1   **Title:** Effector-specific motor simulation supplements core action recognition processes in

2   adverse conditions

3   **Running title:** Motor simulation in action recognition

4

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17 **Abstract**

18 Observing other people acting activates imitative motor plans in the observer. Whether, and if so when

19 and how, such "effector-specific motor simulation" contributes to action recognition remains unclear. We

20 report that individuals born without upper limbs (IDs) – who cannot covertly imitate upper limb

21 movements – are significantly less accurate at recognizing degraded (but not intact) upper-limb than lower-limb

22 actions (i.e., point-light animations). This finding emphasizes the need to reframe the current controversy

23 regarding the role of effector-specific motor simulation in action recognition: instead of focusing on the

24 dichotomy between motor and non-motor theories, the field would benefit from new hypotheses

25 specifying when and how effector-specific motor simulation may supplement core action recognition processes

26 to accommodate the full variety of action stimuli that humans can recognize.

27

28 **Keywords:** Action recognition, working memory, motor simulation

Introduction

Every day, we see people executing sequences of body movements under a wide range of illumination, viewpoints, and occlusion in more or less cluttered and crowded environments. Despite the challenges imposed by these complicating factors, most of the time we recognize what they are doing, e.g., that they are "texting while walking", "smiling" or "running" (e.g., Fademrecht, Nieuwenhuis, Bülthoff, Barraclough, & de la Rosa, 2017; Ikeda & Watanabe, 2016; Ikeda, Watanabe, & Cavanagh, 2013). By action recognition, we refer to the ability to categorize observed body movements and postures as a specific instance of a known category of action – to "recognize" that the observed body movements constitute an instance of the action "doing a cartwheel", for instance. Studies exploring the cognitive and neural bases of this ability have consistently reported that observing other people performing actions activates effector-specific imitative motor plans in the observer's mind/brain (Buccino et al., 2001; Caspers, Zilles, Laird, & Eickhoff, 2010; Cracco et al., 2018; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). However, whether, and if so when and how, such effector-specific "motor simulation" contributes to action recognition remains unclear.

The most influential early motor simulation theories attributed a critical role to effector-specific motor simulation in action recognition (Blakemore & Decety, 2001; Jeannerod, 2001; Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). The most popular of these theories is the direct-matching hypothesis, proposed by Rizzolatti and colleagues following the discovery of mirror neurons in the macaque monkey's brain. Based on the properties of these neurons, the authors proposed that they constitute a matching system that automatically translates the results of the visual analysis of observed body movements into their corresponding motor commands in the observer's brain. Mirror neurons would allow action recognition because the observer "knows" what s/he is doing when s/he performs the same action (but see Csibra, 2007 for critical discussion). Thus, on this view, although actions may be recognized purely visually (without effector-specific motor simulation), direct visuomotor matching is the only mechanism "by which the meaning of the acts that are being observed are understood immediately"

55 (Rizzolatti & Sinigaglia, 2008, p. 136) without the need of "additional complex inference processes"

56 (Giese & Rizzolatti, 2015; Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014), and by which the

57 observer is able to understand an observed action at a level that goes beyond its mere visual features

58 (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005; Rizzolatti & Sinigaglia, 2010). Accordingly,

59 Rizzolatti and colleagues refer to the finding that some brain-damaged individuals with motor circuit

60 lesions become unable to recognize pictures or videoclips of familiar actions as a "compelling argument

61 for the crucial role of mirror neurons in this function" (Rizzolatti & Sinigaglia, 2010, 2016).

62

63 It has since become clear that such strong versions of the motor simulation theories, in which effector-

64 specific motor simulation is necessary for efficient action recognition, are untenable. Many studies have

65 reported action recognition difficulties in patients suffering from brain damage involving different parts

66 of the motor system in the context of different aetiologies: patients with Apraxia (a disorder affecting the

67 capacity to perform actions despite preserved basic motor and somatosensory functions), Motor-Neuron

68 Disease, Parkinson's Disease, and Cortico-Basal Degeneration present with difficulty to recognize action

69 pictures and pantomimes (Buxbaum et al., 2005; Cotelli et al., 2006; Grossman et al., 2008; Negri et al.,

70 2007; Papeo et al., 2010; Pazzaglia, Pizzamiglio, et al., 2008; Pazzaglia, Smania, et al., 2008; Silveri &

71 Ciccarelli, 2007). However, the reported action recognition impairments cannot unambiguously be

72 ascribed specifically to *motor system* damage because, in these disorders, brain lesions generally extend

73 outside the motor system and most patients also present with other cognitive difficulties, such as

74 executive function, attentional, and/or visuospatial disorders. Furthermore, at odds with the prediction of

75 the strong versions of the motor simulation theories, there are also many reports of brain-damaged

76 patients who, despite impaired action production, achieve normal performance in naming, or matching-to-

77 a-word, pictures, video-clips, and pantomimes of actions (Kalénine, Buxbaum, & Coslett, 2010; Negri et

78 al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010). In a three-year longitudinal study, for instance, patient

79 J.R. presented with increasing action production difficulty resulting from progressive bilateral atrophy in

80 cortical and subcortical regions involved in the sensorimotor control of actions, notably the superior

81   parietal cortex, the primary motor and premotor cortex, the inferior frontal gyrus, and the basal ganglia.

82   Despite the extensive damage to these structures, which are assumed to underlie motor simulation, J.R.'s

83   ability to recognize actions remained intact and comparable to that of control participants in both

84   accuracy and speed (Vannuscorps, Dricot, & Pillon, 2016).

85

86   The hypothesis that action recognition is mediated by effector-specific motor simulation is also difficult to

87   reconcile with reports of typically efficient action recognition in individuals who cannot rely on such

88   mediation because of congenitally absent or paralyzed limbs (Vannuscorps & Caramazza, 2016b; Vannuscorps,

89   Andres, & Caramazza, 2020; Vannuscorps, Andres, Carneiro, Rombaux, & Caramazza, 2020; Vannuscorps,

90   Andres, & Pillon, 2013). Action recognition through direct-matching is a two-steps process: (1) observed body

91   movements are translated into the corresponding effector-specific motor commands in the observer's brain and,

92   (2) the simulation allows observers to "retrieve" information about what action these movements allow them to

93   produce when they carry them out. In this scenario, previous motor experience with observed body movements is

94   critical for effector-specific motor simulation to occur, and action recognition efficiency is assumed to depend on

95   the similarity between the observed movements and those produced by the viewer (Calvo-Merino et al., 2006;

96   Swaminathan et al., 2013; Turella et al., 2013; Tye-Murray et al., 2013). These two steps in action recognition are

97   not available to observers with congenitally absent or paralyzed limbs. Extant evidence suggests that the motor

98   cortex does not contain representations of congenitally absent or paralyzed limbs (Reilly & Sirigu, 2011; Striem-

99   Amit et al., 2018). Rather, the specific parts of the somatosensory and motor cortices that would normally

100   represent the "absent" or paralyzed limbs are allocated to the representation of adjacent body parts (Funk et al.,

101   2008; Kaas et al., 1983; Makin et al., 2015; Stoeckel et al., 2009; Striem-Amit et al., 2018). In addition, and in

102   any event, individuals with congenitally missing or paralyzed limbs have obviously never themselves executed

103   any action using these missing or paralyzed limbs. Nevertheless, individuals born without upper limbs have

104   been shown to be as fast and accurate as control participants at recognizing pictures and video-clips of

105   upper-limb actions (Vannuscorps, Andres, & Pillon, 2013), and the quantitative and qualitative

106   performance of some individuals born with facial paralysis is indistinguishable from that of control

107 participants in challenging lip-reading and facial expression recognition tasks (Vannuscorps, Andres,

108 Carneiro, Rombaux, & Caramazza, 2020; Vannuscorps, Andres, & Caramazza, 2020).

109

110 These findings challenge the central premise of effector-specific motor simulation theories: they

111 demonstrate that it is possible to account for efficient action recognition without effector-specific motor

112 simulation. Instead, they support theories of action recognition according to which action recognition results

113 from a matching of observed body postures and movements to mental representations (descriptions) of the

114 body postures and movements that characterize known actions stored in memory (Rothi et al., 1991;

115 Giese & Poggio, 2003; see Figure 1).

116

117 In the study of language, the term "input lexicon" is used to describe components of the language system

118 that store abstract information about words that one has previously read ("input orthographical lexicon")

119 or heard ("input phonological lexicon"). This information is deemed "abstract" in the sense that it is

120 invariant to low-level sensory features. For instance, at this stage of processing a large capital letter "M"

121 printed in red ink in Times New Roman refers to the same "abstract" representation of the letter "M" as a

122 lowercase "m" printed in green in Arial (Grainger et al., 2008). By analogy, in the field of action

123 recognition, Heilman and Rothi used the term "input praxicon" to refer to abstract representations of

124 known actions stored in memory (Heilman & Rothi, 1993). Although what exactly is represented in the

125 input praxicon remains insufficiently articulated, representations of known actions likely include

126 information about a series of "units" of body postures and movements that together make up human

127 actions. These likely include what are the parts of the body involved (vs. those whose posture and

128 kinematic are not relevant), and for these body parts their characteristic configuration (e.g., fingers

129 stretched, elbow flexed), position, orientation and kinematic (orientation, amplitude, number of

130 repetitions, speed, velocity).

131

132   When one sees an action, it may be recognized in three stages. First, a visuo-perceptual analysis of that

133   action decomposes it into its constituent postural and kinematic units (Giese & Poggio, 2003; Csibra,

134   2007). In the field of object recognition, such initial parsing of the visual scene, referred to as "mid-level"

135   vision, is assumed to compute a series of visual features such as, for example, the objects' elongation axis,

136   center, and curvature (Palmer & Rock, 1994; Sekuler, 1996; Ungerleider & Bell, 2011; Vannuscorps,

137   Galaburda, & Caramazza, 2021). When one sees an action, the set of "units" computed is likely to

138   correspond to the set of representational units that characterize known actions in the input praxicon. The

139   result of this operation is compared with representations of known actions stored in the input praxicon. If

140   a reasonably good match is found, the observed action is automatically, rapidly, effortlessly "recognized"

141   as an instance of a known category of actions (e.g., as an instance of "waving goodbye"). Once

142   recognized as an action of a certain type, access to a conceptual system allows the observer to retrieve

143   knowledge about the action, like its typical cause, purpose and results, the typical agent and instrument

144   involved, the needed force, approximate duration, and so on. Following a similar proposal in the field of

145   object recognition (DiCarlo & Cox, 2007), we refer to the rapid, effortless, automatic recognition of

146   actions that results from these three stages as "core action recognition".

147

148   On this view, the observation of body movements is accompanied by two distinct types of "motor

149   simulation" in the service of imitation, emulation, and motor learning (Buccino et al., 2004; Heilman &

150   Rothi, 1993). Once analyzed as a set of relevant gestural "units", observed body movements and/or

151   postures are automatically translated into the motor commands that the observer would use to execute the

152   same body postures and/or movements (e.g., Brass & Heyes, 2005). This "gesture-to-gesture" or

153   "effector-specific" imitation/simulation must be distinguished from "action-to-gesture" or "effector-

154   independent" emulation/motor simulation, which results from action recognition. Once conceptual

155   knowledge has been accessed, it activates associated representations such as the phonological and

156   orthographic lexicons that encode the spoken and written forms associated with the action (to name it;

157   Shelton & Caramazza, 1999), and the "output praxicon" that stores learned motor programs associated

158   with action execution and object use (to execute it; Heilman & Rothi, 1993). In other words, once

159   observed body movements have been recognized as an act of a particular type, the motor programs that

160   the observer would use to execute that action are automatically evoked. The automatic activation of post-

161   conceptual representations is supported by a range of findings, such as the demonstration that pictures of

162   objects automatically activate their related phonological (Navarrete & Costa, 2005; Meyer & Damian,

163   2007) and motoric (Bub & Masson, 2006) content, and that observers born without upper limbs activate

164   brain regions involved in the execution of mouth and lower-limb actions when they observe hand action

165   (Aziz-Zadeh, Sheng, Liew & Damasio, 2011; Gazzola et al., 2007).

166

167   However, evidence that efficient action recognition is possible without effector-specific motor simulation

168   does not imply that action recognition may not, in some conditions, require additional processing

169   resources. Indeed, the idea that the core cognitive and neural mechanisms underpinning a given function

170   may be supplemented by other ones when tasks or stimuli become more challenging is widely accepted.

171   Although not necessary for auditory speech perception, for instance, it is well documented that lipreading

172   enhances speech perception under difficult listening conditions (Akeroyd, 2008; Rönnberg et al., 2013).

173   Although object recognition may be largely solved by feedforward visual processing, additional recurrent

174   processes become necessary under challenging conditions (Tang et al., 2014, 2018).

175

176   Core action recognition is, by design, limited to cases in which the result of the visuo-perceptual analysis

177   of the actors' body posture and movements may be matched onto a corresponding memory trace. When

178   this is not possible, one must necessarily rely on additional resources and mechanisms. In line with this,

179   for instance, information about the context in which an action takes place (e.g., the room) has been shown to

180   facilitate specifically the recognition of actions that are unfamiliar (Wurm et al., 2017) or made perceptually

181   ambiguous (Wurm & Schubotz, 2017).

182

183 As discussed above, "action-to-gesture" "effector-independent" motor simulation results from, and

184 therefore cannot contribute to action recognition (Csibra, 2008; Gazzola et al., 2007). However, we see at

185 least two ways by which effector-specific motor simulation may support the recognition of actions when

186 core action recognition fails (see Figure 1). Previous evidence has shown that the ability to maintain

187 meaningless, uninterpreted, body movements and postures in memory, even for just a few seconds, is

188 augmented by effector-specific motor simulation (Galvez-Pol et al., 2020; Gao et al., 2015; Moreau,

189 2013). Individuals born without upper limbs have been shown to be significantly less good than typically

190 developed participants at maintaining hand postures in memory even for a few seconds (Vannuscorps &

191 Caramazza, 2016a). In cases such as these, when core action recognition fails, one way in which effector-

192 specific motor simulation may contribute to action recognition is by allowing the rehearsal of the

193 observed gestures/postures, extending the time they will be available (in a motor format) for the more

194 effortful recognition process. During this time window, the rapid decay of the initial transient visual trace

195 is likely to transform action recognition from a process of matching a visual input onto a representation

196 stored in memory to a process of attempting to identify which known action corresponds to the covertly

197 executed movements (Figure 1A). In other words, although action recognition may operate rapidly on a

198 pure visuo-perceptual basis when an action is familiar and perceived in optimal viewing conditions, motor

199 simulation may offer to any observer able to covertly imitate the observed gestures a useful "tool" to

200 extend the processing time window available to interpret actions when stimuli are more difficult to match

201 rapidly onto memory representations – a role akin to that attributed to the articulatory loop component of

202 working memory (Baddeley, 2012) in the ability to recognize speech under adverse conditions (Rönnberg

203 et al., 2010).

204

205 --- Figure 1 ---

206

207 During this time window, effector-specific motor simulation may also contribute by activating

208 corresponding actions (if any) in the observer's motor repertoire or "output praxicon" (Heilman & Rothi,

209   1993; Figure 1B). This contribution would be akin to the one described by Rizzolatti and Sinigaglia :

210   "…observing actions performed by another individual elicits a motor activation in the brain of the

211   observer similar to that which occurs when the observer plans their own actions, and the similarity

212   between these two activations allows the observer to understand the actions of others without needing

213   inferential processing" (Rizzolatti & Sinigaglia, 2010, p. 268). As such, this process would be similar to

214   that available to brain-damaged patients with pure alexia, who are unable to match perceptual

215   representations of letters with their stored representations but may circumvent this disorder by tracing the

216   shape of the letters (overtly or covertly) and, thereby, recognize the letter because they know what letter

217   they trace when they typically use these motor programs (Kashiwagi, 1989; Lott et al., 2010; Starrfelt et

218   al., 2013).

219

220   In a previous study (Vannuscorps & Caramazza, 2016b), we addressed this possibility by comparing the ability

221   of 5 individuals born without upper limbs and matched control groups of typically developed participants

222   to recognize upper limb actions presented in either a familiar or unfamiliar format. In a first experiment,

223   we showed them video-clips of an actress executing pantomimes of various familiar upper limb actions

224   (e.g., playing the guitar, cutting with scissors) and used a gradual unmasking paradigm to measure the

225   quantity of information (i.e. number of frames) necessary for the participants to recognize these

226   pantomimes. By showing familiar actions in a familiar format, we aimed at assessing the efficiency of

227   participants' core action recognition system. To test the hypothesis that effector-specific motor simulation

228   may enhance action recognition when core action recognition fails, we also needed stimuli that were

229   sufficiently dissimilar from stored representations of known actions to hamper their automatic, rapid

230   recognition by visuo-perceptual matching. Therefore, in a second experiment, we also measured their

231   ability to recognize point light animations (PLAs) of upper limb (e.g., playing the violin) and lower limb

232   (e.g., moonwalking) actions. PLAs of actions are extremely impoverished stimuli in which the stimulus is

233   reduced to only a few dots depicting the spatiotemporal location of the major joints of the actor's body.

234 Participants had never experienced PLAs before and these stimuli are very different from natural stimuli.

235 Therefore, we assumed that these stimuli could benefit from effector-specific motor simulation.

236

237 The results of the first experiment were clear-cut: all five IDs performed as well as the control

238 participants. The results of the second experiment were mixed, however. In line with the possibility that

239 effector-specific motor simulation may contribute to action recognition when core action recognition fails,

240 three IDs recognized significantly fewer upper-limb than lower-limb actions (in comparison to the

241 controls). However, two others were slightly better at recognizing PLAs of upper limb than lower limb

242 actions in comparison to the controls. We concluded that the performance of these two individuals

243 "…demonstrate(s) the ability of the visuo-perceptual system, in the absence of motor simulation, […] to

244 perceive and interpret observed actions efficiently even when they are presented in extreme, impoverished

245 conditions" (Vannuscorps & Caramazza, 2016b, p. 89).

246

247 We have since found reason to moderate and clarify this conclusion. A reanalysis of the performance of

248 the two IDs who performed slightly better for manual than non-manual actions by means of the Bayesian

249 Standardized Difference Test (Crawford & Garthwaite, 2007) indicated that this advantage was

250 nevertheless smaller than that of approximately 30% of the typically developed population. This left a

251 narrow space for a role of motor experience in the ability to recognize actions in adverse condition. This

252 reconsideration of the original results led to the follow-up study reported herein. The goal was to gain

253 more power to detect an impact of motor simulation on action recognition, if any, by testing additional

254 individuals born without upper limbs. The results of the new analyses led us to reconsider our previous

255 conclusions. In line with the conclusion of our previous study, we found conclusive evidence that the IDs

256 recognize upper limb actions presented as pantomimes as efficiently as typically developed individuals.

257 However, and in contrast with the conclusion of the previous study, we also found that the IDs, as a group, are

258 significantly less accurate at recognizing PLAs of upper-limb than lower-limb actions.

259

260 **Material and Methods**

261 The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc,

262 Brussels, Belgium, and all participants gave written informed consent prior to the study.

263

264 Participants

265 We report here the results of 2 individuals born without upper limbs (ID 6-7) and of one individual born

266 without upper or lower limbs (ID 8) in addition to the 5 IDs (ID 1-5) already reported in our previous

267 study (Vannuscorps & Caramazza, 2016b) and compared the performance of this group (4 females and 4

268 males; mean age ± SD: 48 ± 12) to that of the 27 typically developed age-matched control participants

269 reported in the original study (all right-handed, 17 females and 10 males; mean age ± SD: 45 ± 10)

270 without any history of psychiatric or neurological disorder. Information about the IDs' body schema was

271 obtained through visual examination and interview. Information about prosthetic and phantom limb

272 history was obtained through a questionnaire and complemented by interview when necessary. None of

273 the ID reported any history of phantom limb sensation. All the IDs had typical lower limbs, except ID4

274 who had a shortened right leg and ID8, who had missing lower limbs. Other relevant information is

275 summarized in Table 1.

276

277 Note that we also recruited and tested another individual born without upper or lower limb in the context

278 of this study (ID9). We decided against reporting his results because he could not be tested in the same

279 conditions as the other participants. During testing, ID9 was lying face down next to the 5.5 inch.

280 smartphone screen on which he performed the experiment. Therefore, the size of the stimuli had to be

281 severely reduced.

282

283 Stimuli and procedure

284 All participants performed three experiments. The first two were identical to those reported in the original

285 article (Experiments 1 and 2 in Vannuscorps & Caramazza, 2016b). In Experiment 1, participants viewed

286   video clips of an actress pantomiming 20 different upper-limb instrumental actions (e.g., playing a guitar;

287   Agostini, Papeo, Galusca, & Lingnau, 2019). Only body movements were shown, without any object or

288   context. In most of the stimuli (n=16) only the upper limb(s) moved (the face remained neutral and the

289   body did not move). In the four other stimuli (to shoot a basketball, to play golf, to throw a ball, to shoot a

290   bow and arrow) the upper limb movements were accompanied by coarse movements of the body and

291   shoulders. All video clips were sized 978x550 pixels and had 30 frames/seconds. From each original

292   movie we created 14 clips in which the number of frames ranged from 10 (330 msec) to 75 (2640 msec)

293   in steps of 5 (165 msec). During the experiment, participants viewed the 14 versions of each video in a

294   row, from the shortest to the longest one. The size of the actress on the computer screen was

295   approximately 10 cm. Each trial began with the presentation of a black screen for 1000 msec, followed by

296   the video clip and a screen on which was written the question "What was the action mimed by the

297   actress?". Participants responded orally to the question and the experimenter wrote down their responses.

298   They were encouraged to provide a response at each step, even if they were not sure. There was no time

299   constraint for responding but participants were asked not to respond before the end of each video clip. An

300   item was scored correct at a given level of demasking (from 1 to 14) if it was identified correctly also at

301   all subsequent levels and was scored 15 if not recognized.

302

303   In Experiment 2 (Experiment 2 in Vannuscorps & Caramazza, 2016b), participants viewed video clips

304   depicting an actor reduced to 12 light dots (approximately 5 mm of diameter) corresponding to captors

305   originally placed on his main joints (center of the head, shoulders, elbows, wrists, center of pelvis, knees,

306   and ankles; "Point-Light Animations", PLA) executing 20 upper limb (e.g., fishing) and 20 non upper

307   limb actions (e.g., walking backward). The video clips were sized 700x1024 pixels, had 33

308   frames/seconds and lasted 5 seconds. These stimuli were chosen from a set of 83 point-light animations of

309   actions created from a motion capture database (asf/amc format obtained from the Carnegie Mellon

310   University Motion Capture Database) with a software developed locally. These 83 point-light displays

311   were shown to two groups of 20 control subjects. Participants of Group 1 (Mean Age= 24.8; 10 males)

312   were presented the PLAs and asked to name them. Participants of Group 2 (Mean Age= 23; 5 males) were

313   presented the same PLAs as Group 1 except that the upper limbs were masked (elbows and wrist

314   removed) in order to determine the role of these limbs in the identification of each action. From this

315   preliminary study, 20 upper-limb actions (Group1's mean = 87.75%, Group 2's mean = 8.25%) and 20

316   lower-limb actions (Group 1's mean = 93.75%, Group 2's mean = 92%) were selected. During the

317   experiment, participants viewed the 40 video-clips in the same pseudo-randomized order. The size of the

318   actor on the computer screen was approximately 9 cm. Each trial began with the presentation of a black

319   screen for 1000 msec, followed by the video clip and a screen on which was written the question "What

320   was the action?". Participants responded orally to the question and the experimenter wrote down their

321   responses. They were encouraged to provide a response for each stimulus, even if they were not sure.

322   There was no time constraint for responding but participants were asked not to respond before the end of

323   each video clip.

324

325   In Experiment 3, participants viewed video clips of an actor pantomiming the 20 upper-limb actions

326   depicted as PLAs in Experiment 2. Only body movements were shown, without any object or context. All

327   video clips were sized 720x1280 pixels, had 25 frames/seconds and lasted 5 seconds. During the

328   experiment, the size of the actor on the computer screen was approximately 7 cm. Each trial began with

329   the presentation of a grey screen for 1000 msec, followed by the video clip and a screen on which was

330   written the question "What was the action mimed by the actor?". Participants responded orally to the

331   question and the experimenter wrote down their responses. They were encouraged to provide a response,

332   even if they were not sure. There was no time constraint for responding but participants were asked not to

333   respond before the end of each video clip.

334

335   During the experiments, the control participants and IDs 1-5 were seated in front of a computer screen

336   located at a distance of about 60 cm. The experiments were controlled with the E-Prime software

337   (Psychological Software, 2002, Pittsburgh, PA) and presented on a 15.6 inch Dell Latitude E5530 anti-

338   glare laptop screen set at 1366 x 768 pixels and 60Hz. IDs 6-8 were tested remotely under supervision of

339   the experimenter through a visual conference system. The experiments were controlled by the online

340   testable.org interface (http://www.testable.org), which allows precise spatiotemporal control of online

341   experiments. At the beginning of each experiment, IDs 6-8 were sitting in front of a computer screen and

342   instructed to set the browsing window of the computer to full screen and minimize possible distractions

343   (e.g., TV, phone, etc). Next, a calibration procedure ascertained a homogeneous presentation size and time

344   on all computer screens. Finally, the participants started the experiment.

345

346   **Results**

347   The results of Experiments 1 and 2 are displayed in Figure 2. We first analyzed the data of Experiment 1 and

348   tested whether the IDs' (1-8) lack of motor experience with the upper limbs impacted their ability to recognize

349   manual actions depicted as pantomimes. This was not the case. Descriptive analysis of the data indicated that the

350   IDs (Median = 4.3) needed on average fewer steps of demasking than the controls (Median = 4.7) and the

351   results of a Mann-Whitney U test provided no support for the hypothesis that the IDs are less efficient than the

352   controls at identifying pantomimes of actions (W = 147.5, p = 0.94). An additional Bayesian Mann-Whitney

353   U test performed with a Cauchy prior centered around zero and with a width parameter of r = 0.707 for

354   effect size on the alternative hypothesis indicated that the data was 6.02 times (Bayes Factor) more likely

355   under the hypothesis that IDs are better or as good as the controls at identifying pantomimes of actions

356   than under the hypothesis that the IDs are less efficient.

357

358   --- Figure 2 ---

359

360   Then, we analyzed the data of the PLA naming task. We first tested whether the IDs 1-7, as a group, were less

361   accurate at recognizing upper limb than lower limb actions, everything else being equal – that is, in comparison to

362   the baseline provided by the performance of the typically developed controls for both action categories.

363   Descriptive analysis of the data indicated that there was indeed a larger difference between manual and non-

364   manual actions in the IDs (Medians = 10 and 18, respectively) than in the controls (Medians = 14 and 17,

365   respectively). The results of an ANOVA with GROUP as between-subject factor and EFFECTOR as within-

366   subject factor on the data transformed by an Adjusted Rank Transform (ART) procedure (Leys &

367   Schumann, 2010) indicated that this interaction between GROUP and EFFECTOR was significant ($F_{(1, 32)}$

368   = 8.08, p = 0.008, η^2 = 0.2). The results of an additional Bayesian repeated measure ANOVA indicated

369   that the model including an interaction between GROUP and EFFECTOR was 6.8 times (Bayes Factor) more

370   likely that the model including only the main effects. Second, we tested whether ID8, who is missing both

371   upper and lower limbs, was less accurate than control participants for both lower and upper-limb actions.

372   The results of two modified t-tests (Crawford & Howell, 1998) indicated that this was the case (both

373   modified ts < -3.23, both ps < 0.002). Finally, we tested whether IDs 1-8, as a group, were less accurate at

374   recognizing PLAs of upper limb actions than the typically developed controls. The results of both frequentist (W

375   = 155, p = 0.03) and Bayesian (same parameters as above for the alternative; BF = 1.6) Mann-Whitney U tests

376   supported this hypothesis over the alternatives.

377

378   Third, we analyzed the data of Experiment 3 and tested whether the IDs' (1-8) lack of motor experience with the

379   upper limbs impacted their ability to recognize pantomimes of the upper limb actions depicted as PLAs in

380   Experiment 2. The goal was to ensure that the difficulty to recognize upper limb actions detected in Experiment

381   2 could be attributed to the format of the stimuli (PLAs), rather than to the manual actions being less familiar or

382   harder to recognize than in Experiment 1. In line with this, both the IDs (Mean = 19.89, SD = 0.35) and the

383   controls (Mean = 19.48, SD = 0.89) recognized these actions accurately. In the IDs, only ID2 failed to

384   recognize one action (playing golf). This suggested that the upper-limb actions used in Experiment 2 were

385   not difficult to recognize when presented in a more familiar format. Yet, to directly test the hypothesis that

386   the IDs' difficulty with the manual actions in Experiment 2 could be attributed to the format of the PLAs,

387   we conducted an ANOVA with GROUP as between-subject factor and FORMAT (PLAS VS. PANTOMINES) as

388   within-subject factor on the data transformed by an Adjusted Rank Transform (ART) procedure (Leys &

389   Schumann, 2010). The interaction between GROUP and FORMAT was significant ($F_{(1, 33)}$ = 15.4, p <

390   0.001, $\eta^2 = 0.32$). The results of an additional Bayesian repeated measure ANOVA indicated that the

391   model including the interaction between GROUP and EFFECTOR was 128 times (Bayes Factor) more likely

392   that the model including only the main effects.

393

394

395

396   **Discussion**

397   Perceiving the body movements of someone else activates not only brain areas in the observer's visual perceptual

398   system, but also in his/her motor system. This finding has generated a debate about the role of motor

399   representations and processes in recognizing others' actions. According to a strictly perceptual view, action

400   recognition relies on a visuo-perceptual analysis of the actor's body shape and motion, which provides the visual

401   description that "activates" a representation of the corresponding action category stored in memory (Giese

402   & Poggio, 2003; Rothi, Ochipa, & Heilman, 1991; Jellema & Perrett, 2005; Johansson, 1973). On this view,

403   although automatically activated, motor representations are not involved in the processes of action recognition. In

404   contrast, "motor theories" of action recognition propose that the recognition of others' actions is supported by

405   covert unconscious imitation of the observed body movements in the observer's motor system (Rizzolatti,

406   Fogassi, & Gallese, 2001; Rizzolatti & Sinigaglia, 2010). To address this issue, we extended a previous study

407   that examined whether individuals born without upper limbs (congenital aplasia) have difficulty in recognizing

408   upper limb actions – actions that they are unable to covertly imitate (Vannuscorps & Caramazza, 2016b). In line

409   with the conclusion of that previous study, the results of the current study indicate that the IDs are able to

410   recognize manual actions presented as pantomimes as efficiently as typically developed individuals. However,

411   and in contrast with the conclusion of the previous study, we now find clear evidence that the IDs are

412   significantly less accurate at recognizing PLAs of actions that they are unable to imitate than PLAs of actions that

413   they can imitate.

414

415   These results contribute to constrain the contribution of effector-specific simulation to a narrower scope

416   than that initially hypothesized by motor simulation theories. Previous studies had shown that individuals

417   with brain damage or a congenital disorder could 1) recognize carefully crafted pictures and video clips of

418   familiar actions that they could not covertly imitate ("effector-specific motor simulation") as rapidly as

419   typically developed participants (Vannuscorps, Andres & Pillon, 2013; Vannuscorps, Dricot & Pillon, 2016)

420   and 2) even use fine-grained kinematic information to draw different types of inferences, such as the mental state

421   of an actor or the most likely outcome of an action, as efficiently as typically developed participants

422   (Vannuscorps & Caramazza, 2016b; Vannuscorps & Caramazza, 2017). The results of Experiment 1

423   additionally demonstrate that individuals who cannot covertly imitate observed postures and movements

424   do not require more information to recognize an action. This finding cannot be explained by a lack of

425   sensitivity of the measure, or as a mere null effect. The measure is sensitive, with no ceiling or floor effect

426   and a Bayes Factor provided positive evidence in favor of the hypothesis that the IDs are at least as good

427   as the control participants in this task.

428

429   Of course, this does not *imply* that effector-specific motor simulation does not support the recognition of

430   actions presented as pantomimes in typically developed participants. Correlated sensorimotor experience

431   may be necessary for the development of motor contributions to action perception (e.g., Catmur and

432   Heyes, 2019) and the IDs may have developed an atypically efficient visual system to compensate for

433   their congenitally missing limbs. In this case, our results would have to be interpreted as useful evidence

434   about the range of computational and neural plasticity that is possible in a system that typically relies on

435   motor simulation. However, this alternate conclusion faces several challenges. First, it seems difficult to

436   reconcile with evidence of efficient action recognition in patients with acquired motor disorders

437   (Kalénine, Buxbaum, & Coslett, 2010; Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010;

438   Vannuscorps, Dricot & Pillon, 2016), and with evidence that individuals with congenitally missing or

439   paralyzed limbs are not only as efficient as control participants in recognizing actions, but also engage the

440   very same neural network (Vannuscorps, Wurm, Striem-Amit & Caramazza, 2019) and perform tasks in a

441   way that is qualitatively very similar (Vannuscorps, Andres & Caramazza, 2020; Vannuscorps &

442   Caramazza, 2016b). In addition, and more importantly, we are not aware of experimental evidence that

443   would justify favoring this less parsimonious alternative conclusion. As reviewed elsewhere, the

444   interpretation of the results from neuroimaging, behavioral, neuropsychological, and TMS studies, which

445   have been cited in support of motor simulation theories of perception, has been challenged (Vannuscorps

446   & Caramazza, 2016b; Hickok, 2014; Caramazza, Anzelotti, Strnad & Lingnau, 2014). For instance,

447   although there is clear evidence that action recognition may be modulated by concurrent motor tasks and

448   transcranial magnetic stimulation (TMS) over the motor cortex, such evidence would be compelling only

449   if one were to assume that TMS and concurrent motor tasks affect specifically and *only* motor simulation

450   (Hamilton et al., 2004; Ipser & Cook, 2016; Maringer et al., 2011; Oberman et al., 2007; Paracampo et al.,

451   2017; Rychlowska et al., 2014). There is clear evidence against this assumption. In addition to mobilizing

452   the motor system itself, moving one's limb feeds efferent copies and corollary discharges of the motor

453   commands to the sensory and perceptual pathways involved in motor control (Wolpert et al., 2003). For

454   example, moving one's body parts activates not only the motor system but also parts of the visual cortex

455   involved in the perception of these body parts (Astafiev et al., 2004; Dinstein et al., 2007; Orlov et al.,

456   2010). Likewise, TMS applied to an area may have distant effects on other areas to which it projects

457   (Papeo et al., 2015; Ruff et al., 2009; Siebner et al., 2009). Thus, TMS applied to the motor system may

458   have functional effects upon action recognition by modulating the visuo-perceptual system to which it is

459   naturally connected to support the control of one's movements. Although it is possible that the IDs' ability to

460   recognize upper-limb actions is supported by idiosyncratic computational and neural mechanisms, at this

461   juncture experimental evidence on the ability to recognize familiar actions depicted in a familiar format is

462   better and more parsimoniously explained without effector-specific motor simulation. In line with this

463   conclusion, the results of fMRI studies conducted to identify the brain areas underlying core action

464   recognition (i.e., the recognition of familiar actions presented in a familiar format) collectively suggest

465   that it relies on visuo-perceptual (i.e., lateral occipito-temporal cortex and inferior parietal lobule) rather

466   than motor areas of the brain (see Wurm & Caramazza, 2022 for review).

467

Nevertheless, there remains ample space for a role of effector-specific motor simulation in action recognition. The demasking paradigm used in Experiment 1 measures the amount of information required to recognize an action. However, performance in this task may reflect both immediate recognition and the result of other processes (e.g., decision, guessing), which may have differently contributed to the performance of the controls and of the IDs. Therefore, it remains possible that effector-specific motor simulation contributes to the ease or speed of action recognition. At odds with this possibility, two previous studies had reported individuals with acquired and congenital motor disorders who were able to recognize (name) pictures and video clips of actions that they could not imitate as accurately and as rapidly as typically developed participants (Vannuscorps et al., 2013, 2016b). However, the main statistical tool used in these studies to test for a deficit in an individual patient, the modified t test (Crawford & Howell, 1998), has a power of only approximately 60% to detect a 2SD deficit. Therefore, it remains possible that effector-specific motor simulation may contribute to some extent to the speed of action recognition. Another possibility is that effector-specific motor simulation contributes to decrease the cognitive cost of action recognition, a hypothesis that, to our knowledge, has yet to be tested, or to the recognition of challenging action stimuli. The findings from the PLA naming task support this possibility: IDs 1-7 recognized upper limb actions presented as PLAs significantly less accurately than lower limb actions in PLAs (everything else being equal) and ID8 recognized PLAs of both upper and lower limb actions less accurately than control participants. This finding corroborates those of previous studies showing that patients with hemiplegia and paraplegia suffer from difficulties to recognize actions depicted as PLAs (Arrighi et al., 2011; Serino et al., 2010). Note, however, that the latter findings were interpreted, and have been cited so far, as evidence of a contribution of the motor system to core action recognition, that is, to action recognition *in general*. Our findings challenge this conclusion: the ID's specific difficulty for upper limb actions restricted to those presented as PLAs, and not to pantomimed actions, suggests that motor simulation may contribute only to the recognition of challenging action stimuli.

492

493   Future studies will be needed to explore whether effector-specific motor simulation also plays a role in the

494   recognition of challenging real-life action stimuli. We chose to use PLAs in this study because of their

495   widespread use in the field of action and body movement perception (Blake & Shiffrar, 2007) and previous

496   evidence suggesting that PLAs were difficult to recognize for patients with different types of motor disorders

497   (Arrighi, Cartocci, & Burr, 2011; Serino et al., 2010). One could object that the PLAs have low ecological

498   validity, raising the question whether our findings have any implication for the recognition of challenging stimuli

499   in real-life. Three main lines of evidence mitigate this concern, however. First, motor involvement during action

500   recognition has been shown to increase in various types of challenging conditions, such as when offline

501   transcranial magnetic stimulation (TMS) interferes with the observer's visuo-perceptual system (Avenanti et al.,

502   2013), when the stimuli are meaningless (Hétu et al., 2011), or when they are less familiar (Stapel et al.,

503   2010). Second, and more convincingly, the effect of various methods that interfere with motor simulation on

504   action recognition (such as TMS and transcranial random noise stimulation applied on the observer's premotor

505   cortex) has been shown to be larger (Paracampo et al., 2018) or even specific (Penton et al., 2017; Yang &

506   Banissy, 2017) to individuals for whom the task is most challenging (i.e., with low baseline performance). Third,

507   although we have previously shown that the IDs perform at a typical level of efficiency in the hand laterality

508   judgment task with simple hand postures (Vannuscorps & Caramazza, 2015; Vannuscorps, Pillon, & Andres,

509   2012), a recent study found atypical performance in individuals born with congenital unilateral hand dysplasia in

510   laterality judgments using more complex hand postures involving atypical finger and wrist orientations (Maimon-

511   Mor et al., 2020). For all these reasons, it is likely that motor simulation helps action recognition in a variety of

512   challenging conditions in real-life. As a first approximation, we hypothesize that motor simulation might

513   contribute to action recognition whenever core action recognition fails. Potential reasons for core action

514   recognition to fail include, but are not limited to, limitations linked to the observer (e.g., low visual acuity,

515   familiarity with some actions) and information loss at the level of the stimulus itself such as when a

516   stimulus/an action is occluded, insufficiently informative, or too unfamiliar to be automatically matched

517   onto an action representation stored in memory. A different level of familiarity with the actions depicted as PLAs

518   may explain, for instance, the large variability of performance in the IDs.

519

In sum, our findings are consistent with previously apparently diverging results, cited either in favor or against the direct-matching hypothesis of action recognition, and in fact reconciles them. Thus, they are consistent both with the finding that at least some patients with apraxia, despite their action production deficit, perform within the normal range in identifying actions from pantomimes or pictures, and with the finding that patients with hemiplegia or paraplegia have difficulties in naming or detecting PLAs of actions. This emphasizes the need to reframe the current controversy regarding the role of effector-specific motor simulation in action recognition: instead of focusing on the dichotomy between motor and non-motor theories, the field would benefit from new hypotheses specifying when and how effector-specific motor simulation may contribute to the recognition of actions. Beyond this question, our findings encourage future theoretical work and empirical studies to consider with more attention the nature of the stimuli used to study the cognitive and neural bases of action recognition. Eventually, the goal should be not only to develop models detailing the cognitive and neural mechanisms underlying core action recognition, but also to describe what, when and how effector specific motor simulation may supplement core action recognition processes to accommodate the full variety of action stimuli that humans can recognize.

534

As a first attempt in that direction, we propose to distinguish three different routes to action recognition, schematized in Figure 1. Of course, this hypothesis is at an early stage of development, in several respects, and future studies will be needed to evaluate and refine this proposal. However, we believe that this proposal has some value in that it provides a much-needed tractable framework for thinking about when and how effector-specific motor simulation may contribute to action recognition. In this spirit, we wish to conclude by making explicit that we assume that the contribution of these different routes to action recognition depends on their availability and their efficiency. The role of availability is trivial: when one or several routes are unavailable, for instance because the stimulus is unfamiliar, or because the observer is deprived of the motor representations required to covertly imitate the observed body movements, then action recognition depends on the other route(s). The efficiency claim proposes that

545   when several routes are simultaneously available, action recognition efficiency depends uniquely on the

546   most efficient of these routes. The availability assumption is motivated by the IDs' specific deficit for the

547   upper-limb actions (that they are not able to imitate) presented as PLAs (that are not depicted in a familiar

548   format). In turn, the efficiency assumption seems necessary to explain the IDs' typically efficient

549   recognition of pantomimes, pictures, and video-clips of upper-limb actions reported in this and previous

550   studies.

555 **Competing interests**

556 The authors declare no conflict of interest.

557

558 **Data availability**

559 The data underlying this article are displayed in the article (Figure 2). They will be promptly shared by

560 the corresponding author upon request.

561

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844   **Figure legends**

845   Figure 1. Schematic representation of three different "routes" to action recognition. Core action

846   recognition refers to the automatic, effortless matching of familiar body postures and movements onto a

847   corresponding stored action representation. When core action recognition fails, action recognition may be

848   supplemented by effector-specific motor simulation (see text for detail).

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850   Figure 2. Results of Experiments 1 and 2 by individual participant and group.

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