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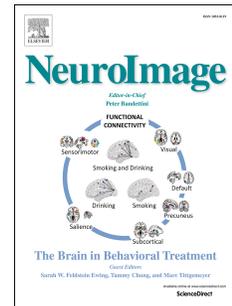
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## Predicting domain-specific actions in expert table tennis players activates the semantic brain network

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# 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 ( $20.04 \pm 1.67$  years of age; 10 males) and a  
157 control group of 25 college students ( $20.68 \pm 1.57$  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.

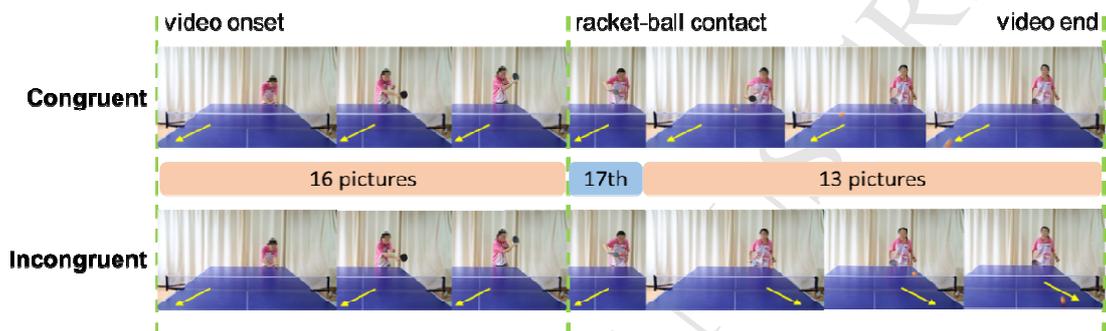
166

### 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,  $1280 \times 720$  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,  $640 \times 360$  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



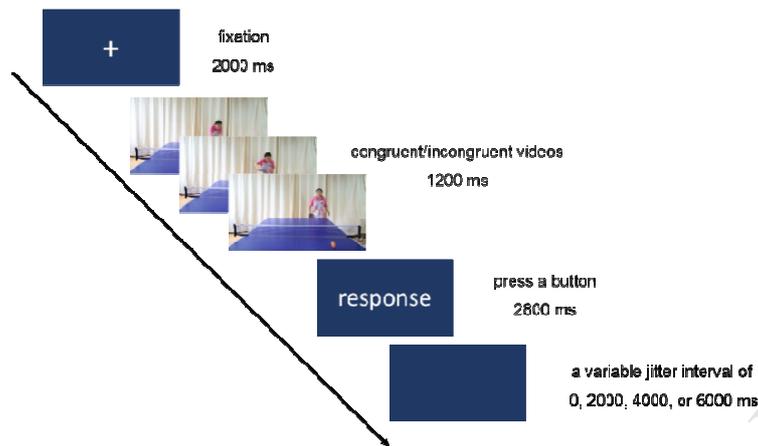
187

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,  $90^\circ$ ; 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,  $12^\circ$ ;  
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 ( $\eta^2_p$ ) 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 mm × 3 mm × 3 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 × 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

316

Table 1. Results of the whole-brain analysis

| Region  | BA | Number of Cluster | T value | MNI coordinates |     |     |
|---|----|-------------------|---------|-----------------|-----|-----|
|   |    |                   |         | X               | Y   | Z   |
| <b>Expert table tennis players: incongruent condition &gt; congruent condition</b>    |    |                   |         |                 |     |     |
| 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  |
| <b>Expert &gt; nonexpert players: incongruent condition minus congruent condition</b> |    |                   |         |                 |     |     |
| 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  |

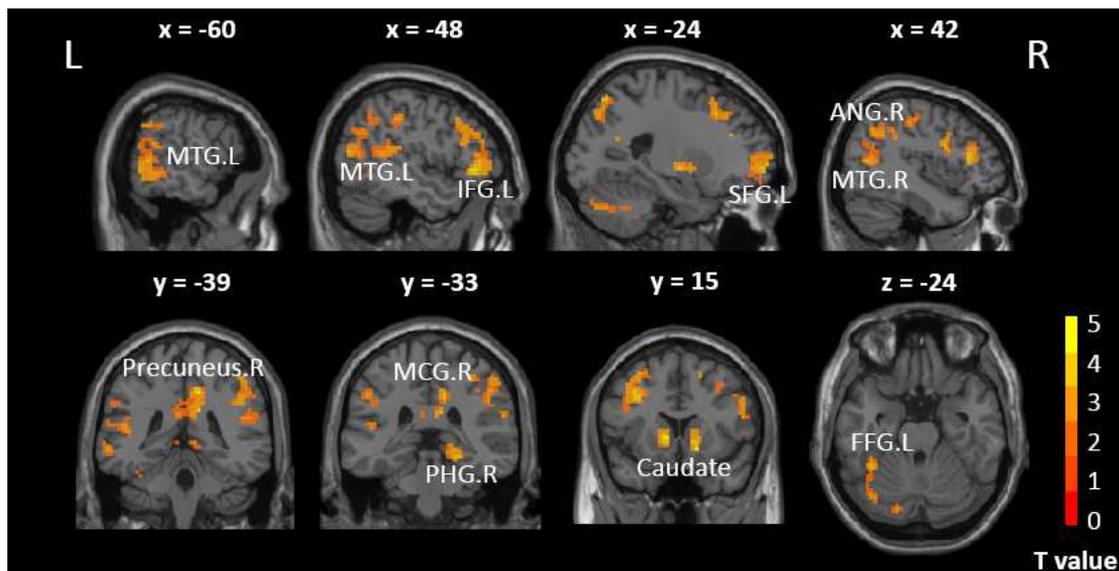
317 *Note:* Clusters with  $p_{(FWE)} < 0.05$  were considered statistically significant. Coordinates

318 (XYZ) are in Montreal Neurological Institute (MNI) space. BA indicates Brodmann

319 Area.

320

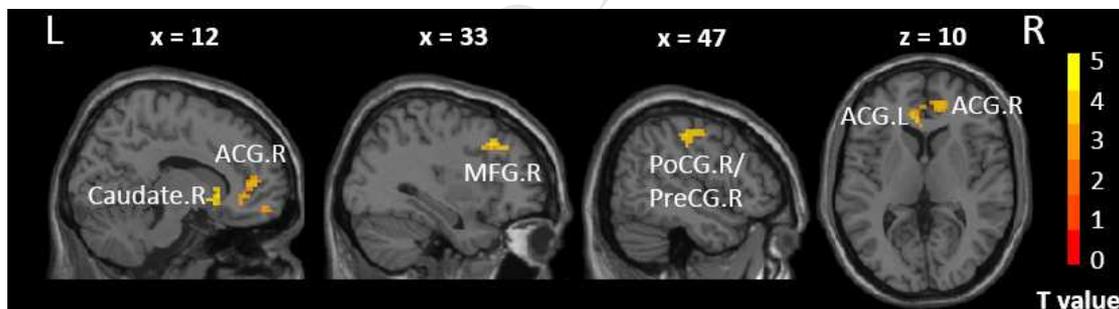
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322

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



332

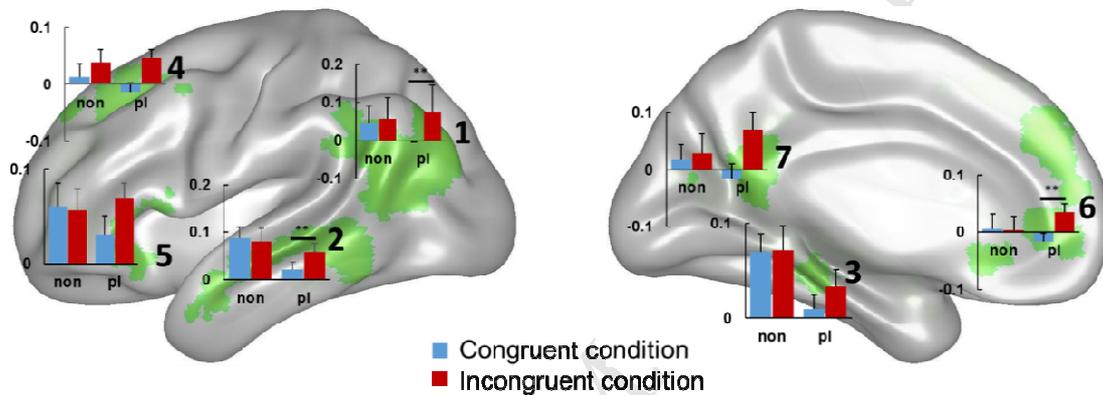
333 Figure 4. Areas showing greater activation for expert table tennis players (incongruent  
 334 condition minus congruent condition) compared with nonexperts (incongruent  
 335 condition minus congruent condition). Clusters with  $p_{(FWE)} < 0.05$  (corrected) were  
 336 considered statistically 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.

340

341

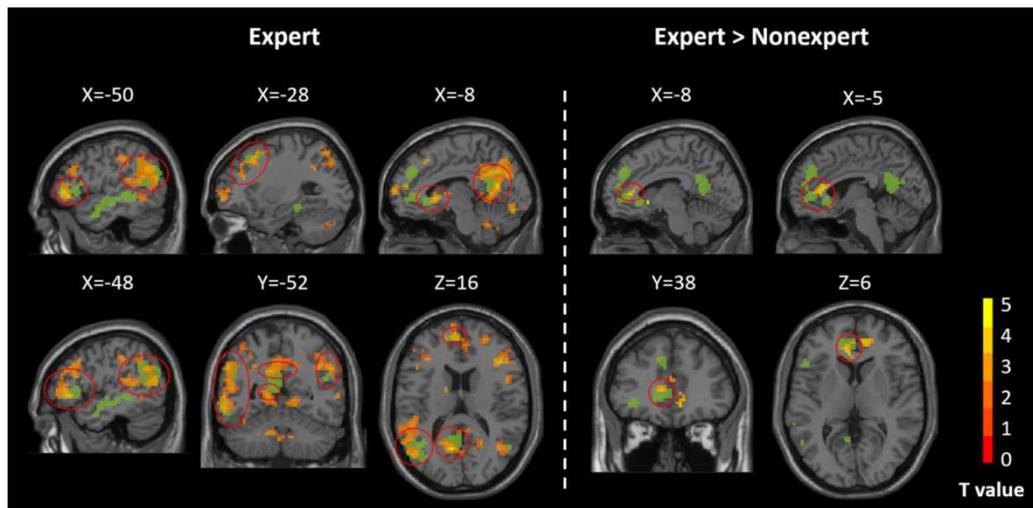
342 To further explore whether action processing also involved the semantic network, we  
 343 conducted an ROI analysis. The intensity of the activations for all participants in each  
 344 condition was extracted from the ROIs and was entered into a  $2$  (group)  $\times$   $2$   
 345 (condition) 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 ( $F_{(1,48)} = 4.065$ ,  $p = 0.049$ ,  $\eta^2_p$   
 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

524 **References**

- 525 Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C., 2008. Action anticipation and motor resonance in  
526 elite basketball players. *Nat Neurosci* 11(9), 1109-1116. doi:10.1038/nn.2182
- 527 Amoruso, L., Gelormini, C., Aboitiz, F., Gonzalez, M. A., Manes, F., Cardona, J. F., & Ibanez, A., 2013.  
528 N400 ERPs for actions: building meaning in context. *Frontiers in Human Neuroscience* 7.  
529 doi:10.3389/fnhum.2013.00057
- 530 Amoruso, L., Sedeno, L., Huepe, D., Tomio, A., Kamienskowski, J., Hurtado, E., . . . Ibanez, A., 2014.  
531 Time to Tango: expertise and contextual anticipation during action observation. *Neuroimage*  
532 98, 366-385. doi:10.1016/j.neuroimage.2014.05.005
- 533 Balconi, M., & Caldiroli, C., 2011. Semantic violation effect on object-related action comprehension.  
534 N400-like event-related potentials for unusual and incorrect use. *Neuroscience* 197, 191-199.  
535 doi: 10.1016/j.neuroscience.2011.09.026
- 536 Balconi, M., & Pozzoli, U., 2005. Comprehending semantic and grammatical violations in Italian.  
537 N400 and P600 comparison with visual and auditory stimuli. *J Psycholinguist Res* 34(1),  
538 71-98. doi: 10.1007/s10936-005-3633-6
- 539 Balsler, N., Lorey, B., Pilgramm, S., Stark, R., Bischoff, M., Zentgraf, K., . . . Munzert, J., 2014.  
540 Prediction of Human Actions: Expertise and Task-Related Effects on Neural Activation of the  
541 Action Observation Network. *Human Brain Mapping* 35(8), 4016-4034.  
542 doi:10.1002/hbm.22455
- 543 Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L., 2008. Sports  
544 experience changes the neural processing of action language. *Proc Natl Acad Sci U S A*  
545 105(36), 13269-13273. doi:10.1073/pnas.0803424105
- 546 Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L., 2009. Where is the semantic system? A  
547 critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*  
548 19(12), 2767-2796. doi:10.1093/cercor/bhp055
- 549 Blakemore, S. J., & Decety, J., 2001. From the perception of action to the understanding of intention.  
550 *Nat Rev Neurosci* 2(8), 561-567. doi:10.1038/35086023
- 551 Brass, M., Schmitt, R. M., Spengler, S., & Gergely, G., 2007. Investigating action understanding:  
552 inferential processes versus action simulation. *Curr Biol* 17(24), 2117-2121.  
553 doi:10.1016/j.cub.2007.11.057
- 554 Cañal-Bruland, R., van Ginneken, W. F., van der Meer, B. R., & Williams, A. M., 2011. The effect of  
555 local kinematic changes on anticipation judgments. *Human movement science* 30(3), 495-503.  
556 doi:10.1016/j.humov.2010.10.001
- 557 Causer, J., Smeeton, N. J., & Williams, A. M., 2017. Expertise differences in anticipatory judgements  
558 during a temporally and spatially occluded task. *Plos One* 12(2).  
559 doi:10.1371/journal.pone.0171330
- 560 Chaddock, L., Erickson, K. I., Prakash, R. S., Kim, J. S., Voss, M. W., VanPatter, M., . . . Hillman, C.  
561 H., 2010. A neuroimaging investigation of the association between aerobic fitness,  
562 hippocampal volume, and memory performance in preadolescent children. *Brain Research*  
563 1358, 172-183. doi:10.1016/j.brainres.2010.08.049
- 564 Chen, X., Lu, B., & Yan, C.-G., 2018. Reproducibility of R-fMRI Metrics on the Impact of Different  
565 Strategies for Multiple Comparison Correction and Sample Sizes. *Human Brain Mapping* 39,  
566 300-318. doi:10.1002/hbm.23843
- 567 Colcombe, S. J., Kramer, A. F., Erickson, K. I., Scalf, P., McAuley, E., Cohen, N. J., . . . Elavsky, S.,

- 568 2004. Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National*  
569 *Academy of Sciences of the United States of America* 101(9), 3316-3321.  
570 doi:10.1073/pnas.0400266101
- 571 Cross, E. S., Liepelt, R., Hamilton, A. F. D., Parkinson, J., Ramsey, R., Stadler, W., & Prinz, W., 2012.  
572 Robotic movement preferentially engages the action observation network. *Human Brain*  
573 *Mapping* 33(9), 2238-2254. doi:10.1002/hbm.21361
- 574 de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H., 2008. Complementary systems  
575 for understanding action intentions. *Curr Biol* 18(6), 454-457. doi:10.1016/j.cub.2008.02.057
- 576 di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G., 1992. Understanding motor  
577 events: a neurophysiological study. *Experimental brain research* 91(1), 176-180.
- 578 Doricchi, F., Macci, E., Silvetti, M., & Macaluso, E., 2009. Neural correlates of the spatial and  
579 expectancy components of endogenous and stimulus-driven orienting of attention in the  
580 Posner task. *Cerebral Cortex* 20(7), 1574-1585. doi:10.1093/cercor/bhp215
- 581 Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., & May, A., 2004. Neuroplasticity:  
582 changes in grey matter induced by training. *Nature* 427(6972), 311-312. doi:10.1038/427311a
- 583 Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., ... & Wojcicki, T. R.,  
584 2011. Exercise training increases size of hippocampus and improves memory. *Proceedings of*  
585 *the National Academy of Sciences of the United States of America* 108(7), 3017-3022.  
586 doi:10.1073/pnas.1015950108
- 587 Farrow, D., Abernethy, B., & Jackson, R. C., 2005. Probing expert anticipation with the temporal  
588 occlusion paradigm: Experimental investigations of some methodological issues. *Motor*  
589 *control* 9(3), 330-349. doi:10.1123/mcj.9.3.330
- 590 Ferrari, P. F., Bonini, L., & Fogassi, L., 2009. From monkey mirror neurons to primate behaviours:  
591 possible 'direct' and 'indirect' pathways. *Philos Trans R Soc Lond B Biol Sci* 364(1528),  
592 2311-2323. doi:10.1098/rstb.2009.0062
- 593 Friston, K., 2005. A theory of cortical responses. *Philos Trans R Soc Lond B Biol Sci* 360(1456),  
594 815-836. doi:10.1098/rstb.2005.1622
- 595 Gerson, S. A., Meyer, M., Hunnius, S., & Bekkering, H., 2017. Unravelling the contributions of motor  
596 experience and conceptual knowledge in action perception: A training study. *Sci Rep* 7, 46761.  
597 doi:10.1038/srep46761
- 598 Glover, S., & Dixon, P., 2002. Semantics affect the planning but not control of grasping. *Experimental*  
599 *Brain Research* 146(3), 383-387. doi:10.1007/s00221-002-1222-6
- 600 Graziano, M. S., Taylor, C. S., & Moore, T., 2002. Complex movements evoked by microstimulation of  
601 precentral cortex. *Neuron* 34(5), 841-851. doi:10.1016/S0896-6273(02)00698-0
- 602 Grodzinsky, Y., & Friederici, A. D., 2006. Neuroimaging of syntax and syntactic processing. *Curr Opin*  
603 *Neurobiol* 16(2), 240-246. doi:10.1016/j.conb.2006.03.007
- 604 Hickok, G., 2009. Eight problems for the mirror neuron theory of action understanding in monkeys and  
605 humans. *J Cogn Neurosci* 21(7), 1229-1243. doi:10.1162/jocn.2009.21189
- 606 Holzsneider, K., Wolbers, T., Röder, B., & Hötting, K., 2012. Cardiovascular fitness modulates brain  
607 activation associated with spatial learning. *Neuroimage* 59(3), 3003-3014.  
608 doi:10.1016/j.neuroimage.2011.10.021
- 609 Jin, H., Xu, G., Zhang, J. X., Gao, H., Ye, Z., Wang, P., . . . Lin, C. D., 2011. Event-related potential  
610 effects of superior action anticipation in professional badminton players. *Neurosci Lett* 492(3),  
611 139-144. doi:10.1016/j.neulet.2011.01.074

- 612 Kilner, J. M., 2011. More than one pathway to action understanding. *Trends in cognitive sciences* 15(8),  
613 352-357. doi:10.1016/j.tics.2011.06.005
- 614 Kilner, J. M., & Lemon, R. N., 2013. What We Know Currently about Mirror Neurons. *Current*  
615 *Biology* 23(23), R1057-R1062. doi:10.1016/j.cub.2013.10.051
- 616 Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., & Hommer, D., 2001. Dissociation of reward  
617 anticipation and outcome with event-related fMRI. *Neuroreport* 12(17), 3683-3687.  
618 doi:10.1097/00001756-200112040-00016
- 619 Kutas, M., & Hillyard, S. A., 1980. Reading senseless sentences: brain potentials reflect semantic  
620 incongruity. *Science* 207(4427), 203-205. doi:10.1126/science.7350657
- 621 Lauwereyns, J., Watanabe, K., Coe, B., & Hikosaka, O., 2002. A neural correlate of response bias in  
622 monkey caudate nucleus. *Nature* 418(6896), 413-417. doi:10.1038/nature00892
- 623 Lee, C. L., Huang, H. W., Federmeier, K. D., & Buxbaum, L. J., 2018. Sensory and semantic  
624 activations evoked by action attributes of manipulable objects: Evidence from ERPs.  
625 *Neuroimage* 167, 331-341. doi:10.1016/j.neuroimage.2017.11.045
- 626 Libby, L. A., Hannula, D. E., & Ranganath, C., 2014. Medial temporal lobe coding of item and spatial  
627 information during relational binding in working memory. *J Neurosci* 34(43), 14233-14242.  
628 doi:10.1523/JNEUROSCI.0655-14.2014
- 629 Mcgregor, K. M., Nocera, J. R., Sudhyadhom, A., Patten, C., Manini, T. M., Kleim, J. A., . . . Butler, A.  
630 J., 2013. Effects of Aerobic Fitness on Aging-Related Changes of Interhemispheric Inhibition  
631 and Motor Performance. *Frontiers in Aging Neuroscience* 5(11), 66.  
632 doi:10.3389/fnagi.2013.00066
- 633 Molenberghs, P., Cunnington, R., & Mattingley, J. B., 2012. Brain regions with mirror properties: a  
634 meta-analysis of 125 human fMRI studies. *Neurosci Biobehav Rev* 36(1), 341-349.  
635 doi:10.1016/j.neubiorev.2011.07.004
- 636 Nishitani, N., & Hari, R., 2000. Temporal dynamics of cortical representation for action. *Proceedings*  
637 *of the National Academy of Sciences of the United States of America* 97(2), 913-918.  
638 doi:10.1073/pnas.97.2.913
- 639 Ondobaka, S., de Lange, F. P., Wittmann, M., Frith, C. D., & Bekkering, H., 2014. Interplay between  
640 conceptual expectations and movement predictions underlies action understanding. *Cerebral*  
641 *Cortex* 25(9), 2566-2573. doi:10.1093/cercor/bhu056
- 642 Opacic, T., Stevens, C., & Tillmann, B., 2009. Unspoken knowledge: implicit learning of structured  
643 human dance movement. *Journal of Experimental Psychology: Learning, Memory, and*  
644 *Cognition* 35(6), 1570. doi:10.1037/a0017244
- 645 Patterson, K., Nestor, P. J., & Rogers, T. T., 2007. Where do you know what you know? The  
646 representation of semantic knowledge in the human brain. *Nature reviews. Neuroscience* 8(12),  
647 976. doi:10.1038/nrn2277
- 648 Pomiechowska, B., & Csibra, G., 2017. Motor activation during action perception depends on action  
649 interpretation. *Neuropsychologia* 105, 84-91. doi:10.1016/j.neuropsychologia.2017.01.032
- 650 Postle, N., McMahan, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I., 2008. Action word  
651 meaning representations in cytoarchitecturally defined primary and premotor cortices.  
652 *Neuroimage* 43(3), 634-644. doi:10.1016/j.neuroimage.2008.08.006
- 653 Proverbio, A. M., Riva, F., & Zani, A., 2010. When neurons do not mirror the agent's intentions: sex  
654 differences in neural coding of goal-directed actions. *Neuropsychologia* 48(5), 1454-1463. doi:  
655 10.1016/j.neuropsychologia.2010.01.015

- 656 Pulvermuller, F., 2005. Brain mechanisms linking language and action. *Nat Rev Neurosci* 6(7),  
657 576-582. doi:10.1038/nrn1706
- 658 Reid, V. M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., & Striano, T., 2009. The neural  
659 correlates of infant and adult goal prediction: evidence for semantic processing systems. *Dev*  
660 *Psychol* 45(3), 620-629. doi:10.1037/a0015209
- 661 Reid, V. M., & Striano, T., 2008. N400 involvement in the processing of action sequences. *Neurosci*  
662 *Lett* 433(2), 93-97. doi:10.1016/j.neulet.2007.12.066
- 663 Rizzolatti, G., & Craighero, L., 2004. The mirror-neuron system. *Annu Rev Neurosci* 27, 169-192.  
664 doi:10.1146/annurev.neuro.27.070203.144230
- 665 Rizzolatti, G., & Luppino, G., 2001. The cortical motor system. *Neuron* 31(6), 889-901.  
666 doi:10.1016/S0896-6273(01)00423-8
- 667 Ruotsalainen, I., Renvall, V., Gorbach, T., Syväoja, H. J., Tammelin, T. H., Karvanen, J., & Parviainen,  
668 T., 2019. Aerobic fitness, but not physical activity, is associated with grey matter volume in  
669 adolescents. *Behavioural brain research* 362(19), 122-130. doi:10.1016/j.bbr.2018.12.041
- 670 Sitnikova, T., Kuperberg, G., & Holcomb, P. J., 2003. Semantic integration in videos of real-world  
671 events: an electrophysiological investigation. *Psychophysiology* 40(1), 160-164.  
672 doi:10.1111/1469-8986.00016
- 673 Smith, D. M., 2016. Neurophysiology of action anticipation in athletes: A systematic review.  
674 *Neuroscience & Biobehavioral Reviews* 60, 115-120. doi:10.1016/j.neubiorev.2015.11.007
- 675 Smith, S. M., & Nichols, T. E., 2009. Threshold-free cluster enhancement: addressing problems of  
676 smoothing, threshold dependence and localisation in cluster inference. *Neuroimage* 44(1),  
677 83-98. doi:10.1016/j.neuroimage.2008.03.061
- 678 Spunt, R. P., & Lieberman, M. D., 2012. Dissociating modality-specific and supramodal neural systems  
679 for action understanding. *J Neurosci* 32(10), 3575-3583.  
680 doi:10.1523/JNEUROSCI.5715-11.2012
- 681 Stapel, J. C., Hunnius, S., Meyer, M., & Bekkering, H., 2016. Motor system contribution to action  
682 prediction: Temporal accuracy depends on motor experience. *Cognition* 148, 71-78.  
683 doi:10.1016/j.cognition.2015.12.007
- 684 Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H., 2010. Motor activation during observation of  
685 unusual versus ordinary actions in infancy. *Social Neuroscience* 5(5-6), 451-460.  
686 doi:10.1080/17470919.2010.490667
- 687 Swick, D., & Turken, U., 2002. Dissociation between conflict detection and error monitoring in the  
688 human anterior cingulate cortex. *Proceedings of the National Academy of Sciences* 99(25),  
689 16354-16359. doi:10.1073/pnas.252521499
- 690 Tan, L. H., Laird, A. R., Li, K., & Fox, P. T., 2005. Neuroanatomical correlates of phonological  
691 processing of Chinese characters and alphabetic words: a meta-analysis. *Human Brain*  
692 *Mapping* 25(1), 83-91. doi:10.1002/hbm.20134
- 693 Tomeo, E., Cesari, P., Aglioti, S. M., & Urgesi, C., 2012. Fooling the kickers but not the goalkeepers:  
694 behavioral and neurophysiological correlates of fake action detection in soccer. *Cerebral*  
695 *Cortex* 23(11), 2765-2778. doi:10.1093/cercor/bhs279
- 696 Tricomi, E. M., Delgado, M. R., & Fiez, J. A., 2004. Modulation of caudate activity by action  
697 contingency. *Neuron* 41(2), 281-292. doi:10.1016/S0896-6273(03)00848-1
- 698 van Elk, M., van Schie, H., & Bekkering, H., 2014. Action semantics: a unifying conceptual framework  
699 for the selective use of multimodal and modality-specific object knowledge. *Physics of life*

- 700 reviews 11(2), 220-250. doi:10.1016/j.plrev.2013.11.005
- 701 Vannuscorps, G., & Caramazza, A., 2015. Typical action perception and interpretation without motor  
702 simulation. *Proceedings of the National Academy of Sciences of the United States of America*  
703 113(1), 86-91. doi:10.1073/pnas.1516978112
- 704 Voss, M. W., Chaddock, L., Kim, J. S., VanPatter, M., Pontifex, M. B., Raine, L. B., . . . Kramer, A. F.,  
705 2011. Aerobic fitness is associated with greater efficiency of the network underlying cognitive  
706 control in preadolescent children. *Neuroscience* 199, 166-176.  
707 doi:10.1016/j.neuroscience.2011.10.009
- 708 Voss, M. W., Prakash, R. S., Erickson, K. I., Basak, C., Chaddock, L., Kim, J. S., . . . White, S. M.,  
709 2010. Plasticity of Brain Networks in a Randomized Intervention Trial of Exercise Training in  
710 Older Adults. *Frontiers in Aging Neuroscience* 2(1), : 32. doi:10.3389/fnagi.2010.00032
- 711 Wang, Y., Ji, Q., & Zhou, C., 2019. Effect of prior cues on action anticipation in soccer goalkeepers.  
712 *Psychology of Sport and Exercise*. doi:10.1016/j.psychsport.2019.02.001
- 713 Ward, P., Williams, A. M., & Bennett, S. J., 2002. Visual search and biological motion perception in  
714 tennis. *Res Q Exerc Sport* 73(1), 107-112. doi:10.1080/02701367.2002.10608997
- 715 Williams, A. M., Huys, R., Cañal-Bruland, R., & Hagemann, N., 2009. The dynamical information  
716 underpinning anticipation skill. *Human movement science* 28(3), 362-370.  
717 doi:10.1016/j.humov.2008.10.006
- 718 Winkler, A. M., Ridgway, G. R., Douaud, G., Nichols, T. E., & Smith, S. M., 2016. Faster permutation  
719 inference in brain imaging. *Neuroimage* 141, 502-516. doi:10.1016/j.neuroimage.2016.05.068
- 720 Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B., 2010. Functional MRI reveals  
721 expert-novice differences during sport-related anticipation. *Neuroreport* 21(2), 94-98.  
722 doi:10.1097/WNR.0b013e328333dff2
- 723 Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B., 2011. Cortical fMRI activation to  
724 opponents' body kinematics in sport-related anticipation: expert-novice differences with  
725 normal and point-light video. *Neurosci Lett* 500(3), 216-221.  
726 doi:10.1016/j.neulet.2011.06.045
- 727 Xu, H., Wang, P., Ye, Z., Di, X., Xu, G., Mo, L., . . . Jin, H., 2016. The Role of Medial Frontal Cortex in  
728 Action Anticipation in Professional Badminton Players. *Front Psychol* 7, 1817.  
729 doi:10.3389/fpsyg.2016.01817
- 730 Yan, C., & Zang, Y., 2010. DPARSF: a MATLAB toolbox for " pipeline" data analysis of resting-state  
731 fMRI. *Frontiers in systems neuroscience* 4, 13. doi:10.3389/fnsys.2010.00013
- 732 Yarrow, K., Brown, P., & Krakauer, J. W., 2009. Inside the brain of an elite athlete: the neural processes  
733 that support high achievement in sports. *Nature Reviews Neuroscience* 10(8), 585.  
734 doi:10.1038/nrn2672
- 735
- 736
- 737

**Conflict of Interest:**

The authors declare no competing financial interests.

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