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State-dependent TMS reveals representation of affective body movements in the anterior intraparietal cortex

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TITLE: State-dependent TMS reveals representation of affective body movements in the anterior intraparietal cortex

ABBREVIATED TITLE: TMS over aIPS reversed adaptation effect to fearful PLDs

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1 **ABSTRACT**

2 In humans, recognition of others' actions involves a cortical network that comprises, among other
3 cortical regions, the posterior superior temporal sulcus (pSTS), where biological motion is coded and the
4 anterior intraparietal sulcus (aIPS), where movement information is elaborated in terms of meaningful goal-
5 directed actions. This action observation system (AOS) is thought to encode neutral voluntary actions, and
6 possibly some aspects of affective motor repertoire, but the role of the AOS' areas in processing affective
7 kinematic information has never been examined. Here we investigated whether the action observation system
8 plays a role in representing dynamic emotional bodily expressions. In the first experiment, we assessed
9 behavioural adaptation effects of observed affective movements. Participants watched series of happy or
10 fearful whole-body point-light displays (PLDs) as adapters and were then asked to perform an explicit
11 categorization of the emotion expressed in test PLDs. Participants were slower when categorizing any of the
12 two emotions as long as it was congruent with the emotion in the adapter sequence. We interpreted this effect
13 as adaptation to the emotional content of PLDs. In the second experiment, we combined this paradigm with
14 TMS applied over either the right aIPS, pSTS and the right half of the occipital pole (corresponding to
15 Brodmann's area 17 and serving as control) to examine the neural locus of the adaptation effect. TMS over
16 the aIPS (but not over the other sites) reversed the behavioural cost of adaptation, specifically for fearful
17 contents. This demonstrates that aIPS contains an explicit representation of affective body movements.

18 **SIGNIFICANCE STATEMENT:** In humans, a network of areas – the action observation system (AOS) -
19 encodes voluntary actions. However, the role of these brain regions in processing affective kinematic
20 information has not been investigated. Here we demonstrate that the aIPS contains a representation of
21 affective body movements. Firstly, in a behavioural experiment, we found an adaptation after-effect for
22 emotional PLDs, indicating the existence of a neural representation selective for affective information in
23 biological motion. To examine the neural locus of this effect, we then combined the adaptation paradigm
24 with TMS. Stimulation of the aIPS (but not over pSTS and control site) reversed the behavioural cost of
25 adaptation, specifically for fearful contents, demonstrating that aIPS contains a representation of affective
26 body movements.

27

28 **Introduction**

29 Perception of movements of other living beings is crucial for survival in most species, to the extent
30 that many vertebrate species have specialized neural systems for action observation. In humans, a
31 widespread network of interconnected brain areas (known as the action observation system - AOS) underlies
32 the comprehension of conspecifics' body movements and actions. This network includes the posterior
33 superior temporal sulcus (pSTS) (Puce and Perrett, 2003), and two mirror system areas, the putative human
34 anterior intraparietal area (aIPS) and the ventral premotor/caudal inferior frontal gyrus complex (PMv/cIFG)
35 (Cattaneo and Rizzolatti, 2009). Several TMS studies have demonstrated that stimulating the pSTS, the aIPS
36 and the PMv/cIFG regions produces selective impairment in visual recognition of neutral actions (Candidi et
37 al., 2008; Cattaneo et al., 2010; Grossman et al., 2005; van Kemenade et al., 2012; Pobric and Hamilton,
38 2006). But is the AOS also important for the encoding of the emotional aspects of biological motion?

39 The perception of affective stimuli, irrespective of stimulus type, generally enhances the neural
40 response of core affective systems, situated within the limbic system (Adolphs, 2002; Phillips et al., 2003)
41 but emotional body movements are complex and their perception activates also a more widespread network
42 of subcortical and cortical regions, related to analysis of visual body features and more generally to action
43 observation and preparation (de Gelder et al., 2006, 2010, 2015; Tamietto and de Gelder, 2011). It is thus
44 crucial to understand whether the activation within the AOS is a mere side-effect of the type of stimuli (body
45 actions), independent from their content or whether AOS activity is causally linked to emotional recognition.
46 This issue has been explored in the literature in only two TMS studies; these found that perturbation of pSTS
47 (Candidi et al., 2011) and IPL (Engelen et al., 2015) selectively improved the recognition of fearful body
48 images. However, a limitation of both of these studies was that participants observed static images; human
49 bodies are dynamic in nature and the brain substrates used in processing static postures are likely to differ
50 from those engaged in perception of body movements. Furthermore, while conventional TMS paradigms can
51 reveal the causal role of cortical regions in cognitive functions, they do not inform us about the neural
52 representations in those regions.

53 Here we examined whether specific regions of the action observation network contain
54 representations of affective body movements. This was accomplished by the use of state-dependent TMS
55 which enables the selectivity of neural representations in a cortical region to be assessed (Romei et al., 2016;

56 Silvano et al., 2008). This approach has been previously used to examine the selectivity of neural
57 representations in various cognitive functions such as colour and motion perception (Silvano et al., 2007;
58 Cattaneo and Silvano, 2008), numerical cognition (Kadosh et al., 2010) and action observation (Cattaneo et
59 al., 2011, 2010; Jacquet and Avenanti 2015; Sato et al. 2011). In order to examine the role of AOS in
60 encoding the emotional aspects of dynamic biological motion, we used point-light displays (PLDs), also
61 referred to as biological motion (BM) stimuli (Johansson, 1973), which allow isolation of motion signals
62 from others visual cues. Kinematic information contained in PLDs is sufficient for detection of emotional
63 content of human movements (Alaerts et al. 2011; Atkinson et al. 2004, 2007, 2012; Chouhorelou et al.,
64 2006; Clarke et al., 2005; Dittrich et al. 1996). In Experiment 1, we examined behavioural adaptation effects
65 of observed affective PLDs. We found an adaptation-like bias with incongruent stimuli recognized faster
66 than congruent ones. In Experiment 2, we used the TMS-adaptation paradigm to examine the cortical locus
67 of adaptation effects observed in Experiment 1. TMS over the aIPS – but not over pSTS nor over a visual
68 control area - reversed the behavioural adaptation for fearful stimuli, indicating that this region contains
69 neural representations selective for the fearful characteristics of human movements.

70

71 **Material and methods**

72 *Visual stimuli and validation of emotional valence.* A total of 20 PLDs were presented, depicting 10
73 different expressions of happiness and fear, respectively. These stimuli are part of a wider dataset created by
74 Atkinson and collaborators (Atkinson et al., 2004, 2012). The PLDs consisted of 2 second-long digitalized
75 video clips (see Atkinson et al. 2012 for details), displaying a single actor represented as 13 white dot-lights
76 moving on a black background. The dots were positioned over the head and the main joints (one dot over
77 each ankle, knee, hip, elbow, shoulder, and hand) of the actor. Examples of the stimuli can be viewed at
78 <http://community.dur.ac.uk/a.p.atkinson/Stimuli.html>. We selected happy and fearful stimuli because they
79 are roughly equally arousing emotions, with opposite emotional valence (positive or negative). Prior to the
80 main experiments, we ran a pilot study to validate the PLDs in terms of quantity of movement contained in
81 the PLDs and of type and intensity of portrayed emotion. Sixteen healthy adults took part in this pilot
82 experiment (13 females, mean age = 29.63 (SD = 7.65)). All the participants provided informed consent
83 before taking part in the experiment. They were seated in front of a 24-inch monitor at a distance of about 60

84 centimetres. The stimuli were presented foveally. Each PLD was presented once, and for each video
85 participants were asked to recognize the conveyed emotion among 4 options (Fear, Happiness, Neutral and
86 Other) by pressing the corresponding button on the keyboard. The response options (appearing on the screen
87 after each stimulus) were indicated with a label placed over the keys “F, G, H, J” and were randomized
88 across participants. After the emotion recognition task, participants were asked to rate the “Intensity of the
89 emotion” and the “Quantity of movement” on a scale from 1 to 5, using the numeric keys on the top of the
90 keyboard. Stimuli were presented and responses recorded with E-Prime 2.0® (Psychology Software Tools,
91 Inc.). For each individual PLD we calculated the accuracy of emotion categorization, the rated intensity of
92 the emotion and the rated quantity of movement. Data distribution was tested for normality with Shapiro-
93 Wilk test. Accuracy, Intensity and Movement were not normally distributed, so they were analysed using a
94 non-parametric test for paired data, the Wilcoxon signed rank test with continuity correction. Significance
95 thresholds were Bonferroni-corrected for 3 multiple comparisons (for each variable, we compared results
96 between the three emotional valences, hence the critical alpha was set as $p < .017$). There were no significant
97 differences between the happy and fearful movements for Accuracy, Movement, and Intensity, while –
98 predictably - the neutral movements were rated as less intense compared with the two emotions (Table 1).
99 This implies that the stimuli used in Experiment 1 and 2 (i.e. fearful and happy PLDs) do not differ in terms
100 of: i) recognizability between the emotional categories, ii) intensity of the expressed emotion or iii) quantity
101 of movement contained in the stimuli.

102

Insert Table 1

103

104 **Experiment 1: behavioural assessment of adaptation to observed emotional body movements.**

105 *Participants.* Twenty-six healthy adults (14 females and 12 males, age mean = 23.58 years (SD =
106 2.95 years)) took part in the behavioural study (Experiment 1). All participants had normal or corrected-to-
107 normal vision. Prior to the experiment, all participants provided written informed consent, in accordance
108 with the Declaration of Helsinki.

109 *Design and procedure.* Participants were seated in a comfortable chair in front of a 24-inch computer
110 screen at a distance of around 60 cm. E-Prime version 2.0 (Psychology Software Tools, Inc.) software was
111 used for stimulus presentation and response recordings. The study consisted of 12 adaptation blocks (6 with
112 happy and 6 with fearful adapters), consisting of a 1 minute adapting period followed by 8 test trials. Each
113 trial began with a white central fixation cross over a black background, lasting for 10 seconds. This was
114 followed by an adaptation period in which the same PLD was repeated 30 times (for a total duration of 60
115 sec). Participants were asked to simply watch the stimuli and focus on the emotion expressed by the actor.
116 The order of adaptation blocks was randomized. At the end of adaptation, a screen appeared asking
117 participant to “Get ready for the task”, after which 8 test stimuli (4 fearful and 4 happy PLDs) were
118 presented. Half of the test stimuli were emotionally congruent and half were emotionally incongruent with
119 the adapter, and their order was randomized. The test stimuli and the adapter stimuli belong to the same
120 dataset, i.e. the same stimulus could be used as an adapter in one block or as a test stimulus in another block.
121 However, in single blocks, the adapter stimulus was always different from the test stimuli presented
122 thereafter. In other words, every stimulus could appear randomly as adapter or as a test in different blocks,
123 but not in the same block. The movie clip was presented centrally. Simultaneously with the stimulus
124 presentation, the question “Which emotion?” appeared on the upper part of the screen, and the two response
125 options (“Fear” and “Happiness”) were presented on the lower part of the monitor. For each test stimulus,
126 participants were asked to categorize the expressed emotion as fast as possible by key-press. The response
127 options were indicated with a label placed over the keys “G” and “H”, and the key-emotion correspondence
128 was randomized across participants. Participants were asked to respond using the index and the middle finger
129 of their right hand. The PLD was presented for a maximum of 2 seconds, while the question and the response
130 period lasted until participants responded. Accuracy and response time (RTs) were recorded.

131 *Data analyses.* The dependent variable was mean response times (RTs). Only correct responses were
132 included in the analyses (the overall error rate was 4.43%). Data distributions failed the normality (Shapiro-
133 Wilk’s test) and homoscedasticity of variance (Bartlett’s test) tests. To normalize the distribution, the
134 averaged RTs were log-transformed prior to analyses (logRT). A two-way repeated-measures ANOVA was
135 conducted with emotional content of the test stimuli (“emoTest”: Fear or Happiness) and emotional
136 congruence between test and adapter stimuli (congruent or incongruent) as within-subject factors. Post hoc

137 comparisons were performed with two-tailed paired-samples t-tests with correction of the significance
138 threshold for multiple comparisons whenever appropriate. All analyses were performed using R, version
139 3.3.1 (R Development Core Team, 2016).

140

141 **Experiment 2: Effects of TMS on perceptual adaptation**

142 *Participants.* Seventeen healthy adults (11 females and 6 males, mean age = 25.63 (SD = 5.17))
143 participated in the TMS experiment (Experiment 2). Three participants were excluded from the analysis
144 because of difficulties in determining their resting motor threshold. In these participants, the TMS
145 stimulation over M1 did not produce any visible hand twitch, and no motor sensation was perceived. Hence,
146 the final analyses were performed on a total of 14 participants. Participants in the TMS experiment were
147 screened for MRI and TMS contraindication prior to the experiment and received a £ 15 voucher refund for
148 their participation. All participants had normal or corrected-to-normal vision. Prior to the experiment, all
149 participants provided written informed consent. The protocol was approved by the University of
150 Westminster's ethical committee, in accordance with the Declaration of Helsinki.

151 *Neuronavigation and identification of stimulation sites on individual anatomy.* We used MRI-guided
152 neuronavigation (BrainInnovation BV, the Netherlands) for accurate positioning of the TMS coil. For each
153 participant, a high resolution T1-weighted MPAGE scan (176 partitions, 1 x 1 x 1 mm, flip angle = 7°, TI =
154 1,000 ms, TE = 3.57 ms, TR = 8.4 ms) was acquired before the TMS experiment. Structural MRI images
155 were obtained with a 1.5 T whole-body TIM Avanto System (Siemens Healthcare), at the
156 Birkbeck/University College London Centre for NeuroImaging (BUCNI), with a 32-channel head coil. A 3D
157 reconstruction of the gray matter surfaces and the scalp was created for each participant, which were co-
158 registered to the participant's head in order to position the coil over the site of stimulation and to control coil
159 position throughout the experiment. In each participant, three different sites in the right hemisphere were
160 stimulated: the posterior part of the right superior temporal sulcus (pSTS), the anterior part of the right
161 intraparietal sulcus (aIPS) and a posterior occipital control area located next to the midline. The three loci
162 were identified on the basis of macro-anatomical landmarks. Specifically, pSTS was targeted over the
163 transition between its posterior segment and its horizontal segment (see Ochiai et al. 2004 for an overview of

164 STS anatomy). We defined the aIPS as the most rostral part of the IPS at the intersection between the
165 postcentral gyrus and the IPS (Caspers et al., 2006). Control TMS was applied to a site corresponding to a
166 secondary visual area not primarily implied in coding for emotional aspect of visual stimuli, located between
167 BA 17 and BA 18 (see Figure 1)

168 *TMS.* Biphasic TMS pulses were applied with a figure-of-eight coil (D70mm coil) connected to a
169 Magstim Rapid2 stimulator (Magstim Co Ltd, Whitland, UK). At first we searched in each participant the
170 visually assessed resting motor threshold (rMT), defined as the stimulator's output intensity necessary to
171 obtain a visible twitch in the contralateral intrinsic hand muscles in exactly 50% of trials in a series of at least
172 eight consecutive pulses (Rossini et al, 1994). The intensity of stimulation in the actual experiment was set to
173 120% of the individual's rMT with a maximum of 65% maximal stimulator output due to coil overheating
174 and limiting discomfort to participants. The coil was attached to a Magstim coil stand and placed tangentially
175 to the scalp. Coil orientation was medial-lateral with the handle pointing laterally and slightly posteriorly
176 (70° from the midline) for the aIPS position, in order to induce a current in the underlying cortical tissue
177 roughly perpendicular to the IPS. A similar orientation was used for the stimulation of pSTS, but with the
178 coil handles pointing upwards. Due to pSTS proximity to the ears, in some participants the coil orientation
179 was changed to minimize discomfort. For the occipital (control) stimulation, the coil was positioned
180 perpendicular to the midline with the handle pointing outward. TMS was delivered in triplets. In every trial
181 participants received three 10 Hz pulses time-locked to the onset of the PLD, starting synchronously with the
182 visual stimulus.

183

184

Insert Figure 1

185

186 *Procedure.* The TMS paradigm was identical to that used in Experiment 1 described above. Every
187 block consisted of 1 minute of adapting period followed by 8 test trials. A total of 12 adapter stimuli (6
188 happy and 6 fearful PLDs) and 96 test stimuli were presented for each of the three sites of stimulation. The
189 order of adaptation blocks was randomized. During the adaptation period the same PLD was repeated 30
190 times (for 60 sec). Participants were asked to simply watch the adapter stimuli and focus on the emotion
191 expressed by the actor. At the end of adaptation, 8 test stimuli (4 fearful and 4 happy PLDs) were presented.

192 Half of the test stimuli were emotionally congruent (i.e. same emotion) and half were emotionally
193 incongruent (i.e. different emotion) with the adapter, and their order was randomized. Participants were
194 asked to categorize the expressed emotion (Fear or Happiness) as fast as possible by key-press, using the
195 index and the middle finger of their right hand. Accuracy and response time (RTs) were recorded. The three
196 stimulation sites (right pSTS, right aIPS and the control site) were stimulated on the same day, with 30
197 minutes of delay between sessions. The order of stimulation sites was counterbalanced between participants.
198 Participants wore earplugs and were seated in a comfortable chair in a quiet room, in front of a 24-inch
199 computer screen at a distance of 60 cm, with their head on a chin-rest.

200

201

Insert Figure 2

202

203 Data analyses: All analyses were performed using R, version 3.3.1 (R Development Core Team,
204 2016). The dependent variable was the mean of response time (RTs). Only correct responses were included
205 in the analyses. Data were tested for normality (Shapiro test) and homoscedasticity of variance (Bartlett test).
206 To normalize the distribution, the averaged RTs were log-transformed prior to analyses (logRT). A three-
207 way repeated-measures ANOVA (3x2x2) was performed. The site of TMS stimulation (“stimSite”), the
208 emotional valence of the test stimuli (“emoTest”) and the emotional congruence between test and adapter
209 stimuli (“congruence”) were entered as within-subject factors. Post hoc comparisons were performed with
210 two-tailed paired-samples t-tests. The significance threshold for the p-values was corrected for multiple
211 comparisons when appropriate. As a measure of the effects size, the Generalized Eta squared (η^2) is reported
212 when appropriate. In addition, we calculated the Cohen’s d for the significant comparisons using bootstrap
213 resamples method (Gerlanc and Kirby, 2015). The number of bootstrap resamples (R) was set at 2000.
214 Bootstrap Cohen’s d effect size measures and their corresponding 95% confidence intervals (CIs) are also
215 reported when appropriate.

216

217 **Results**

218 **Experiment 1: behavioural evidence of perceptual adaptation to the emotional content of PLDs.**

219 In Experiment 1, the overall error rate was 4.43%. A summary of the results of Experiment 1 is
220 presented in Table 2 and in Figure 3. The two-way ANOVA showed a significant main effect of
221 “Congruence” ($F_{(1,25)} = 7.31$, p -value = .012) with incongruent stimuli being recognized faster than congruent
222 ones, while the interaction between “emoTest” and “Congruence” was not significant ($F_{(1, 25)} = 0.856$, p -value
223 = .364; $\eta^2 = 0.014$; Cohen’s $d = -0.236$, C.I. = -0.660; 0.166).

224

225

Insert Table 2.

226

227

Insert Figure 3.

228

229 **Experiment 2: state-dependent effects of TMS over aIPS on explicit categorization of fearful PLDs.**

230 In Experiment 2 the overall error rate was 3.87%. The three-way ANOVA showed a significant main
231 effect of “Congruence” ($F_{(1,13)} = 14.994$, p -value = .002), with congruent stimuli being recognized slower than
232 incongruent ones (mean RTs: congruent = 1194 ms; incongruent = 1148 ms), suggesting the presence of an
233 adaptation after-effect for affective PLDs and confirming the results of the behavioural experiment
234 (Experiment 1). More importantly, we found a significant three-way interaction between “stimSite, emoTest
235 and Congruence” ($F_{(2,26)} = 3.546$, p -value = .043). To better understand this interaction, we performed three
236 2x2 repeated measures ANOVAs in the three stimulation sites separately, with “emoTest” and “Congruence”
237 as within factors. We found a significant main effect of “Congruence” in the control site ($F_{(1,13)} = 9.329$; p -
238 value = .009; $\eta^2 = .017$) and in pSTS ($F_{(1,13)} = 9.393$; p -value = .009; $\eta^2 = .029$), showing that the adaptation
239 after-effect persisted and hence suggesting that TMS stimulation did not have any effect on those two brain
240 areas. On the contrary, ANOVA in aIPS showed a significant interaction between “emoTest and
241 Congruence” ($F_{(1,13)} = 8.474$; p -value = .012; $\eta^2 = .022$), but no significant main effects. In particular, the
242 adaptation after-effect was still present for happy test stimuli (p -value = .009; Cohen’s $d = -0.311$, C.I. = -

243 1.114, 0.459) with incongruent stimuli recognized faster than congruent ones. Conversely, the adaptation
244 after-effect was completely abolished for fearful test stimuli, to the point that we observed a trend towards an
245 inversion of the adaptation effects, i.e. congruent test stimuli were recognized *faster* than congruent ones (p-
246 value = 0.066; Cohen's d = 0.267, C.I. = -0.459, 1.075).

247 *Insert Figure 4*

248

249 **DISCUSSION**

250 *Perceptual adaptation to emotional content of PLDs.* In the first experiment, we examined
251 behaviourally whether adaptation to the emotional content of PLD produces perceptual aftereffects. When
252 categorizing an affective PLD, participants' performance was markedly biased (slower RTs) by their
253 previous exposure to congruent emotions. Adaptation aftereffects for features contained in PLDs have been
254 reported previously. For example, prolonged exposure to human actions conveying gender characteristics
255 generates an aftereffect that biases the perception of gender in subsequently observed actions (Troje et al.,
256 2006). Similar adaptation-like aftereffects have been observed for action category (de la Rosa et al., 2014;
257 van Boxtel & Lu, 2013) and for spatial components of the observed bodily trajectories (Jackson and Blake
258 2010; Theusner et al., 2011). Also judgments about the interaction between a human hand and an object have
259 been shown to be susceptible to visual adaptation, with viewing the grasping of a light object biasing
260 subsequent grasped objects to appear heavier (Barraclough et al., 2009). Besides, a number of studies
261 reported adaptation aftereffect to affective facial (Fox and Barton, 2007; Russell and Fehr, 1987; Webster
262 and MacLeod, 2011; Webster et al., 2004) and vocal expressions (Skuk and Schweinberger, 2013;
263 Bestelmeyer et al., 2014). However, the extent to which emotional bodily expression can produce adaptation
264 aftereffects has remained unexplored so far. Our study fills this gap, providing the first evidence that
265 perception of emotional whole body movements can undergo selective perceptual adaptation. The finding is
266 indicative of the existence of a neural representation selective for affective information in biological motion.

267 *Absence of state-dependent effects of TMS on the early visual cortex (control condition).*

268 The aim of Experiment 2 was to examine the neural locus of this adaptation effect for affective dynamic
269 bodily expressions. We found adaptation after-effects similar to those observed in Experiment 1 following
270 control stimulation, consisting in a behavioural disadvantage in recognizing PLDs emotionally congruent
271 with the adapter sequences (Figure 4). Given the assumptions of TMS-adaptation paradigms, we did not
272 expect any effect of TMS on this region, because the adapted features (bodily movements) are not supposed
273 to be coded in the early visual cortex. The earliest visual body representation to be found along the visual
274 pathways is in the lateral occipital complex, way more rostral than the area that we chose as control
275 (Downing et al., 2001). Studies in blindsight patients suggest that the processing of emotional information
276 can efficaciously occur in spite of lesions of the early visual areas, either when conveyed by faces (de Gelder
277 et al., 1999; Morris et al., 2001) or by body postures (De Gelder and Hadjikhani, 2006). Accordingly, in
278 another study, TMS perturbation of V1 impaired the discrimination of neutral – but not emotional - body
279 postures, supporting the hypothesis that the encoding of the emotional content does not depend on V1
280 (Filmer and Monsell, 2013).

281 *Absence of state-dependent effects of TMS on the pSTS.*

282 In contrast to the early visual cortex, the pSTS is tuned to biological motion. However, to our
283 surprise, no state-dependent effects of TMS were found. We interpreted this finding in the light of the
284 functional specialization of the pSTS. The integrity of STS is fundamental to biological motion identification
285 (Vaina et al., 1990; Grossman et al., 2005; Saygin, 2007), it encodes low-level pictorial aspects of BM
286 (Cattaneo et al., 2010), and it represents bodily movements separately for different body parts (upper limb,
287 face, whole body, gaze) (Hein and Knight, 2008), probably in a viewpoint-invariant manner (Grossman et
288 al., 2010). In one TMS study, stimulation of pSTS *improved* the visual match of body forms specifically for
289 fearful body postures (Candidi et al, 2011). However this type of task relies on pictorial analysis likely
290 encoded in pSTS, while we asked to recognize the emotional meaning of dynamic PLDs, potentially related
291 to higher level of action representation implemented in aIPS (Cattaneo et al., 2010; Fogassi et al., 2005;
292 Shmuelof and Zohary, 2005; Hamilton and Grafton, 2006). Similarly, another study (Tseng et al., 2010)
293 showed that the specific effects of static fearful facial displays as distracters in a visual search task could be
294 disrupted by anodal transcranial direct current stimulation (tDCS) over the right pSTS.

295 *State-dependent effects of TMS on the aIPS.*

296 TMS stimulation over aIPS reduced significantly the cost of adaptation, and even produced a
297 reversal of the cost of this effect, turning it into behavioural advantage. According to the TMS-adaptation
298 assumption, this finding is diagnostic for the presence neurons that were affected by adaptation changes in
299 the stimulated area (Silvanto, 2008). Interestingly, the effects of TMS over aIPS were limited to fearful
300 PLDs, and were virtually absent for happy PLDs. What do we know about action representation in the aIPS?
301 Several lines of evidence in both human (Arfeller et al., 2013) and nonhuman primates (Borra et al., 2008;
302 Matelli and Luppino, 2001; Nelissen et al., 2011; Rizzolatti et al., 2014) indicate that the action
303 representation is hierarchically organized between a low-level pictorial representation in pSTS, and a more
304 abstract high-level representation of action goal and intention in the parieto-frontal system (Cattaneo et al.
305 2010). Notably, among the AOS, the coding of action goals occurs exactly in the aIPS (Tunik et al., 2007).
306 The aIPS cortex generalizes actions across effectors (Cattaneo et al. 2010) and is capable of encoding action
307 invariants such as action end-points, action outcomes, and environmental changes produced by actions
308 (Hamilton and Grafton, 2006; 2008). In Experiment 2, we found evidence that the explicit recognition of the
309 emotional component of body movements relies in part on the parietal node of the AOS. Visual observation
310 of emotional body movements produces activity in several brain networks, such as visual regions, the limbic
311 network, and the AOS (de Gelder et al. 2004, 2010; Meeren et al. 2013; Pichon et al. 2008; Tamietto et al.
312 2007; van de Riet et al. 2009). There are several different neural mechanisms by which the human brain can
313 identify and categorize observed affective displays. The capacity to recognize non-verbal affective
314 communications generally relies on a core system that is likely to be located within the limbic system
315 (Adolphs & Tranel, 2003; LeDoux, 1996; Ohman & Mineka, 2001). However, our findings indicate that
316 (limitedly to explicit processes) some subtypes of emotional body movements may be encoded as purposeful,
317 goal-directed actions in the aIPS. Conversely, the pSTS, being the site of simple movement representation,
318 does not seem to contain a specific representation of affective movements.

319 *Dissociation between fear and happiness in the aIPS.*

320 State-dependent effects of TMS in aIPS were specific to fearful PLDs (Figure 4). Why do fearful
321 stimuli seem to be predominantly represented in the aIPS compared to happy stimuli? A possible explanation

322 is that the affective state of fear itself is represented in the aIPS. Alternatively, it is possible the motor pattern
323 expressing fear has characteristics that are best encoded by the aIPS, which preferentially processes goal-
324 directed, purposeful movements (Cattaneo et al., 2010). The fearful bodily movements represented in our
325 stimuli were in most cases directed towards a position in space as they depicted self-protective or avoidance
326 body movements directed away from specific threatening agents (See example videos at
327 <http://community.dur.ac.uk/a.p.atkinson/Stimuli.html>). On the contrary, happy stimuli (e.g. exulting,
328 clapping hands, joyful hopping) were not directed towards or away from specific sectors in space. Therefore,
329 the fear-happiness dissociation could be explained by a higher goal-directed or space oriented in fearful
330 movements, compared to happy ones. From an evolutionary point of view, the emotional movements are
331 communicative in nature, and our brain's prompt reactions to them is essential for the survival (Darwin,
332 1872; Ekman, 1957; Grèzes et al., 2007). In this sense, each emotional subtype has an own identity, and its
333 affective state is not dissociable from its stereotyped communicative motor behaviour. The effective
334 communication of fearful content is more likely relied on goal-directed and spatially-oriented actions than
335 happiness. We therefore favour the hypothesis that fearful movements have a more “praxic” and “goal-
336 directed” quality compared to happiness. In line with that, several studies has reported that the motor system
337 is specifically tuned to fearful body movements as shown by changes in corticospinal excitability in response
338 to fearful body postures (Borgomaneri et al., 2012; Borgomaneri et al., 2015), fearful facial expressions
339 (Borgomaneri et al., 2014), and negative natural complex scenes (Schutter et al., 2008). However, the role of
340 activity in the corticospinal system in action comprehension remains unclear.

341

342 *Conclusions*

343 We conclude that, while performing explicit categorizations (i.e. high-level cognitive task), the
344 human brain considers fearful emotional body movements as goal-directed actions. This conclusion is
345 supported by the specific recruitment of the cortical network that is specialized in processing actions. The
346 AOS therefore contains representations of affective movements, as long as these are interpreted as finalistic,
347 goal-directed, meaningful actions. On the contrary, the pSTS is known to encode biological motion
348 according to its characteristic kinematic, distinguishing it from non-human motion and is apparently not
349 encoding specifically neither fearful nor happy bodily actions.

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532 **Legend of Figures**

533 Figure 1 p. 10

534 **Figure 1. Representation of stimulation sites and respective anatomical landmarks.** Right panel:
535 individual renderings of the gray-white matter border in each of the 14 participants. Left panel: the same
536 brains as in the right panel are shown with the main anatomical landmarks used for localization of TMS
537 targets. Blue: central sulcus; green: postcentral sulcus; yellow: intraparietal sulcus; purple: Sylvian fissure;
538 red: superior temporal sulcus. The 3 stimulation sites (aIPS, pSTS and control) are represented with white
539 spots.

540

541 Figure 2 p. 11

542 **Figure 2: Timeline of TMS Experiments.**

543

544 Figure 3 p. 13

545 **Figure 3. Visualization of results in Experiment 1.** The performance of each participant is represented
546 with a black bar. The grey columns represent the mean of RTs in congruent and incongruent conditions.
547 Main analysis revealed an adaptation after-effect for affective PLDs, with congruent stimuli being
548 recognized significantly slower than incongruent ones.

549

550 Figure 4 p. 14

551 **Figure 4: Visualization of Results of Experiment 2.** Mean RTs are shown, classified according to emotion
552 in the test PLD (happiness or fear); congruence with the adapter sequence (congruent or incongruent); and to
553 the site of TMS (aIPS, pSTS or occipital control). The vertical bars represent the standard errors.

554

555 **Legend of Tables**

556 Table 1 p. 6

557 **Table 1.** Results of comparisons between the three emotional valences of PLDs for Accuracy,
558 Intensity and Movement assessed in the pilot study. V is the value of the test statistic (Wilcoxon Signed-
559 Rank Test for paired samples).

560

561 Table 2 p. 12

562 **Table 2:** Mean and Standard Errors of RTs in all the conditions in Experiment 1.

563

Figure 1

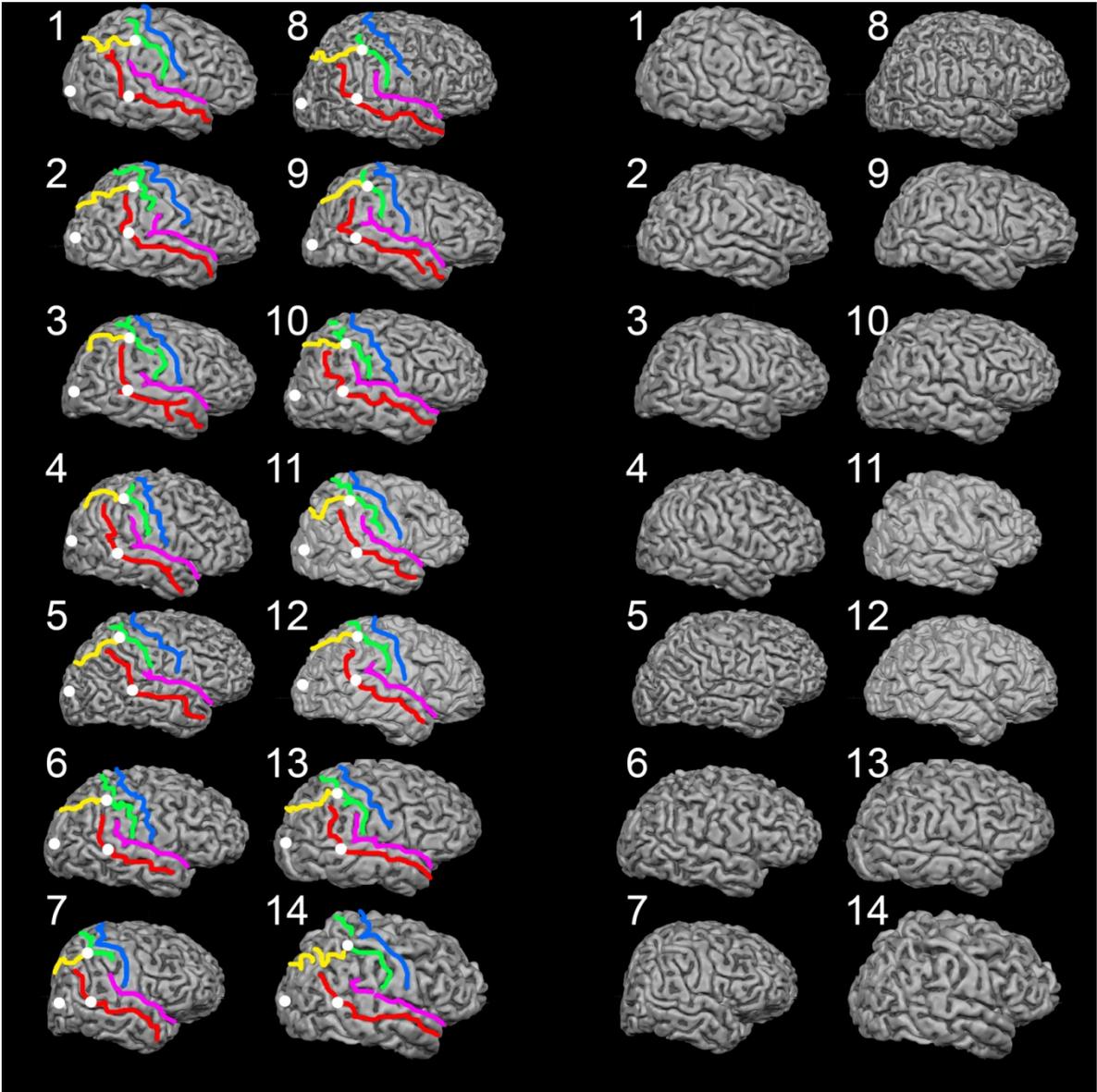


Figure 2

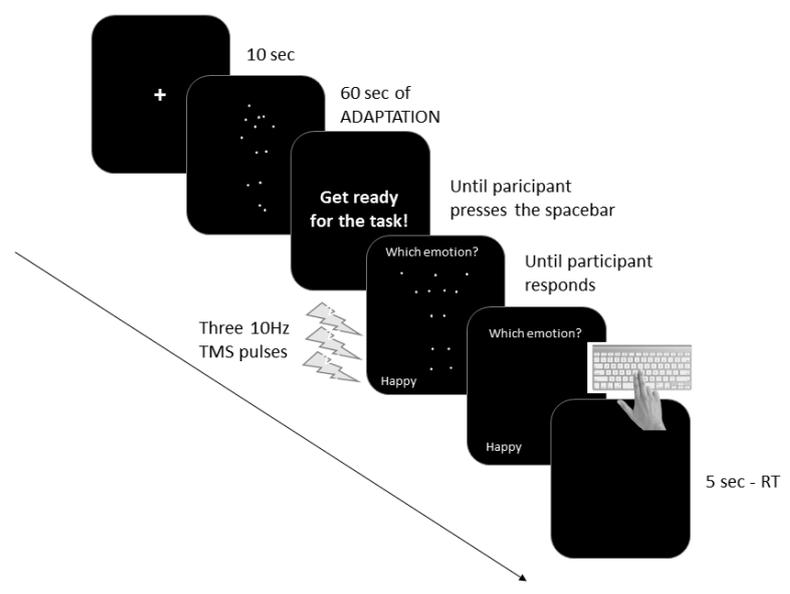


Figure 3

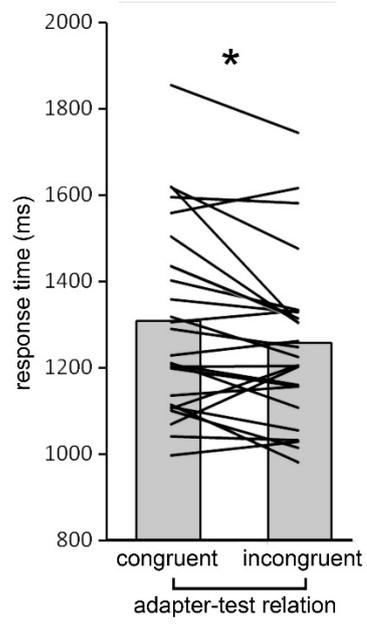
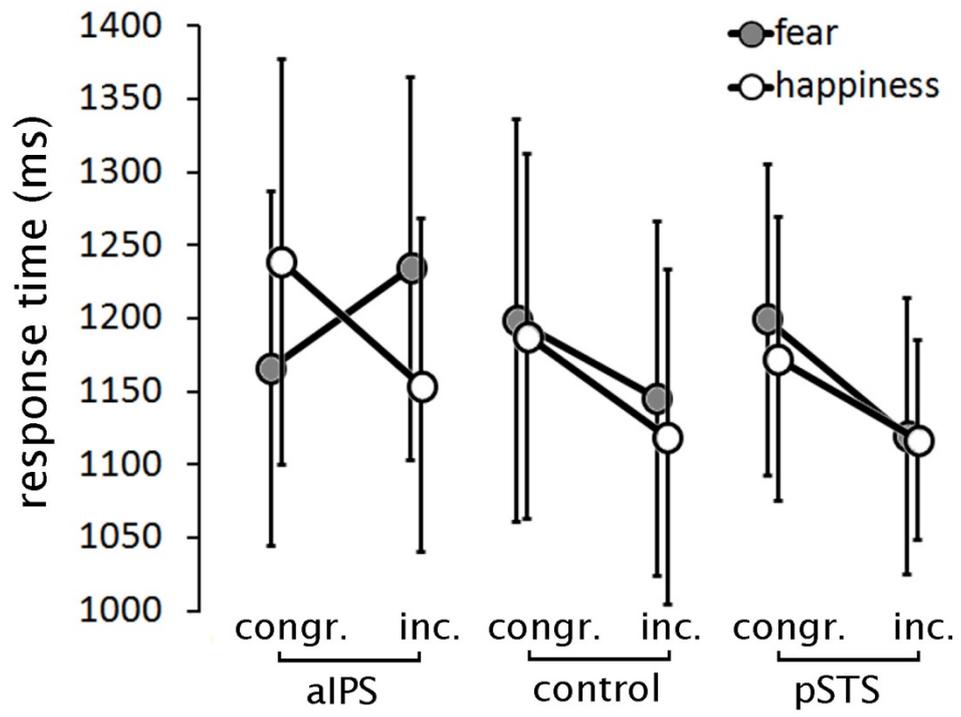


Figure 4



564 **Table 1**

	Accuracy		Movement		Intensity	
	V	p-value	V	p-value	V	p-value
Fearful vs Happy	30	0.39	12.5	0.139	26	0.919
Fearful vs Neutral	21	0.034	31	0.759	55	0.002
Happy vs Neutral	28.5	0.154	45	0.083	55	0.002

565

566 **Table 2**

emoTest	Congruence	Mean RT (ms)	SE (ms)
Fear	Congruent	1317	50.32
Fear	Incongruent	1219	46.75
Happiness	Congruent	1267	43.92
Happiness	Incongruent	1252	36.84

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