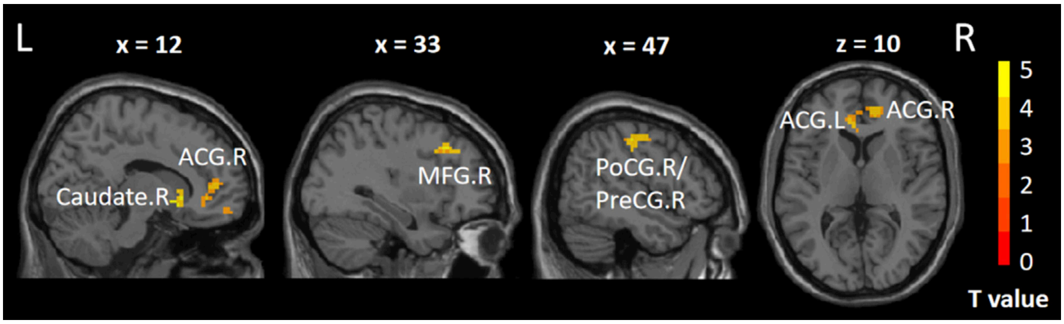

Fig. 4. Areas showing greater activation for expert table tennis players (incongruent condition minus congruent condition) compared with nonexperts (incongruent condition minus congruent condition). Clusters with $p_{(FWE)} < 0.05$ (corrected) were considered statistically significant. Caudate.R indicates right caudate; ACG.R, right anterior cingulate gyrus; MFG.R, right middle frontal gyrus; PoCG.R, right postcentral gyrus; PreCG.R, right precentral gyrus; and ACG.L, left anterior cingulate gyrus. Color bar indicates *t* values; L, left; R, right.

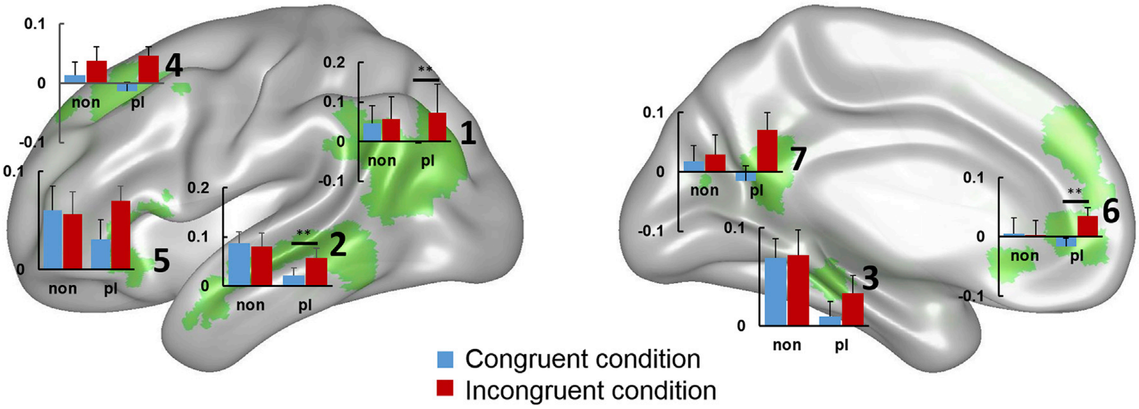

Fig. 5. The activation intensity (signal change % BOLD) in seven brain regions associated with semantics for the incongruent condition and for the congruent condition based on a meta-analysis, including the ① posterior inferior parietal lobe (angular gyrus), ② middle temporal gyrus, ③ fusiform and parahippocampal gyri, ④ dorsomedial prefrontal cortex, ⑤ inferior frontal gyrus, ⑥ ventromedial prefrontal cortex, and ⑦ posterior cingulate gyrus. The MNI coordinates of each region are shown in the supplementary materials (Table S3). $^{**}p < 0.01$ between the two conditions; non indicates nonexperts; pl, expert table tennis players.

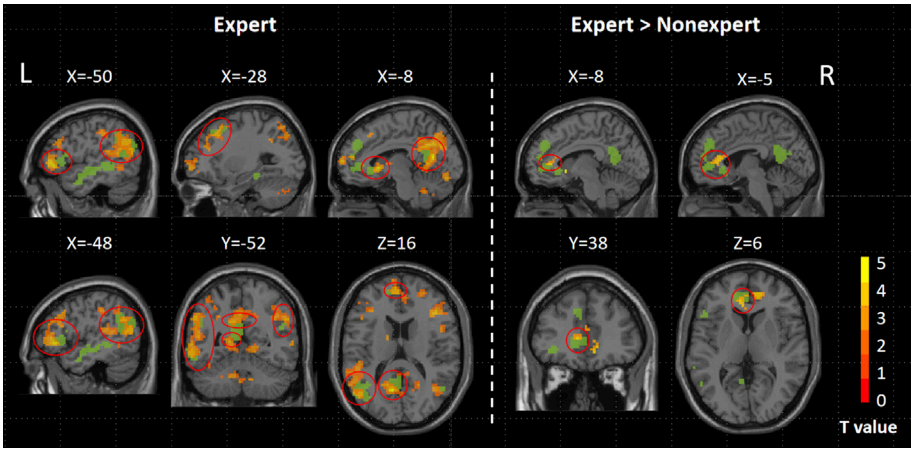

Fig. 6. The semantic ROIs (green) and activation maps of the whole-brain analyses for experts only (left panel) and for expert table tennis players compared with nonexperts (right panel). Red circles have been placed around the overlap foci.

gyrus) in the incongruent vs. congruent condition. Although in these regions the group vs. condition interaction was not significant, the general patter of incongruent > congruent was comparable to the regions where expert players showed stronger activation than novices. Not all semantic regions, however, were activated by the task, such as the fusiform and parahippocampal gyri and the inferior frontal gyrus. One plausible explanation is the difference in abstract processing of actions vs. words. Inferior frontal gyrus is often implicated in phonological processing, articulatory planning, and syntactic analysis rather than semantic processing (Binder et al., 2009; Grodzinsky and Friederici, 2006; Tan et al., 2005). In the same way, although the specific roles of the fusiform and parahippocampal gyri are still unknown (Binder et al., 2009), they may be more distinctively related to word processing. Therefore, we speculate that this pattern of activation influenced by expertise serves as a network to make these actions appear meaningful to expert players, and reflects quite different system from the general semantic network. It is however important to note, that the task in our study was only indirectly linked to actual intentions, and further studies are need to explore action processing with explicit conceptual intentions.

Our results on the differential brain activations between the incongruent vs. congruent action processing are well in line with predictive coding hypotheses. This framework suggests that the brain is predisposed to process expected incoming input, and more resources are devoted when predictions are not met (Friston, 2005). Our data on expert tennis players can be interpreted to reflect acquired experience implemented in the sensorimotor prediction pattern. Our results also suggest that brain processes linked to abstract level of processing appear to code relevant information for the athletic expertise–related prediction. This interpretation aligns with results from neuromagnetic studies that have extended the classic semantic N400 effect to the perceived "mismatch" between predicted and observed actions (Balconi and Pozzoli, 2005; Kutas and Hillyard, 1980; Sitnikova et al., 2003). Indeed, our results could be taken as support for the general notion of the importance of prediction at multiple levels, and the idea of build-up of predictions at multiple systems through accumulation of experience.

In some previous neuroimaging studies, the general level of physical activity and fitness has been linked to differences in brain function and structure (Erickson et al., 2011; Mcgregor et al., 2013; Ruotsalainen et al., 2019; Voss et al., 2010). In principle, our results could be influenced by a general difference in fitness between the participant groups. However, our results are likely to be attributable to specific expertise rather than to training in general or to physical fitness because cardiovascular training or physical fitness has mainly been associated with general cognitive functions, such as executive control and memory, which are primarily subserved by the prefrontal cortex and hippocampus (Chaddock et al., 2010; Colcombe et al., 2004; Holzschneider et al., 2012; Voss et al., 2011).

In conclusion, our findings suggest a multitiered network underlying action perception and predicting domain-specific actions that involve both semantic and sensorimotor regions, which were associated with a skilled action anticipation ability in expert table tennis players.

Ethics statement

The experimental protocol was approved by the ethics committee of Shanghai University of Sport.

Conflicts of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.06.035.

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