

1        **Inhibitory theta burst stimulation highlights the role of left aIPS and right TPJ during**  
2        **complementary and imitative human-avatar interactions in cooperative and competitive**  
3                            **scenarios**

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13

14 **Abstract**

15 Competitive and cooperative interactions are based on anticipation or synchronization with the  
16 partner's actions. Both forms of interaction may either require performing imitative or  
17 complementary movements with respect to those performed by our partner. We explored how  
18 parietal regions involved in the control of imitative behavior (temporo-parietal-junction, TPJ), goal  
19 coding and visuo-motor integration (anterior intraparietal sulcus, aIPS) contribute to the execution  
20 of imitative and complementary movements during cooperative and competitive interactions. To  
21 this aim, we delivered off-line non-invasive inhibitory brain stimulation to healthy individuals' left  
22 aIPS and right TPJ before they were asked to reach and grasp an object together with a virtual  
23 partner by either performing imitative or complementary interactions. In different blocks  
24 participants were asked to compete or cooperate with the virtual partner that varied its behaviour  
25 according to cooperative or competitive contexts. Left aIPS and right TPJ inhibition impaired  
26 individuals' performance (i.e. synchrony in cooperative task and anticipation in competition) during  
27 complementary and imitative interactions, respectively, in both cooperative and competitive  
28 contexts, indicating that aIPS and TPJ inhibition affects own-other action integration and action  
29 imitation (that are different in complementary vs imitative interactions) more than action  
30 synchronization or anticipation (that are different in cooperative vs competitive contexts).

31 **Keywords:** competition, cooperation, motor interactions, aIPS, TPJ

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33

## 34 **Introduction**

35 Competitive and cooperative interactions deeply differ in their execution. While competition is  
36 mainly based on the anticipation of the actions of competitors, cooperation mainly relies on  
37 synchronization with partners' actions. These two interaction modalities are supported by the ability  
38 to predict the interactor's actions and to integrate one's own action goal with that of the partner  
39 (Dumas et al., 2019). For example, when playing football, members of the same team must predict  
40 and adapt their movements to successfully perform an action together (cooperation). In a similar  
41 vein, opposing team members must predict each other's actions and anticipate them (competition).  
42 In cooperative (Sacheli et al., 2013) and competitive (Naber et al., 2013; Tomeo et al., 2013)  
43 contexts, automatic imitation of the partner's movements ((in the form of visuo-motor interference,  
44 Kilner et al., 2003) or cortico-spinal facilitation, (Tomeo et al., 2013)) emerges when predictions  
45 about the partner's goals are needed (Era et al., 2018a, see Panasiti et al., 2017 for a review).  
46 Neuroimaging studies indicate that both motor cooperation and competition recruit the activation of  
47 the fronto-parietal Action Observation Network (AON) (Decety et al., 2004).  
48 Virtually all interactions may be divided in complementary or imitative interactions and cooperative  
49 and competitive ones are no exception to this. Neuroimaging studies indicate that the activity of the  
50 fronto-parietal AON is associated with both these interaction types (Newman-Norlund et al., 2007),  
51 perhaps because it supports sensory-motor transformation and integration (Freund, 2001). Recent  
52 studies have supported the notion that frontal nodes of the fronto-parietal network (primary motor  
53 cortex and dorsal premotor cortex) support the ability to coordinate in musical synchronous and  
54 turn-taking interactions (Novembre et al., 2014; Hadley et al., 2015). Within the fronto-parietal  
55 network, the left anterior intraparietal sulcus (aIPS) is activated when coding the goal of both self-  
56 executed (Tunik et al., 2005) and observed actions (Hamilton and Grafton, 2006; Fogassi et al.,  
57 2005). Crucially for the present study, this region has been shown to support the performance of  
58 cooperative complementary motor interactions with virtual partners when predictions about the  
59 partner's action are needed in order to perform one's own (Sacheli et al., 2015; 2018). Recently,

60 inhibitory non-invasive brain stimulation (continuous theta burst stimulation) was used to interfere  
61 with the activity of left aIPS in one member of interacting human-human pairs (Era et al., 2018b).  
62 The results of this study showed that aIPS functioning is more fundamental to effective motor  
63 synchronization during cooperative, human-human, complementary interactions than during  
64 imitative ones. Moreover, left aIPS inhibition effect was correlated negatively with the pair's ability  
65 to mutually adapt, indicating that this process is a crucial marker of human-human interactions (Era  
66 et al., 2018b; Era et al., 2019). Thus, it has been demonstrated that aIPS is crucial to perform  
67 complementary interactions in cooperative contexts (Sacheli et al., 2015; Era et al., 2018).  
68 However, these studies left unexplored whether aIPS activity supports the ability to synchronize  
69 with another person per se, which characterizes cooperative conditions, or rather the ability to  
70 integrate ones' own and the other's action independently to whether synchronization (during  
71 cooperation) or anticipation (during competition) is needed.

72 The right temporo-parietal-junction (rTPJ) has been suggested to play a role in self-other distinction  
73 across a variety of low-level (agency discrimination (Farrer and Frith, 2002), visual perspective  
74 taking (Aichhorn et al., 2006; Martin et al., 2018), control of imitation (Spengler et al., 2009;  
75 Spengler et al., 2010)) and high-level (mentalizing, empathy (Spengler et al., 2009; Saxe et al.,  
76 2003; Volm et al., 2006)) domains, which may be extremely relevant during competitive  
77 interactions when one needs to anticipate the behavior of the interactor, thus dissociating one's own  
78 behavior from that of the competitor. This region has been shown to control the automatic tendency  
79 to imitate observed, task irrelevant, finger movements while individuals are asked to execute an  
80 incongruent movement (Santiesteban et al., 2012; Santiesteban et al., 2015; Sowden and Catmur  
81 2015). Measuring cortico-spinal excitability (MEP), a tDCS-TMS study further specified this notion  
82 by showing that TPJ activity enhances the instructed motor plan rather than suppressing task-  
83 irrelevant imitation (Bardi et al., 2017). Moreover, in another study where participants were asked  
84 to perform congruent or incongruent movements with respect to the observed ones, inhibitory  
85 stimulation of rTPJ facilitated the performance of incongruent, task-relevant actions (Giardina et al.,

86 2015). However, the role of TPJ during realistic motor interactions has not been studied, and it is  
87 also not known whether TPJ activity may support the ability to perform competitive interactions,  
88 where self-other distinction is needed to anticipate the action of the other (Decety et al., 2004).

89 Imitative interactions are thought to be based on the direct mapping of the observed action of the  
90 partner onto one's own motor behaviour. Crucial to this process is the ability to transform the  
91 observed action in visuo-spatial terms. It has been shown, for example, that observing an action  
92 from a third-person perspective (i.e. face-to-face) reduces the ability to imitate the action compared  
93 to when the same action is observed from a first-person perspective (Ishikura and Inomata, 1995).  
94 Similarly, Jackson et al. (2006) reported that participants performed better (i.e smaller reaction  
95 times) when imitating in first person perspective compared to third one. Accordingly, studies  
96 indicate that different neural processes are involved in the parietal cortex when observing and  
97 imitating models seen from a first- or third-person perspective (Jackson et al., 2006; Watanabe et  
98 al., 2011; Shmuelof and Zohary, 2008; Vingerhoets et al., 2012). Within the parietal cortex, the  
99 difference between first- and third-person perspective seems to be evident at the level of the right  
100 Temporo-Parietal Junction (rTPJ). This area has been shown to be active in visuo-spatial  
101 perspective-taking tasks (Ruby and Decety, 2001; Donaldson et al., 2015). Brain  
102 stimulation/modulation (TMS/tDCS) studies investigating perspective taking and control of  
103 imitation targeted the right TPJ (Blanke et al., 2005; Sowden and Catmur, 2015; van Elk et al.,  
104 2017) and support the idea that the rTPJ is fundamental for 1) rotating body-centred perspective, 2)  
105 imitating others' movements.

106 In the present study, we used non-invasive brain stimulation (continuous theta burst stimulation,  
107 cTBS) to inhibit left aIPS and right TPJ activity in human participants interacting with a virtual  
108 partner. Our goal was to investigate whether these areas play a causal role in supporting real-time  
109 complementary and imitative interactions in cooperative vs competitive contexts. In keeping with  
110 previous reports from our own (Sacheli et al., 2015; 2018; Era et al., 2018b) and other (Tunik et al.,

111 2005) laboratories we targeted left aIPS because fMRI studies showed that this region is involved in  
112 coding for the goal of actions (Hamilton and Grafton, 2006) and because TMS studies show deficits  
113 in right-arm pointing in response to left IPS stimulation only (Desmurget et al., 1999). Following a  
114 similar logic, we targeted the right TPJ because, although recent studies may suggest bilateral TPJ  
115 involvement in control of imitation and visual perspective taking (Santiesteban et al., 2015), meta-  
116 analytic studies hint at a predominant role of the right TPJ in perspective-taking and theory of mind  
117 (Decety and Sommerville 2003; Decety and Lamm 2007). In the present study, participants were  
118 asked to grasp a bottle-shaped object by employing either precision or power grips (see Materials  
119 and Methods), (Figure 1) and to coordinate their movements with a virtual partner in two different  
120 interactive contexts. While action goal had always to be on-line selected according to the avatar's  
121 movement, humans had to synchronize their actions with the avatar in the cooperative context and  
122 anticipate the action of the virtual partner in the competitive one. Either opposite (complementary:  
123 the avatar performs a precision grip while the human participant performs a power grip, or vice-  
124 versa) or same (imitative) actions were performed. Participants did not know in advance whether  
125 they would have to perform a precision grip or a power grip, but they were asked to either imitate or  
126 complement the avatar's actions. In order to make the cooperative and competitive scenarios  
127 equally difficult, the virtual partner reacted to the speed of human partner's movements in previous  
128 trials by changing the speed of its own movements (as in Era et al., 2018a). This manipulation  
129 forced the participant to adapt to the movements of the partner, a fundamental mechanism of  
130 human-human motor interactions (Era et al., 2018b), giving our task ecological validity to study  
131 social motor interactions (Reader and Holmes, 2016; Moreau and Candidi, 2016).

132 Participants were divided into groups before performing the joint-grasping task. One group received  
133 off-line cTBS of left aIPS (target site) and sham (control stimulation), while the other received  
134 cTBS of right TPJ (target site) and sham (control stimulation). Grasping Asynchrony (see Materials  
135 and Methods) was considered the dependent variable indexing the success of interpersonal  
136 coordination and anticipation. Contrasting Cooperative vs Competitive contexts of the interaction

137 allowed us to test whether aIPS and TPJ: 1) support the ability to synchronize with the action of the  
138 partner (based on self-other movements/goals integration in the cooperation context), or anticipate  
139 them (based on self-other distinction in the competition context), or 2) whether their contribution  
140 should be attributed to functions that are in common in these two contexts. Implementing  
141 Complementary and Imitative conditions, conversely, allowed us to test whether aIPS and TPJ play  
142 different roles in supporting 1) the ability to integrate one's own and the partner actions/goals  
143 during complementary interactions, or 2) the ability to imitate the observed actions/goals of the  
144 partner. Implementing imitative and complementary interactions in cooperative and competitive  
145 contexts made the two manipulations orthogonal and allowed us to test whether aIPS and TPJ  
146 support functions that are shared between the contexts or selective for one of the two. More in  
147 details, goal integration (aIPS) and imitation (TPJ) are different in complementary and imitative  
148 interactions because in the first case there is the need to integrate one's own and the others'  
149 movement, while the second scenario is characterized by the need to control imitation. We thus  
150 hypothesized that the effect of left aIPS and rTPJ inhibition might be independent from the  
151 interactive (cooperative and competitive) contexts, because the two contexts have in common  
152 prediction and planning processes.

153

## 154 **Materials and Methods**

### 155 **Participants**

156 Forty-two participants were recruited for the study. Six participants were excluded as outliers (see  
157 statistical analyses) making the final sample thirty-six participants. Participants were divided in two  
158 eighteen-person groups and received cTBS to different brain regions: one group (8 males, group  
159 average age  $25.1 \pm 4.9$ ) received cTBS over left aIPS and a control sham stimulation, while the  
160 other group (5 males, group average age  $23.2 \pm 3.5$ ) received cTBS over right TPJ and a sham  
161 stimulation. The two groups did not differ in terms of age ( $t = 1.33, p = .19$ ). All participants were

162 right-handed as confirmed by the Standard Handedness Inventory (Briggs and Nebes, 1975),  
163 reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.  
164 None of the participants had neurological, psychiatric, or other medical problems, nor any  
165 contraindication for TMS (Rossini et al., 2015). The experimental protocol was approved by the  
166 ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical  
167 standards of the 1964 Declaration of Helsinki and later amendments. Participants gave their written  
168 informed consent to take part in the study and, at the end of the experimental procedures, were  
169 debriefed as to the purpose of the study. No discomfort or adverse effects to rTMS were reported by  
170 any of the participants.

171

## 172 **Stimuli**

173 The virtual partner (avatar) was created in Maya 2011 (Autodesk, Inc.) using a customized Python  
174 script (Prof. Orvalho V., Instituto de Telecomunicacoes, Porto University) and the virtual scenario  
175 was designed in 3DS Max 2011(Autodesk, Inc.). The avatar moved following the kinematics of a  
176 real person's body [SMART-D motion capture system (Bioengineering Technology & Systems  
177 (B|T|S))] (Tieri et al., 2015) that was recorded while performing 6 reach-to-grasp movements  
178 toward the upper part of a bottle (precision grip) and 6 toward the lower part (power grip) with his  
179 right dominant hand. To avoid that participants were influenced by facial expressions, the stimuli  
180 contained only the upper body from the shoulders down, without the neck and head. The standard  
181 duration of each clip (~2000 ms) was the same for the different conditions (up and down  
182 movements), but we created five different clips with five different avatar movement duration times  
183 for each condition by modifying the number of frames per second: 1600 ms; 1800 ms; 2000 ms;  
184 2200 ms; 2400 ms. In order to make the avatar reactive to participants' behaviour on a trial-by-trial  
185 basis, stimuli with different durations were displayed to participants according to their performance  
186 (see below). At the start of each stimulus the avatar was still, with its hand on the table. After a  
187 variable amount of time (i.e. between 200 and 500 ms), the avatar began its movement. The



188 moment in which the avatar touched the object was computed by attaching a photodiode to the  
189 screen (where the videos were displayed) that detected the appearance of a black dot glued to the  
190 frame where the avatar touched the bottle.

191

## 192 **Interactive task**

193 We used an ecological human-avatar interactive task “Joint-Grasping task” (Sacheli et al., 2015a,  
194 2015b; Candidi et al., 2017; Era et al., 2018a; Moreau et al., 2018; Gandolfo et al., 2019, Figure 1)  
195 that recruits mechanisms similar to the ones characterizing human-human interaction, namely  
196 mutual adjustment and automatic imitation (Sacheli et al., 2012, 2013; Candidi et al., 2015; Curioni  
197 et al., 2017; Era et al., 2018a). Indeed, the participants’ action goal cannot be achieved without  
198 taking the virtual partner’s movements into account and adapting to them in real time. Participants  
199 sat in front of a rectangular table, where a bottle-shaped object was placed 45 cm away from them.  
200 Behind the bottle-shaped object there was a monitor displaying a virtual partner facing the  
201 participant and a virtual bottle-shaped object identical to that of the participants (Fig.1). Participants  
202 positioned their right hand over a start-button placed 40 cm from the bottle-shaped object and 10 cm  
203 to the right of the midline, with their index finger and thumb touching. To record the moment in  
204 which participants touched the bottle, touch-sensitive copper plates were placed at 15 cm and 23 cm  
205 of the total height of the object. Because of the shape of the object, to grasp the lower part  
206 participants had to perform a whole-hand grasp (power grip), while to grasp the upper part they had  
207 to perform a thumb-index finger precision grip. Participants were required to perform different  
208 (complementary) or same (imitative) actions with respect to the virtual partner. In the Imitative  
209 movements condition, participants had to grasp the same portion of the object as the virtual partner  
210 by performing a power or precision grip to the lower or upper part of the bottle, respectively. In the  
211 Complementary movement’s condition, conversely, participants had to perform opposite  
212 movements with respect to the virtual partner (one grasping the lower part via power grip, the other  
213 grasping the upper part via precision grip, or vice-versa) (Fig.1). In one experimental session,

214 participants were asked to cooperate with the virtual partner, grasping the object as synchronously  
215 as possible with their partner (Cooperative session). In another experimental session, participants  
216 were asked to compete with the virtual partner, grasping the object before virtual partner  
217 (Competitive session). Participants needed to on-line adapt to the partner's movement by  
218 performing the same action or a different one, without knowing in advance whether this would  
219 imply performing a precision grip on the upper part or a power grip on the lower part. In 20% of the  
220 trials, in order to keep the participant's attention, the virtual partner performed a movement change  
221 by switching from a precision to a power grip (or vice versa) during the reaching movement. These  
222 trials were not included in the analyses. The trial timeline was as follows: participants heard the  
223 Imitative/Complementary auditory instruction, and, upon receiving it, they were allowed to release  
224 the start button and reach-to-grasp the bottle-shaped object. When participants started before  
225 hearing the instruction, the trial was discarded from the analyses. At the end of each trial,  
226 participants received a feedback (by way of green or red LED lights) concerning their performance  
227 (win/loss trial). A win trial meant that participants had followed their auditory instructions and  
228 correctly performed complementary/imitative movements. In addition, a win trial in the cooperative  
229 session meant the object had been grasped synchronously with the virtual partner, while in the  
230 competitive session it meant the bottle had been grasped before the virtual partner. The action was  
231 considered synchronous in the Cooperative session when the time-delay between the participant's  
232 and avatar's index-thumb bottle contact-times fell within a given time-window. It was considered  
233 fast enough to win a competition trial when the time-delay was smaller than a given time-window.  
234 The time-window was narrowed or widened on a trial-by-trial basis according to a stair-case  
235 procedure. This procedure allowed us to tailor the task difficulty to the specific performance of each  
236 participant. In order to motivate individual commitment during the task, participants knew their  
237 final monetary reward would depend on the number of win trials gained during the experiment. The  
238 virtual partner adapted the duration of its movements according to the participant's performance: in  
239 the Cooperative session, when participant's asynchrony was smaller than the given time-window

240 for two consecutive trials, the avatar changed its speed for the following trial. Otherwise the speed  
241 stayed the same. This was done to make the avatar easier to predict when participants were  
242 performing badly (the avatar became more “committed” to smoothing the interaction) and less easy  
243 when participants were performing well. Indeed, it has been shown that making one’s own behavior  
244 more predictable facilitates coordination during joint-actions (Vesper et al., 2010 for a review). In  
245 the Competitive session, instead, when participants grasped the object before the avatar by a time  
246 exceeding the set time-window for two consecutive trials, the virtual partner increased its speed for  
247 the following trial; when participants grasped the object after the avatar by a time exceeding the  
248 time-window for two consecutive trials, the virtual partner decreased its speed for the following  
249 trial. In the rest of the cases the virtual partner speed remained the same. These procedures allowed  
250 us to tailor the task difficulty to participant performance in the Cooperative and Competitive  
251 interactions. Movements were always performed with the right, dominant hand.

252 In each session (after cTBS), participants performed one 56-trial Cooperative and one 56-trial  
253 Competitive block (in a counterbalanced order between participants). Thus, participants performed  
254 14 trials in the following 2 x 2 design: 2 (Complementary/Imitative) x 2 (Precision/Power grip).  
255 Stimuli presentation and randomization were controlled by E-Prime2 software (Psychology  
256 Software Tools Inc., Pittsburgh, PA).

257

## 258 **Kinematics Recording**

259 See Supplementary Information.

260

## 261 **Transcranial Magnetic Stimulation.**

262 The stimulation method was the same used in Sacheli et al. (2015a; 2018) and Era et al. (2018). To  
263 determine stimulation intensity, we measured individuals’ resting motor threshold (rMT).  
264 Recordings of motor evoked potentials (MEPs) were taken from the first dorsal interosseous (FDI)  
265 muscle of the right hand. Surface Ag/AgCl electrodes were placed in a belly-tendon montage with

266 the active electrode placed over the muscle and the reference one over the interphalangeal joint.  
267 Electromyographic (EMG) recording was performed with Spike 2 electromyography software. The  
268 resting motor threshold, defined as the lowest intensity able to evoke 5 of 10 MEPs with an  
269 amplitude of at least 50  $\mu$ V, was determined by holding the stimulation coil over the optimal scalp  
270 position (OSP). The OSP for inducing MEPs in the right FDI muscle was found by moving the coil  
271 in 1 cm increments over the left primary motor cortex until the largest MEPs were found. These  
272 points were then marked with a pen on a bathing cap worn by the participants. The mean resting  
273 motor threshold (rMT) was  $57\% \pm 9.8\%$  of the stimulator output for participants receiving cTBS  
274 over aIPS and  $54.4\% \pm 5.9$  for participants receiving cTBS over TPJ. The rMTs did not differ  
275 between the two groups ( $t = 0.98$ ,  $p = 0.33$ ). cTBS was applied following Huang and colleagues  
276 (Huang et al., 2005): three 50 Hz pulses were delivered in trains every 200 ms (i.e., at 5 Hz) for 20 s  
277 (300 pulses in total). After the cTBS, but before starting the interactive task, participants rested for  
278 5 minutes with their right arm relaxed on their side. To avoid exceeding the inhibitory time-  
279 window, the task never lasted more than 15 minutes.

280 Stimulation sites were stereotactically identified on the scalp of each participant with the SofTactic  
281 Navigator system (EMS), (see Supplementary Information). TMS was delivered using a 70 mm  
282 figure-eight coil connected to a Magstim Super Rapid Transcranial Magnetic Stimulator (The  
283 Magstim Company). We used a continuous Theta-Burst stimulation paradigm (20 seconds) shown  
284 to have an inhibitory effect over the stimulated site starting 5 minutes after stimulation and lasting  
285 up to 20 minutes (Huang et al., 2005). The SofTactic Neuronavigator system (EMS) allowed us to  
286 find the location of the stimulation sites on the participant's scalp. Skull landmarks (nasion,inion  
287 and two preauricular points) and 61 points forming a representation of the scalp were digitized by  
288 means of a Polaris Vicra Optical Tracking System (NDI). Coordinates in Talairach space (Talairach  
289 and Tournoux, 1988) were automatically estimated by the SofTactic Navigator from an MRI-  
290 constructed stereotaxic template using an individualized probabilistic head model computation. This  
291 individualized head model preserved the anatomical scalp-brain correlates of a mean MR template

292 and provided an accurate set of estimated MRI data specific to the participant under examination.  
293 The neuronavigation system was used to identify and store the sites that optimally targeted the left  
294 aIPS for each participant according to the coordinates reported by Hamilton and Grafton 2006 (MNI  
295  $x = -52, y = -32, z = 44$ , converted in Tal  $x = -47, y = -34, z = 37$  according to (Tunik et al., 2007)).  
296 The same procedure was adopted to target the rTPJ coordinates (Tal  $x = 54, y = -45, z = 26$ ,  
297 Sowdan and Catmur, 2015). The resulting mean stimulation coordinates were  $x = -46.76 \pm 0.9, y = -$   
298  $34.47 \pm 1$  and  $z = 36.35 \pm 0.7$  for left aIPS and  $x = 53.89 \pm 2.17, y = -45.56 \pm 1.09$  and  $z = 25.89 \pm$   
299  $2.32$  for the rTPJ (Talairach coordinates, see Figure 2). The neuronavigator system allowed us to  
300 track the coil focus on these coordinates and monitor online any unwanted movement of the coil  
301 during cTBS. Displacements from the optimal individual scalp locations for aIPS/rTPJ stimulation  
302 never exceeded 2 mm for any of the three axes. In both stimulation Groups, participants also  
303 received a sham stimulation as control stimulation sessions. During sham stimulation, a 3-cm-thick  
304 wooden rectangular-shaped object was placed on the target area between the coil and the  
305 participant's head. The 3-cm-thick wooden rectangular-shaped object was not visible to  
306 participants. We decided to use a sham protocol in which a 3 cm-thick object is introduced between  
307 the scalp and the coil in order to ensure that no current was reaching the brain (Roth et al., 2002,  
308 2007; Zangen et al., 2005), while keeping the acoustic artifact and the contact with the scalp  
309 equivalent to the active stimulation. The same sham protocol has already been used in other studies  
310 (Sacheli et al., 2015; 2018; Fiori et al., 2015; Era et al., 2018; Ellison and Convey, 2006). aIPS/rTPJ  
311 and sham stimulation was counterbalanced between participants.

312

### 313 **Experimental Design and Statistical Analysis**

314 Excluded from the analyses were trials in which participants i) missed the touch-sensitive copper-  
315 plates and thus no response was recorded, ii) released the start button before the go instruction or  
316 iii) did not respect their complementary/imitative instructions. At the group level, participants with

317 a mean 2.5 SDs above or below the group mean were also excluded from the analyses; according to  
318 this criterion, six pairs were outliers in grasping asynchrony.

319 We considered the following to be crucial behavioral measures:

- 320 1. Accuracy, i.e. number of movements executed correctly (according to the instructions).
- 321 2. Reaction Times (RTs), i.e. time from the go-signal to the release of the start button (See  
322 Supplementary Information);

323 Grasping Asynchrony (GAsynchr) for the Cooperative session was the absolute value of time delay  
324 between the participant's and avatar's index-thumb contact-times on the bottle-shaped object. For  
325 the Competitive session it was time delay (with algebraic sign) between the participant's and  
326 avatar's index-thumb contact-times on the bottle-shaped object. To take changes in the avatar's  
327 movement speed into account for the computation of GAsynchr, we corrected its values, trial-by-  
328 trial (as in Era et al., 2018a). More specifically, we gave a 20 ms bonus (meaning we subtracted 20  
329 ms from GAsynchr) in the Cooperative session every time the avatar became more difficult to  
330 predict by changing its speed, while in the Competitive session we added or subtracted a number of  
331 ms to GAsynchr that was equal to the difference between the duration of the standard clip (2000  
332 ms) and the clip actually presented to the participant. For example, when participants were  
333 presented with a clip lasting 1800 ms, we subtracted 200 ms from GAsynchr (bonus on performance  
334 for faster clips); when participants were presented with a clip lasting 2400 ms, we added 400ms to  
335 GAsynchr (malus on performance for slower clips). In order to compare the Cooperation and  
336 Competition factors, we took each trial of GAsynchr in aIPS/TPJ stimulation sessions and  
337 subtracted the means of the GAsynchr in the respective sham sessions. We did so because  
338 GAsynchr was computed as an absolute value in Cooperation, while it retained the algebraic sign in  
339 Competition. This procedure allowed us to look at the effect of stimulating the two brain regions,  
340 net of any baseline difference in performing the task in the two experimental groups. We analyzed  
341 GAsynchr data using multilevel mixed regression analysis (through the package lmer (Bates et al.,  
342 2014)), which belongs to the family of linear mixed models (Pinheiro and Bates, 2000). This

343 approach allows to analyze the data of all the trials (not just mean values of each participant in each  
344 condition) and thus better evaluate the variations of data usually not considered in analysis of  
345 variance. This approach also allows to separately consider the variable manipulated by the  
346 experimenter (fixed effects) and the ones that are not (random effects) (Pinheiro and Bates, 2000).

347 The multilevel mixed regression analysis had GASynchr as dependent variable and CONTEXT  
348 (Cooperative/Competitive), INTERACTION TYPE (Complementary/Imitative), MOVEMENT  
349 (Power/Precision grip) as categorical predictors and the SITE (aIPS/rTPJ) as between group factor.  
350 We considered as apriori random factor the subject (Barr et al., 2013).

351

352 *Motion kinematics analysis*

353 See Supplementary Information.

354

355 Behavioral or kinematic values that fell 2.5 SDs above or below each individual mean for each  
356 experimental condition were excluded as outliers. We used non-parametric tests (Friedman  
357 ANOVA) with regard to Accuracy. All tests of significance were based on an  $\alpha$  level of 0.05. When  
358 appropriate, post-hoc tests were performed using the Bonferroni method. Statistical analyses were  
359 performed using Statistica 8 software (StatSoft) and R (R Development Core Team, 2013).

360

## 361 **Results**

### 362 *Behavioral measures*

#### 363 *Grasping Asynchrony*

364 The multilevel mixed regression analysis showed that the site of stimulation only reached statistical  
365 significance in the INTERACTION TYPE x SITE interaction ( $\chi^2 = 11.45$ ,  $P < 0.001$ , upper CI =  
366 110.82, lower CI = 29.19). Bonferroni corrected post-hoc tests indicated that when performing  
367 complementary actions, independently from the context of interaction, participants receiving left  
368 aIPS inhibition achieved worse performance in comparison to when they performed imitative

369 actions ( $P = 0.0035$ ). On the other hand, participants receiving right TPJ inhibition achieved worse  
370 performance when performing imitative actions in comparison to complementary ones ( $P = 0.029$ )  
371 (Figure 3).

372 Moreover, the analysis showed a significant INTERACTION TYPE x MOVEMENT x CONTEXT  
373 interaction ( $\chi^2 = 7.62$ ,  $P = 0.006$ , upper CI = 146.05, lower CI = 29.15). Post-hoc tests showed that  
374 when performing complementary movements in the Competitive context, participants achieved  
375 worse performance during Precision compared to Power grips ( $P = 0.026$ ). This significant  
376 interaction accounted for the other significant lower level main effects and interactions (Significant  
377 main effect of MOVEMENT ( $\chi^2 = 5.83$ ,  $P = 0.02$ , upper CI = 9.25, lower CI = -68.65; significant  
378 INTERACTION TYPE x MOVEMENT interaction ( $\chi^2 = 5.04$ ,  $P = 0.025$ , upper CI = -10.49, lower  
379 CI = -93.75); significant CONTEXT x MOVEMENT interaction ( $\chi^2 = 7.12$ ,  $P = 0.008$ , upper CI = -  
380 18.43, lower CI = -101.76)).

381

### 382 *Accuracy*

383 Accuracy did not differ across conditions (Chi sq= 10.96,  $P = 0.14$ ).

384

### 385 *Reaction Times*

386 See Supplementary Information.

387

### 388 *Kinematics measures*

389 See Supplementary Information.

390

## 391 **Discussion**

392 Although very different, motor cooperation and competition both require representing and  
393 integrating one's own actions with those of the interaction partners, as well as controlling the



394 imitation of the partner's behavior (Era et al., 2018a). At the same time, cooperative and  
395 competitive motor interactions in humans may often involve the performance of imitative and  
396 complementary movements that in turn likely rely upon different neural and cognitive resources.  
397 While imitative face-to-face interactions might be supported by the ability to control imitative  
398 behavior, complementary interactions require the integration of differently executed and observed  
399 movements that imply the visuo-motor integration of non-overlapping movements. Although  
400 performing imitative and complementary interactions in cooperative and competitive contexts  
401 represents a crucial aspect of our social life, little is known about the causal role of specific brain  
402 regions and networks in supporting these behaviors. One main point of novelty of our study is that,  
403 while transient inhibition of right TPJ induced by continuous theta burst stimulation selectively  
404 impairs the ability to online coordinate with a partner when performing imitative motor responses  
405 (in comparison to complementary ones), inhibition of left aIPS impairs the ability to perform  
406 complementary interactions in comparison to imitative ones.

407

#### 408 **Role of the TPJ for imitative interactions**

409 The temporo-parietal junction (TPJ) is a brain region located at the border of the parietal and  
410 temporal lobes that is heavily involved in social cognition (Goel et al., 1995; Happé et al., 1996;  
411 Gallagher et al., 2000). Studies suggest, for example, that the TPJ plays a critical role in processes  
412 related to social cognition such as mentalizing (Van Overwalle, 2009) and perspective taking  
413 (Aichhorn et al., 2006), two processes of fundamental importance for predicting prosocial behavior  
414 (Tusche et al., 2016; Era et al., 2017). The causal role of the rTPJ in spatial perspective taking has  
415 been highlighted in studies using noninvasive brain stimulation techniques (Donaldson et al., 2015).  
416 In an “own-body transformation” task where participants had to adopt the spatial perspective of an  
417 avatar, TMS disruption of rTPJ activity reduced the ability of participants to take the spatial  
418 perspective of another (Blanke et al., 2005). In a similar vein, TPJ lesions impaired the patients'  
419 performance in imitative control and perspective-taking (both spatial and cognitive) (Spengler et al.,

420 2010). Moreover, TMS studies show that interfering with the activity of rTPJ reduced the ability to  
421 control automatic imitation (Sowden and Catmur, 2015). Two recent studies using anodal excitatory  
422 transcranial direct current stimulation (tDCS) suggest that rTPJ stimulation enhances both the  
423 ability to control automatic imitation in a “control of imitation task” (Brass et al., 2000) and spatial  
424 perspective taking (Santiesteban et al., 2012; Santiesteban et al., 2015).

425 More specifically, Santiesteban and colleagues (2012; 2015) have shown that anodal, excitatory,  
426 tDCS modulation of rTPJ activity results in a reduction of automatic interference during the  
427 execution of finger movements that are incongruent with, task irrelevant, observed ones (i.e. a  
428 relative increased ability to perform finger movements during the incidental observation of  
429 incongruent finger movements compared to a control stimulation condition). The Authors of these  
430 papers interpreted this as a decrease in automatic imitation of task-irrelevant observed movements;  
431 TPJ activity was proposed to strengthen self-other distinction, facilitating own movements and  
432 reducing the tendency to imitate others’, irrelevant, movements. Importantly, this effect was found  
433 when participants were asked to respond to symbolic cues (numbers) while passively observing  
434 task-irrelevant congruent/incongruent finger movements. Using the same task, Bardi et al. (2017)  
435 applied anodal tDCS to up-regulate TPJ activity and measured corticospinal excitability (TMS-  
436 MEP) during the execution of index finger abduction that could either be congruent or incongruent  
437 to the, task irrelevant, observed ones. These Authors described that TPJ activity enhanced the  
438 instructed motor plan rather than suppressing task-irrelevant imitation (Bardi et al., 2017).

439 Here we note that in the study where this visuo-motor interference effect was originally described  
440 (Brass et al., 2000), making the movement of the observed finger ”task-relevant” abolished  
441 (Experiment 1) or diminished (Experiment 2 and 3) the interference effect. Sowden and Catmur  
442 (2013) used a similar task to Brass et al. (2000), Santiesteban et al. (2012 and 2015) and Bardi et al.  
443 (2017) while applying interferential, event-related, rTMS and found that interfering with the activity

444 of rTPJ impaired the ability to control automatic imitation compared to the stimulation of a control  
445 site.

446 Our task differs in significant ways from that used in Sowden et al. (2015), Santiesteban et al.  
447 (2012, 2015), and Bardi et al. (2017) studies. In our task participants are indeed explicitly asked to  
448 imitate, or complement, the actions of the interactor, which are no way task irrelevant but rather  
449 crucial for task execution. Indeed, participants are required to predict the actions of their partner in  
450 order to program and control their own actions. Many studies have shown that the execution of  
451 congruent or incongruent movements is radically different when the observed action is task  
452 irrelevant compared to when it is essential for an interaction (Newmann-Norlund et al., 2007). We  
453 have previously shown in the same experimental set-up used in the present study that  
454 synchronization during complementary and imitative interactions do not differ (Sacheli et al., 2012;  
455 Sacheli et al., 2013; Sacheli et al., 2015; Era et al., 2018) supporting the idea that at a performance  
456 level, during an interactive task, complementing and imitating the action of a partner are not  
457 affected by automatic imitation. Moreover, recent studies demonstrated that automatic imitation is  
458 reduced when two different executed and observed actions are interdependent in contributing to a  
459 shared goal (Clarke et al., 2018).

460 Hogeveen et al., 2015 have shown that anodal tDCS applied to right TPJ reduces the tendency to  
461 imitate, task irrelevant, finger movements incongruent with those that participants had to perform,  
462 but that this inhibition does not appear in more ecological tasks. Conversely stimulating the inferior  
463 frontal gyrus induced an increase in the tendency to imitate other's behavior in an ecological  
464 context and reduced the tendency to inhibit, task irrelevant, imitation. These Authors propose that  
465 "TPJ controls task- appropriate shifts in attention toward representation of the self or the other,  
466 indirectly impacting upon imitation" which is coherent with the evidence that making the behavior  
467 of a partner task relevant might switch the role of TPJ in controlling imitation.

468 More specifically, in the present study we found that inhibiting TPJ activity leads to decreased  
469 synchronization (during cooperation) and anticipation (during competition) in imitative compared to  
470 complementary interactions. Thus, we show that TPJ is necessary to synchronize and anticipate  
471 imitative interactions. Importantly, that interfering with the activity of rTPJ did not compromise the  
472 ability to perform complementary interactions supports the idea that complementary interactions, in  
473 which co-actors need to predict and integrate each other's actions in order to achieve a shared goal,  
474 do not require the control of self-other representations, needed instead in conditions in which co-  
475 actors perform actions at the same time, one independently from the other (Clarke et al., 2018;  
476 Sacheli et al., 2018). Our results show, instead, that TPJ activity supports the ability to perform  
477 imitative interactions, where a direct mapping of the observed action onto one's own motor  
478 representation is needed. This direct mapping might necessitate to transform the observed action in  
479 visuo-spatial terms, a process supported by the activity of rTPJ (Blanke et al., 2005)."

480 Thus, another novel finding of the present study is that rTPJ functioning is crucial in supporting the  
481 ability to perform online imitative motor interactions in both competitive and cooperative contexts.

482

### 483 **Role of the aIPS for complementary interactions**

484 The left anterior intraparietal sulcus (aIPS), has been shown to code for the goals of both executed  
485 and observed actions (Tunik et al., 2007; Hamilton and Grafton, 2006). Indeed, this region has been  
486 shown to have a role in coding motor intentions (Desmurget et al., 2009; Andersen & Buneo, 2002;  
487 Batista and Andersen 2001; Fogassi et al., 2005). Moreover, TMS studies show that aIPS inhibition  
488 impairs participant's ability to switch their action plan and correct their reaching trajectory when the  
489 target of their grasp changes position (Desmurget et al., 1999; Tunik et al., 2005).

490 Crucially, we recently showed that aIPS plays a causal role in integrating predictions about one's  
491 own and others' complementary actions during human-avatar joint-actions (Sacheli et al., 2015a;  
492 Sacheli et al., 2018). Moreover, the inhibitory effect of cTBS delivered to aIPS in one member of an  
493 interacting dyad during complementary interactions was compensated by the dyad's ability to

494 mutually adapt (Era et al., 2018). In a similar vein, another study showed that motor performance of  
495 brain damaged patients with motor disorders (limb-*apraxia*) is improved when engaging in a  
496 realistic form of interaction with a virtual partner compared to when the interaction did not ask for  
497 mutual adjustments (Candidi et al., 2017). Thus, an important feature of realistic joint-action in  
498 which participants link their own action to that their partner is mutual adaptation. In the task used in  
499 the present study, these features were preserved in both the cooperative and competitive context  
500 because participants needed to predict the actions of their virtual partner in order to decide which  
501 action to perform, and because the virtual partner reacted to the movements of its human partner in  
502 order to establish a form of mutual reactivity. The present results confirm that left aIPS plays a  
503 crucial role in mediating complementary interactions and extend this notion by showing that this  
504 region does not merely support the ability to synchronize during cooperation, but rather that it  
505 supports functions that are shared by cooperative and competitive contexts such as the ability to  
506 program and control inter-individual action integration.

507

## 508 **Conclusions**

509 To sum-up, the inhibition of left aIPS impaired individuals' performance during complementary  
510 interactions compared to imitative ones, while the inhibition of rTPJ impaired individuals'  
511 performance during imitative interactions in comparison to complementary ones. Thus, while aIPS  
512 may underpin the integration of one's own and the others' movement required during  
513 complementary interactions (Sacheli et al., 2015a; 2018; Era et al., 2018b), rTPJ may underpin the  
514 ability to imitate the behavior of an interaction partner. That the effects of aIPS and TPJ inhibition  
515 were present in both the cooperative and competitive contexts indicates that the role these regions  
516 play during motor interactions is more linked to action prediction, programming and control, which  
517 may be equally relevant in both contexts, than to their actual execution, where cooperation and  
518 competition may differ radically. Thus, a novel result of the present study is the demonstration that

519 the role of aIPS in supporting complementary motor interactions is independent from the context of  
520 the interaction. This carries out the important implication that aIPS supports the ability to integrate  
521 predictions regarding one's own and other's actions more than action synchronization per se.  
522 Moreover, we demonstrated for the first time that rTPJ plays an active, crucial role in supporting the  
523 ability to perform imitative motor interactions and that it does not specifically support the  
524 performance of competitive interactions, requiring self-other distinction. Given the off-line nature  
525 of our stimulation paradigm, the interpretation of the results needs to keep into account the role of  
526 the targeted areas as well as of those to which they are connected (Ruff et al. 2009, Bestmann et al.  
527 2008). While in the present study we focus on the role of the stimulated 'hub' areas, we endorse the  
528 idea that these areas are part of larger neural networks and that our results might be best interpreted  
529 in terms of functional networks rather than of single regions. Indeed, recent studies indicate that  
530 applying cTBS over a brain region reduces its connectivity with functionally related brain regions  
531 (Rahnev et al., 2013; Valchez et al., 2015). In view of this, our results may rather be interpreted as  
532 the effect of aIPS inhibition on the activity of the fronto-parietal network involved during  
533 complementary motor interactions (Newman-Norlund et al., 2007), and as the effect of TPJ  
534 inhibition on the modulation of the activity of fronto-parietal mirror regions dedicated to action  
535 imitation (see for example the STORM model, Wang and Hamilton, 2012). One limitation of the  
536 present study is that, because of the spatial resolution of cTBS, it is possible that, in some  
537 participants, in addition to inhibiting aIPS the cTBS might have also targeted some neighbouring  
538 portions of the inferior and/or superior parietal lobule. In a similar vein, TPJ stimulation might have  
539 targeted also other portions of the supramarginal gyrus and superior parietal lobule. For this reason,  
540 the present results may also be interpreted as the effect of the inhibition of regions proximal to aIPS  
541 and TPJ and their connected networks.

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545

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794 **Captions to Figures**

795 Figure 1: Participants were asked to reach and grasp the bottle-shaped object placed in front of  
796 them. They needed to perform opposite (complementary) or same (imitative) movements with  
797 respect to the virtual partner. In the Imitative movements condition, participants had to grasp the  
798 same portion of the object as the virtual partner (both performing power or precision grips on the  
799 lower or upper part of the bottles, respectively, lower drawing). In the Complementary movement's  
800 condition, conversely, participants had to perform movements opposite to those of the virtual  
801 partner (one grasping the upper part via precision grip, the other grasping the lower part via power  
802 grip, or viceversa, upper drawing). Moreover, in one of the experimental sessions, participants were  
803 instructed to grasp the object as synchronously as possible with their virtual partner (Cooperative  
804 session, uppermost drawings). In another experimental session (Competitive session, lowermost  
805 drawings), participants were instructed to grasp the object before the virtual partner.

806

807 Figure 2: Mean stimulation sites in Talairach coordinates:  $x = -46.76 \pm 0.9$ ,  $y = -34.47 \pm 1$  and  $z =$   
808  $36.35 \pm 0.7$  for left aIPS and  $x = 53.89 \pm 2.17$ ,  $y = -45.56 \pm 1.09$  and  $z = 25.89 \pm 2.32$  for the rTPJ.

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810 Figure 3: The multilevel mixed regression analysis on Grasping Asynchrony (aIPS/TPJ – Sham)  
811 showed a significant INTERACTION TYPE x SITE interaction ( $\chi^2 = 11.45$ ,  $P < 0.001$ , upper CI =  
812 110.82, lower CI = 29.19). Bonferroni corrected post-hoc tests indicated that when performing  
813 complementary actions, participants receiving left aIPS inhibition achieved worse performance in  
814 comparison to when they performed imitative actions ( $P = 0.0035$ ). On the other hand, participants  
815 receiving right TPJ inhibition achieved worse performance when performing imitative actions in  
816 comparison to complementary ones ( $P = 0.029$ ).

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