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Author(s): Wang, Yingying; Lu, Yingzhi; Deng, Yuqin; Gu, Nan; Parviainen, Tiina; Zhou, Chenglin

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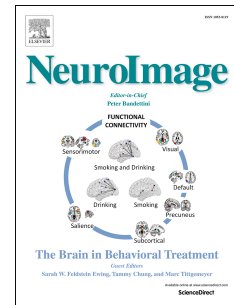
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Predicting domain-specific actions in expert table tennis players activates the semantic brain network

Yingying Wang^a, Yingzhi Lu^a, Yuqin Deng^b, Nan Gu^c, Parviainen Tiina^{d,1}, Chenglin Zhou^{a,1,*}

^a Department of Psychology, Shanghai University of Sport, Shanghai, China, 200438;

^b School of Sports Science, Nantong University, Nantong, China, 226019;

^c China Table Tennis College, Shanghai University of Sport, Shanghai, China, 200438

^d Department of Psychology, University of Jyväskylä, Jyväskylä, Finland, 40014;

Corresponding author:

* Chenglin Zhou: No.399 Changhai Road, Yangpu District, Shanghai, China, 200438;

Tel: +(86)02165508100;

E-mail: chenglin_600@126.com

¹ Shared senior authorship.

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

Highlights

- Involvement of the semantic network in skilled action anticipation was examined.
- Table tennis expert and nonexpert players predicted congruent or incongruent action sequences.
- Functional magnetic resonance imaging assessed brain activation during an action anticipation task.
- Predicting domain-specific actions involves both semantic and sensorimotor networks in experts.

Ethics Statement

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

21 Abstract

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

39

40 Key Words:

41 functional magnetic resonance imaging; semantic expectation; action anticipation;
42 table tennis player, mirror neuron system, action observation

43

44 1. Introduction

45

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

64

65 Professional players of interceptive sports, such as table tennis, provide a useful
66 model to explore the brain correlates of processing movements at an abstract,
67 conceptual level. Expert players must continuously predict the opponents' different
68 ball striking actions during matches and they differ from nonexperts in the repertoire
69 of actions they have learned to perform. Compared with less-experienced or
70 nonexpert players, experienced players show also superior abilities in perceptual
71 processing of other players' actions in a variety of different sport domains (Aglioti,
72 Cesari, Romani, & Urgesi, 2008; Causer, Smeeton, & Williams, 2017; Ward, Williams,
73 & Bennett, 2002; Williams, Huys, Cañal-Bruland, & Hagemann, 2009). The forward
74 model proposes that if we have performed a particular action, the action
75 representations stored in the MNS can be used to simulate the outcome or subsequent
76 actions when we observe the same action (Blakemore & Decety, 2001). Such internal
77 simulation, presumably, makes processing actions faster and more accurate than that
78 using only external feedback. This model is in line with neuroimaging studies, that
79 indicate stronger response in some regions of MNS in expert vs. novice players when
80 observing or anticipating sports-related actions (Balsler et al., 2014; Wright, Bishop,
81 Jackson, & Abernethy, 2010, 2011).

82

83 The mirror neurons were originally described as visuomotor neurons that are activated
84 during both action execution and pure action observation (di Pellegrino, Fadiga,
85 Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti & Craighero, 2004). The human MNS
86 has been suggested to involve at least ventral and dorsal premotor cortices, primary
87 motor cortex, parietal cortex (Kilner & Lemon, 2013), visual cortex and cerebellum

88 (Molenberghs, Cunnington, & Mattingley, 2012), and to contribute especially to
89 action understanding (Nishitani & Hari, 2000). Balsler et al. (2014) found that
90 compared with novices, tennis professionals show increased activation in the superior
91 parietal lobe, intraparietal sulcus, inferior frontal gyrus, and cerebellum when they
92 predict the outcomes of the opponents' actions. Similarly, many other studies have
93 found distinct effects of motor experience (e.g., expert players vs. nonexperts) on
94 behavioral and neural measures of action processing (Draganski et al., 2004; Jin et al.,
95 2011; Wright et al., 2010; Xu et al., 2016).

96
97 Beyond the classic mirror neuron framework, which originally builds on sensorimotor
98 level of processing, the ability to understand the intention of an action, and even the
99 underlying tactic at a more abstract level, is likely to be dependent on brain networks
100 extending to higher-level conceptual representations (Gerson, Meyer, Hunnius, &
101 Bekkering, 2017; Vannuscorps & Caramazza, 2015). Players can acquire conceptual
102 knowledge about actions after long-term sport training (van Elk, van Schie, &
103 Bekkering, 2014), which may help in predicting actions based on the initial portion of
104 a certain action sequence. Efficient analysis of movement sequence may thus be
105 facilitated by segmenting and creating predictions also beyond fine-grained kinematic
106 details. Indeed, movement sequences can be considered as language-like structures
107 where individual movement kinematics build a coherent entity. For example in dance,
108 movement sequences have been described to reflect regularities and "grammar"-like
109 structure, and expert knowledge of this segmentation facilitates e.g. working memory
110 and learning of new sequences (Opacic, Stevens, & Tillmann, 2009). Expert observer,
111 compared to novice observer, may perform also the perceptual analysis of
112 domain-specific movements by relying on a more abstract, conceptual level of
113 processing. Our basic assumption is that processing of opponents movements in
114 interceptive sports utilizes integration between the sensorimotor (mirror neuron)
115 network and the semantic network to understand the intentions and to predict future
116 movements (Kilner, 2011; Ondobaka, de Lange, Wittmann, Frith, & Bekkering, 2014;
117 Spunt & Lieberman, 2012). Whether action processing relies on conceptual
118 expectations at a semantic level, remains elusive.

119
120 Although the MNS and semantic regions are distinct networks in the brain, there are
121 connections between these systems, and they could form an interlinked system (Postle,
122 McMahon, Ashton, Meredith, & de Zubicaray, 2008; Pulvermuller, 2005; Rizzolatti &
123 Luppino, 2001). Some empirical studies, for example, by Glover and Dixon (2002),
124 have found that semantic information (e.g., written words 'large' or 'small') can
125 modulate the planning stage of a reaching movement. In addition, researchers have
126 found that conceptually incongruent actions (those contradicting the semantic
127 knowledge of the observer; e.g., bringing a cup to the ear) elicit an increased response
128 of the MNS (particularly in fronto-central-parietal regions) relative to congruent
129 actions (e.g., bringing a cup to the mouth) (Cross et al., 2012; Stapel, Hunnius, van
130 Elk, & Bekkering, 2010). Studies using event-related potentials also support the
131 involvement of semantic network in action understanding. Although the N400 was

132 initially described following the onset of incongruent verbal stimuli, it has recently
133 been detected also for incongruent non-verbal stimuli such as actions (Michela
134 Balconi & Caldiroli, 2011; Lee, Huang, Federmeier, & Buxbaum, 2018; Proverbio,
135 Riva, & Zani, 2010). Incongruent actions, i.e. movements that mismatch to the
136 preceding context, evoke the classic N400 effect (Amoruso et al., 2014; Reid &
137 Striano, 2008; Sitnikova, Kuperberg, & Holcomb, 2003). Moreover, N400 response
138 seems to be modulated by the degree of congruence and expertise (Amoruso et al.,
139 2014). In the context of interceptive sports, however, it has not been clarified to what
140 extent expert players create expectations of actions based on previously acquired
141 conceptual -level knowledge, utilizing same brain areas as for semantic processing.

142
143 Therefore, the current study aimed to identify the neural basis of action processing in
144 expert table tennis players by using functional magnetic resonance imaging while
145 participants observed an incongruent or congruent ball striking action sequence. We
146 hypothesized that during processing of sport action sequences conceptual knowledge
147 dependent on the semantic regions of the brain is involved, especially in expert
148 players. We further expected that the conceptual violation in incongruent actions
149 would increase activation of both the semantic brain regions and the MNS in expert
150 players compared with that in nonexperts.

151

152 **2. Methods**

153

154 2.1 Participants

155

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

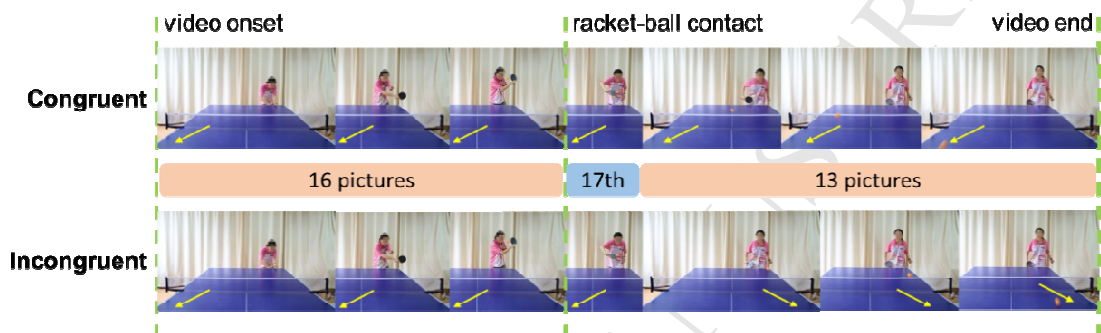
166

167 2.2 Stimuli

168

169 Twenty videos depicting a female table tennis player serving, with an equal
170 probability of serving to the left and right, were recorded from the perspective of her
171 opponent (Canon 5D Mark III; resolution, 1280×720 pixels). The captured videos
172 were processed using Adobe Premiere software (Adobe Systems Incorporated, San
173 Jose, CA, USA). The player's face in the video was blurred to eliminate the influence
174 of facial features and head motion. Each video was interrupted and exported into a file
175 containing 30 continuous pictures (resolution, 640×360 pixels) around the point of

176 racket–ball contact (the seventeenth picture), thus including the initial server’s swing
 177 (body kinematics video clip, 16 pictures) and the visible ball trajectory until the ball
 178 touched the table (ball trajectory video clip, 13 pictures). Each picture was presented
 179 for 40 ms and the duration of the entire video was 1200 ms. Two conditions were
 180 created by manipulating the videos. Each body kinematics video clip was either
 181 combined with its own ball trajectory video clip (congruent video clips) or with the
 182 ball trajectory video clip of a serve in the opposite direction (incongruent video clips;
 183 Fig. 1) (Tomeo, Cesari, Aglioti, & Urgesi, 2012). This resulted in 40 modified videos
 184 including 20 congruent and 20 incongruent action videos (see online Supplementary
 185 material for examples of these two videos, S1 and S2).
 186



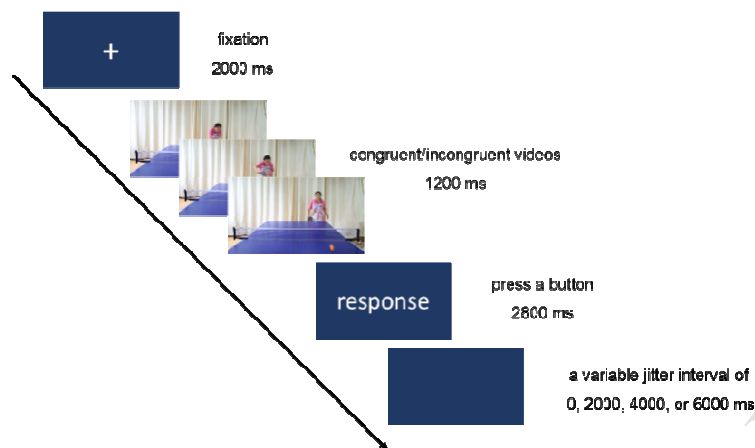
187

188 Figure 1. Exemplar frames of congruent and incongruent videos. A single table tennis
 189 player qualified as a National Player of First Grade was serving. The difference
 190 between the congruent and incongruent videos occurred after the point of racket–ball
 191 contact, with the directions of the body kinematics and ball trajectory being either
 192 matched (top row) or mismatched (bottom row).
 193

194 2.3 Functional Magnetic Resonance Imaging Task

195

196 Participants completed an action anticipation task using E-prime software
 197 (Psychology Software Tools, Pittsburgh, PA) during functional magnetic resonance
 198 imaging (fMRI) scanning. There were 40 trials in total presented randomly, including
 199 20 congruent trials and 20 incongruent trials. Each trial began with the presentation of
 200 a fixation cross that lasted 2 s to alert participants to the upcoming video (Fig. 2).
 201 Then, a 1200-ms action sequence was presented. After the entire video was presented,
 202 the participants were required to report the correct direction (left or right) where the
 203 ball would travel given the preceding body kinematics, as accurately as possible and
 204 regardless of the subsequent ball trajectory. Responses were given by pressing the
 205 corresponding button on a two-button pad. Each trial contained a variable jitter
 206 interval of 0 ms, 2000 ms, 4000 ms, or 6000 ms. Participants had practiced before the
 207 scanning to familiarize with the task.



208
209 Figure 2. Sequence of events within a single trial of the action anticipation task.

210
211 2.4 Procedure and Imaging Parameters

212
213 The fMRI was conducted using a 3T scanner (GE Discovery MR750 3.0T scanner,
214 GE Medical Systems, Waukesha, WI). Functional images were acquired using a
215 gradient echo-planar imaging sequence (repetition time, 2000 ms; echo time, 30 ms;
216 43 slices; voxel size, $3.44 \times 3.44 \times 3.2 \text{ mm}^3$; interslice gap, 3.2 mm; fractional
217 anisotropy, 90° ; field of view, $220 \times 220 \text{ mm}^2$). Additionally, a T1-weighted
218 anatomical MRI was also acquired (repetition time, 8.156 ms; echo time, 3.18 ms;
219 176 slices; voxel size, $1 \times 1 \times 1 \text{ mm}^3$; interslice gap, 1 mm; fractional anisotropy, 12° ;
220 field of view, $256 \times 256 \text{ mm}^2$).

221
222 2.5 Data Analysis

223
224 2.5.1 Behavioral Data Analysis

225
226 We calculated the percentage of correct responses (accuracy) for each experimental
227 condition. Trials in which participants responded earlier than 100 ms or later than
228 2800 ms from the end of the video presentation were discarded from the analysis
229 (Tomeo, Cesari, Aglioti, & Urgesi, 2012). The task was practiced before the scanning
230 session and no trials in either group needed to be discarded. Response accuracy was
231 analyzed by repeated measures analysis of variance (ANOVA) with group (experts
232 versus nonexperts) as a between-subjects factor and condition (congruent versus
233 incongruent action videos) as a within-subjects factor.

234
235 Statistical analysis was performed using SPSS 20.0 (IBM SPSS, Inc., Chicago, IL,
236 USA). The post hoc test of significant main effects was corrected using Bonferroni
237 corrections. A simple effects test, which also used Bonferroni corrections, was
238 conducted when the interaction was significant. All statistical analyses were
239 conducted using a significance level of $p = 0.05$. Partial eta-squared (η^2_p) values were
240 reported to demonstrate the effect size in the ANOVA.

242 2.5.2 fMRI Data Analysis

243

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

249

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

265

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

278

279 3. Results

280

281 3.1 Behavioral Results

282

283 The response accuracy was entered into a repeated measures ANOVA with group
284 (expert vs. nonexpert players) as the between-subject factor and condition (congruent
285 vs. incongruent action) as the within-subject factor. The analysis showed a significant

286 main effect of condition ($F_{(1, 48)} = 116.16, p < 0.001, \eta^2_p = 0.71$); the response
287 accuracy was higher in the congruent condition (mean \pm SE, 77.10% \pm 2.50%) than in
288 the incongruent condition (29.30% \pm 2.98%). The two-way interaction of group \times
289 condition was significant ($F_{(1, 48)} = 6.15, p = 0.017, \eta^2_p = 0.11$). The simple effects
290 analysis of the interaction showed that the response accuracy of the expert table tennis
291 players (mean \pm SE; 37.00% \pm 3.96%) was higher than that of the nonexperts
292 (21.60% \pm 3.96%) in the incongruent condition ($p = 0.008$) but not in the congruent
293 condition ($p = 0.190$). Although the response accuracy was low, expert players who
294 had more table tennis experience were better at anticipating the real ball trajectory
295 based on the preceding body kinematics than nonexperts in the incongruent condition.
296 The simple effects analysis also showed that both expert and nonexpert players
297 showed higher response accuracy in the congruent condition than in incongruent
298 condition ($p < 0.001$ for all).

299

300 3.2 fMRI Results

301

302 The results of the whole-brain analysis are given in Table 1. For expert table tennis
303 players, the incongruent condition elicited greater activations than did the congruent
304 condition in the left fusiform gyrus, right parahippocampal gyrus, left middle
305 temporal gyrus, left orbital inferior frontal gyrus, right precuneus, left and right
306 caudate, left orbital superior frontal gyrus, right middle temporal gyrus, and right
307 middle cingulate gyrus (Fig. 3). There was no brain region for which nonexperts
308 showed higher activation in the incongruent vs. congruent comparison.

309

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

314

315

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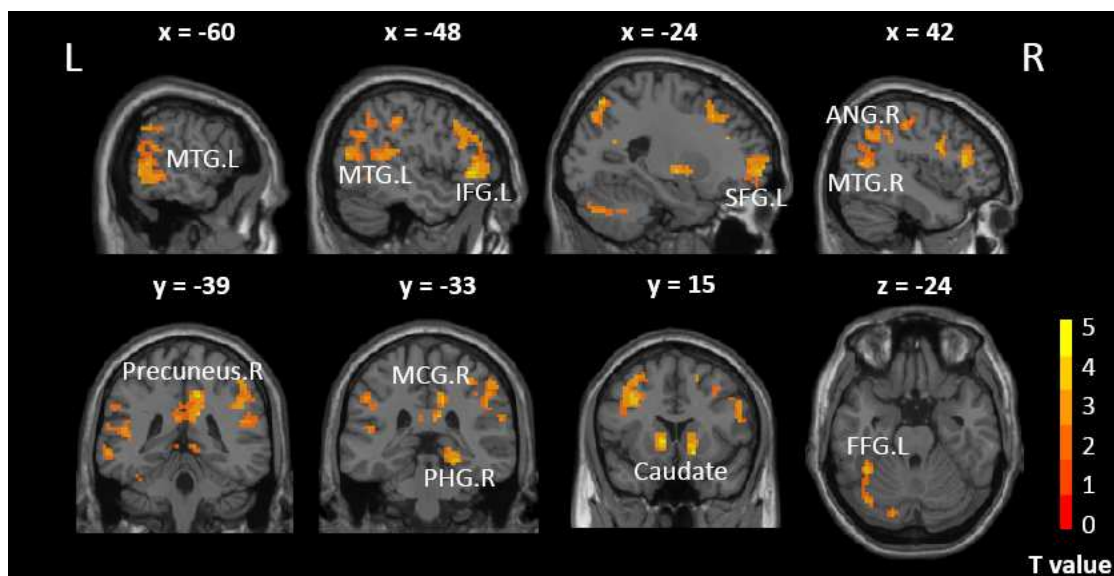
Table 1. Results of the whole-brain analysis

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

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

320

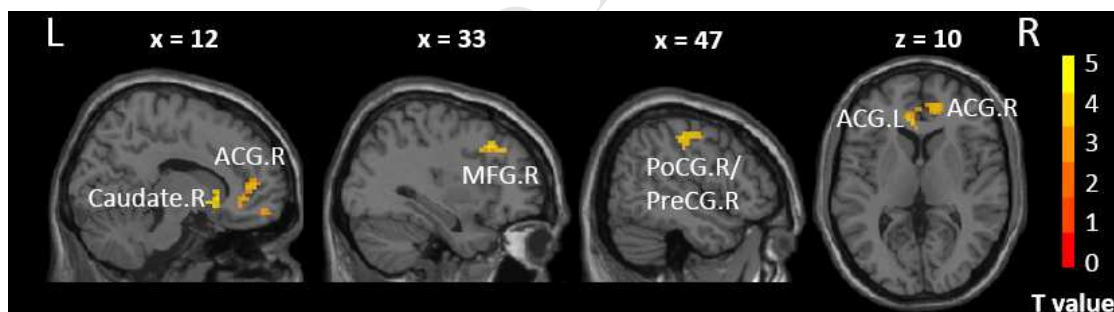
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322

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

331



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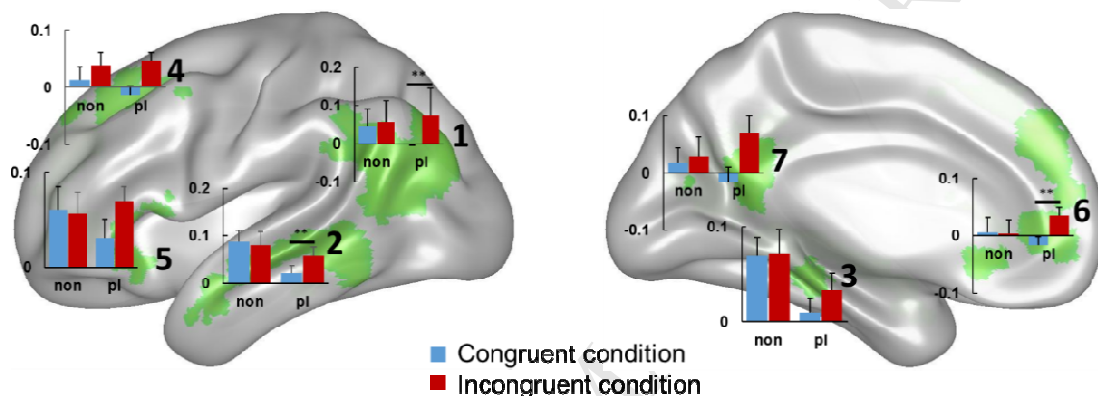
333 Figure 4. Areas showing greater activation for expert table tennis players (incongruent
 334 condition minus congruent condition) compared with nonexperts (incongruent
 335 condition minus congruent condition). Clusters with $p_{(FWE)} < 0.05$ (corrected) were
 336 considered statistically significant.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

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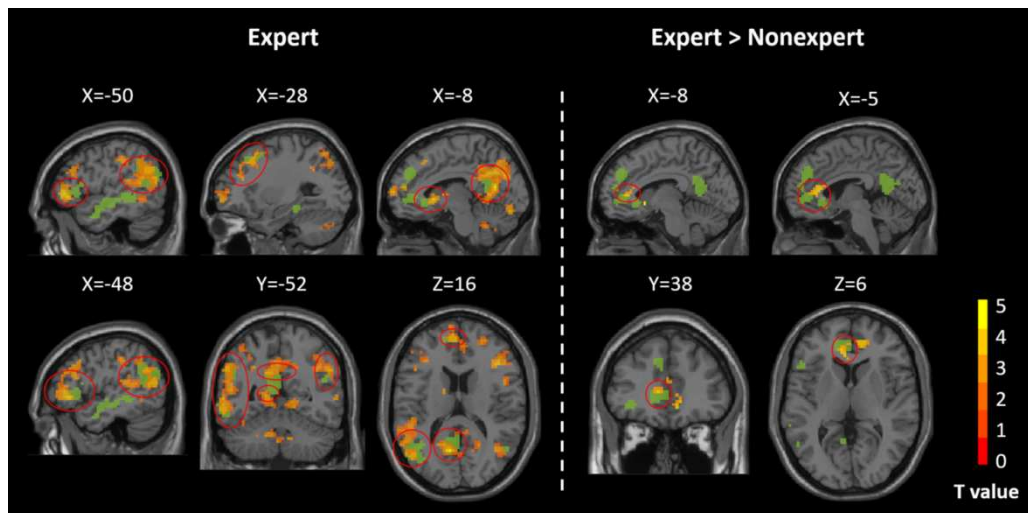
342 To further explore whether action processing also involved the semantic network, we
 343 conducted an ROI analysis. The intensity of the activations for all participants in each
 344 condition was extracted from the ROIs and was entered into a 2 (group) \times 2
 345 (condition) repeated measures ANOVA. The analysis showed a significant interaction

346 of group by condition in the posterior inferior parietal lobe (angular gyrus) ($F_{(1,48)} =$
 347 4.844, $p = 0.033$, $\eta^2_p = 0.092$), middle temporal gyrus ($F_{(1,48)} = 5.437$, $p = 0.024$, $\eta^2_p =$
 348 0.102), and ventromedial prefrontal cortex ($F_{(1,48)} = 4.073$, $p = 0.049$, $\eta^2_p = 0.078$).
 349 The simple effects analysis showed a greater signal change for the incongruent
 350 condition than for the congruent condition in expert table tennis players ($ps \leq 0.008$)
 351 but not in nonexperts ($ps \geq 0.574$) in these three regions (Fig. 5). A significant main
 352 effect of condition was found in the dorsomedial prefrontal cortex ($F_{(1,48)} = 10.772$, p
 353 $= 0.002$, $\eta^2_p = 0.183$) and the posterior cingulate gyrus ($F_{(1,48)} = 4.065$, $p = 0.049$, η^2_p
 354 $= 0.078$); in these areas the incongruent condition showed higher activation than the
 355 congruent condition, but no main effect of group or an interaction between group and
 356 condition was found. No significant effects were found for the other ROIs.
 357



358
 359 Figure 5. The activation intensity (signal change % BOLD) in seven brain regions
 360 associated with semantics for the incongruent condition and for the congruent
 361 condition based on a meta-analysis, including the ① posterior inferior parietal lobe
 362 (angular gyrus), ② middle temporal gyrus, ③ fusiform and parahippocampal gyri,
 363 ④ dorsomedial prefrontal cortex, ⑤ inferior frontal gyrus, ⑥ ventromedial
 364 prefrontal cortex, and ⑦ posterior cingulate gyrus. The MNI coordinates of each
 365 region are shown in the supplementary materials (Table S3). $**p < 0.01$ between the
 366 two conditions; non indicates nonexperts; pl, expert table tennis players.
 367

368 The activation map for the whole-brain analysis and the semantic ROIs are
 369 overlapped in Fig.6. Areas of overlap were found in inferior frontal gyrus, middle
 370 temporal gyrus, angular gyrus, middle frontal gyrus and posterior cingulate gyrus.
 371



372

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

376

377 4. Discussion

378

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

389

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

404

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

417

418 We also found stronger activation in expert players in the right middle frontal gyrus
419 and anterior cingulate gyrus for the incongruent vs. congruent contrast. The right
420 middle frontal gyrus has been shown to be active when reorienting to unexpected
421 stimuli (Doricchi, Macci, Silvetti, & Macaluso, 2009), whereas the anterior cingulate
422 gyrus is involved in error detection (Swick & Turken, 2002). The observed pattern of
423 stronger neural responses in these two regions in expert table tennis players may thus
424 be further related to the successful recruitment of the brain network needed for skilled
425 action anticipation. Indeed, expert observer may better capture the relevant segments
426 in movement trajectory for efficient analysis of the input. Furthermore, the observed
427 activation in the caudate for expert players during the processing of an incongruent
428 action also indicated enhanced action anticipation relative to that in nonexperts, given
429 that the caudate is usually related to anticipation of outcomes (Knutson, Fong, Adams,
430 Varner, & Hommer, 2001; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Tricomi,
431 Delgado, & Fiez, 2004). To sum up, the group comparison in the whole-brain
432 analysis revealed stronger activation in the sensorimotor areas, triggered by a
433 movement trajectory anticipation task, in expert table tennis players. This difference is
434 likely to reflect changes in brain due to experience in interactive sports.

435

436 As hypothesized, the semantic network was involved when expert table tennis players
437 predicted the ball trajectory of table tennis serving actions. The ROI analysis showed
438 that activations in the posterior inferior parietal lobe (angular gyrus), middle temporal
439 gyrus, and ventromedial prefrontal cortex were greater in the incongruent condition
440 than in the congruent condition for expert players only. Activation revealed by the
441 whole brain analyses partially overlapped with several regions in the semantic ROIs
442 (Fig. 6), which together suggested the involvement of semantic areas in action
443 processing. Our results are in line with the model by Kilner (2011), which proposes
444 two pathways underlying skilled action processing. The ability to understand actions
445 at an abstract level is encoded in the ventral pathway, including the middle temporal
446 gyrus, that can help predict the most probable intentions of the observed actions
447 through a process of semantic retrieval of the action representations. Our results were

448 consistent with the hypothesis that expert table tennis players generate conceptual
449 expectations during action processing that support active inference of their opponents'
450 intentions (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Gerson et al., 2017;
451 Ondobaka et al., 2014; Patterson, Nestor, & Rogers, 2007; Vannuscorps & Caramazza,
452 2015).

453

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

467

468 Our ROI analysis also revealed greater activation in two other semantic regions
469 (dorsomedial prefrontal cortex and posterior cingulate gyrus) in the incongruent vs.
470 congruent condition. Although in these regions the group vs. condition interaction was
471 not significant, the general patten of incongruent > congruent was comparable to the
472 regions where expert players showed stronger activation than novices. Not all
473 semantic regions, however, were activated by the task, such as the fusiform and
474 parahippocampal gyri and the inferior frontal gyrus. One plausible explanation is the
475 difference in abstract processing of actions vs. words. Inferior frontal gyrus is often
476 implicated in phonological processing, articulatory planning, and syntactic analysis
477 rather than semantic processing (Binder et al., 2009; Grodzinsky & Friederici, 2006;
478 Tan, Laird, Li, & Fox, 2005). In the same way, although the specific roles of the
479 fusiform and parahippocampal gyri are still unknown (Binder et al., 2009), they may
480 be more distinctively related to word processing. Therefore, we speculate that this
481 pattern of activation influenced by expertise serves as a network to make these actions
482 appear meaningful to expert players, and reflects quite different system from the
483 general semantic network. It is however important to note, that the task in our study
484 was only indirectly linked to actual intentions, and further studies are need to explore
485 action processing with explicit conceptual intentions.

486

487 Our results on the differential brain activations between the incongruent vs. congruent
488 action processing are well in line with predictive coding hypotheses. This framework
489 suggests that the brain is predisposed to process expected incoming input, and more
490 resources are devoted when predictions are not met (Friston, 2005). Our data on
491 expert tennis players can be interpreted to reflect acquired experience implemented in

492 the sensorimotor prediction pattern. Our results also suggest that brain processes
493 linked to abstract level of processing appear to code relevant information for the
494 athletic expertise-related prediction. This interpretation aligns with results from
495 neuromagnetic studies that have extended the classic semantic N400 effect to the
496 perceived “mismatch” between predicted and observed actions (M. Balconi & Pozzoli,
497 2005; Kutas & Hillyard, 1980; Sitnikova et al., 2003). Indeed, our results could be
498 taken as support for the general notion of the importance of prediction at multiple
499 levels, and the idea of build-up of predictions at multiple systems through
500 accumulation of experience.

501

502 In some previous neuroimaging studies, the general level of physical activity and
503 fitness has been linked to differences in brain function and structure (Erickson et al.,
504 2011; McGregor et al., 2013; Ruotsalainen et al., 2019; Voss et al., 2010). In principle,
505 our results could be influenced by a general difference in fitness between the
506 participant groups. However, our results are likely to be attributable to specific
507 expertise rather than to training in general or to physical fitness because
508 cardiovascular training or physical fitness has mainly been associated with general
509 cognitive functions, such as executive control and memory, which are primarily
510 subserved by the prefrontal cortex and hippocampus (Chaddock et al., 2010;
511 Colcombe et al., 2004; Holzsneider, Wolbers, Röder, & Hötting, 2012; Voss et al.,
512 2011).

513

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

518

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523

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Conflict of Interest:

The authors declare no competing financial interests.

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