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► To cite this version:

Nicolas Leclere, Fabrice Sarlegna, Yann Coello, Christophe Bourdin. Sensori-motor adaptation to novel limb dynamics influences the representation of peripersonal space. *Neuropsychologia*, 2019, 10.1016/j.neuropsychologia.2019.05.005 . hal-02129330

HAL Id: hal-02129330

<https://amu.hal.science/hal-02129330v1>

Submitted on 14 May 2019

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1 **Sensori-motor adaptation to novel limb dynamics**
2 **influences the representation of peripersonal space**
3

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14

15 **Abstract**

16 Peripersonal space can be considered as the interface between the body and the environment,
17 where objects can be reached and which may serve as a reference for the central nervous system
18 with regard to possible actions. Peripersonal space can be studied by assessing the perception
19 of the reachable space, which depends on the body's physical characteristics (i.e., arm length)
20 since their modifications have been shown to be associated with a change in peripersonal space
21 representation. However, it remains unclear whether the representation of limb dynamics also
22 influences the representation of peripersonal space. The present study investigated this issue by
23 perturbing the force-field environment. A novel force field was created by rotating an
24 experimental platform where participants were seated while they reached towards visual targets.
25 Manual reaching performance was assessed before, during and after platform rotation.
26 Crucially, perception of peripersonal space was also assessed, with reachability judgments,
27 before and after platform rotation. As expected, sensori-motor adaptation to the perturbed force
28 field was observed. Our principal finding is that peripersonal space was systematically
29 perceived as closer to the body after force-field adaptation. Two control experiments showed
30 no significant difference in reachability judgments when no reaching movements were
31 performed during platform rotation or when reaching movements were performed without
32 platform rotation, suggesting that the change in perceived peripersonal space resulted from
33 exposure to new limb dynamics. Overall, our findings show that sensori-motor adaptation of
34 reaching movements to a new force field, which does not directly influence arm length but
35 results in the updating of the arm's internal model of limb dynamics, interacts with the
36 perceptual categorisation of space, supporting a motor contribution to the representation of
37 peripersonal space.

38

39 **Keywords:** force-field adaptation, internal models, manual reaching, reachability judgment,
40 peripersonal space, space representation

41

42 **1. Introduction**

43 Interacting adequately with the physical world requires fine perceptual and motor skills, such
44 as estimating the distance of an object or anticipating the effect of body movement on the object.
45 As early as the beginning of the 20th century, Poincaré (1902) stated that to localise an object
46 in space, we represent “the movements that are necessary to reach that object” or, in other
47 words, “the muscular sensations which accompany them and which have no geometrical
48 character”. This implies that the central nervous system may use a functional representation of
49 space, and recent research appears to support this view. For instance, the nervous system seems
50 to represent object properties such as being reachable or not, and such attributes can be used to
51 define the peripersonal and the extrapersonal space, respectively (Caggiano et al., 2009;
52 Brozzoli et al., 2010). Behavioural as well as neuroimaging studies of the human neurotypical
53 brain have provided evidence suggesting the specific processing of information in peripersonal
54 and extrapersonal spaces. Object perception, in particular, seems to be associated with an
55 activation of the motor system only when the object appears within the peripersonal space
56 (Mark et al., 1997; Costantini et al., 2010; Iachini et al., 2014; Coello et al., 2008; Gallivan et
57 al., 2009, 2011; Bartolo et al., 2014). Thus, visual presentation of objects in peripersonal space
58 has been found to activate not only occipital but also parietal, ventral and premotor cortices
59 (Chao & Martin, 2000; Chao et al. 2002; Creem-Regehr & Lee, 2005; Kan et al. 2006; Martin,
60 2007), and sensori-motor cortices (Cardellicchio et al., 2011; Grafton et al., 1997; Matelli et al.,
61 1985; Gallivan et al., 2011; Wamain et al., 2016). Wamain et al. (2016), for instance, reported
62 an event-related desynchronisation of the μ rhythm (8-13Hz) over the centro-parietal region
63 when a graspable object was presented in peripersonal space. This typical neural activation
64 related to the motor system was not observed for objects in extrapersonal space, and was
65 congruent with the activation reported when executing a voluntary motor action (Babiloni et

66 al., 1999; Llanos et al., 2013; Salmelin & Hari, 1994; Salenius et al., 1997), observing a human
67 movement (Cochin et al., 1999) or observing the picture of a graspable object (Proverbio, 2002).
68 In addition, Coello et al. (2008) reported that transcranial magnetic stimulation of the left motor
69 cortex altered the neural processing of objects located in peripersonal space, but not of those
70 located in extrapersonal space. Likewise, Cardellicchio et al. (2011) reported greater motor-
71 evoked potentials when observing graspable objects located in the peripersonal space,
72 compared to observing either non-graspable objects or graspable objects outside the
73 peripersonal space. Accordingly, peripersonal space can be viewed as an abstract representation
74 of the near-body space where allocation of attention is multisensorial (Cléry et al., 2015; di
75 Pellegrino et al., 1997; Graziano & Gandhi, 2000) and where objects are coded in terms of
76 possible actions (Coello & Iachini, 2016; de Vignemont & Iannetti, 2015; Di Pellegrino &
77 Làdavas, 2014), as Rizzolatti et al. (1981) put it. It is therefore now generally accepted that the
78 representation of peripersonal space may not be solely based on a perceptual representation of
79 space, but may also be influenced by motor representations allowing the anticipation of possible
80 actions.

81 The relationship between peripersonal space representation and motor representations has
82 been widely investigated, in particular in relation to tool use (Berti & Frassinetti, 2000; Làdavas
83 & Serino, 2008; Cardinali et al., 2009; Canzoneri et al., 2013; Cléry et al., 2015; di Pellegrino
84 & Làdavas, 2015; Gouzien et al., 2017). For instance, Bourgeois et al. (2014) showed that using
85 tools to reach a target modifies the representation of peripersonal space. Their perceptual
86 paradigm investigated peripersonal space representation through reachability judgment tasks
87 that involved judging the reachability of various visual stimuli located at different distances
88 from the body (Bourgeois et al., 2014). In another study, Cardinali et al. (2009) asked
89 participants to repeatedly use long mechanical grabbers to reach objects. This period of repeated
90 tool use modified the kinematics of the same reaching movements using the hand alone,

91 suggesting that the geometry of the arm was perceived as longer after using the grabber. Other
92 work also suggests that after repeated use, the tool is integrated into the body schema, defined
93 as a highly plastic representation of the body in terms of geometry and relative position of limbs,
94 which is used for performed and imagined movements (Haggard & Wolpert, 2005; Medina &
95 Coslett, 2010; De Vignemont, 2010; Martel et al., 2016). However, while it appears clear that
96 the geometrical properties of the body and its hierarchical arrangement are linked to
97 peripersonal space representation, it remains unclear whether dynamic properties also influence
98 this representation.

99 It has been hypothesised that internal models of limb dynamics are used to control
100 movements (Wolpert et al., 1995; Kawato, 1999; Bursztyn et al., 2006; Cullen & Brooks, 2015;
101 Ghez & Sainburg, 1995; Tanaka & Sejnowski, 2013). In reference to the mainstream literature,
102 internal models are separately conceived as a model “within the brain that can predict the
103 sensory consequences of an action”, namely the forward model, and as a model capable “[to
104 transform] a desired sensory consequence into the motor command that would achieve it”,
105 namely the inverse model (Wolpert et al., 2001). These internal models would thus operate at
106 the neural level both as controllers producing motor commands and as predictors anticipating
107 the sensory consequences of these motor commands (Wolpert & Kawato, 1998; Wolpert et al.,
108 2001; Pickering & Clark, 2014). Such internal models could underlie sensori-motor adaptation
109 and learning (Shadmehr et al., 2010). For instance, whenever the dynamic characteristics of the
110 limb change, these highly plastic sensori-motor representations may be updated to maintain a
111 high level of motor performance (Ostry et al., 2010).

112 The effect on motor performance of perturbing upper-limb dynamics has been extensively
113 studied through adaptation to modified gravito-inertial fields (Bourdin et al., 2001; Coello et
114 al., 1996; Lackner & DiZio, 1994; Sarlegna et al., 2010). The force-field environment can be
115 modified by asking individuals to sit on a rotating platform and to perform reaching arm

116 movements. Such experiments are based on the fact that any movement performed during
117 rotation will encounter an inertial force (i.e., the Coriolis force) proportional to the speed of
118 both the reaching movement and the platform rotation. The force is applied to the body segment
119 with an effect orthogonal to the radial trajectory and opposite to the direction of the platform
120 rotation, resulting in lateral deviations of the movements during the first trials. Adaptation to
121 this inertial perturbation typically requires a few trials before the movement characteristics
122 return to baseline values, and produces an after-effect when the rotation (and the perturbation)
123 is interrupted (Lackner & DiZio, 1994; Coello et al., 1996; Bourdin et al., 2001, 2006; Lefumat
124 et al., 2015). Interestingly, the spatio-temporal features of the trajectories before and after
125 adaptation have been found to be similar, suggesting that this adaptation involves changes to
126 the dynamic properties of the motor system with no effect on the body's spatial properties:
127 length of limb segments, their arrangement and configuration in space, and shape of body
128 surface (Morasso et al, 2015).

129

130 We used a classic force-field adaptation protocol (Lackner & DiZio, 1994; Coello et al.,
131 1996; Bourdin et al., 2006; Sarlegna et al. 2010) and measured several kinematic parameters
132 such as initial direction error, endpoint error and maximum perpendicular deviation (Lackner
133 & DiZio, 1994; Lefumat et al. 2015) to validate the strong hypothesis of a sensori-motor
134 adaptation. In the present study, force-field adaptation was a pre-requisite to assess whether the
135 internal model of limb dynamics influences the representation of peripersonal space. Indeed,
136 our subsequent hypothesis was that updating the arm's internal model through sensori-motor
137 adaptation (as revealed by after-effects on reach trajectories) would modify judgments of
138 reachability. To test this hypothesis, we requested participants to perform a reachability
139 judgment task, which enabled us to assess participants' representation of peripersonal space,
140 before and after adapting to new limb dynamics.

141 2. Material and methods

142 2.1. Participants

143 14 healthy right-handed adults (3 females, mean age = 21.9 ± 2.1 years) participated in this
144 experiment. No prior data were available from the literature or pilot experiments to estimate a
145 realistic effect size, so 14 participants were recruited for our main experiment because this
146 number reflects the sample size used in similar studies (Canzoneri et al., 2013; Ambrosini &
147 Costantini, 2013; Grade et al., 2015; Bartolo et al., 2018 for the reachability part and Lackner
148 & DiZio, 1994; Shadmehr & Mussa-Ivaldi, 1994; Wolpert et al., 1995 for the sensori-motor
149 adaptation part). Participants gave their written informed consent prior to inclusion in the
150 study, which was approved by the institutional review board of the Institute of Movement
151 Sciences and was performed in accordance with the ethical standards set out in the 1964
152 Declaration of Helsinki. All participants had normal or corrected-to-normal vision and were
153 naïve to the purpose of the experiment.

154

155 2.2. Experimental set up

156 As illustrated in Figure 1, participants sat at the centre of a motorised rotating platform. An
157 adjustable headrest was used to restrain head movements and to keep the centre of the head
158 aligned with the vertical (Z) axis of the platform, so as to minimise centrifugal forces on the
159 head during platform rotation. When the upper limb was voluntarily moved towards the target
160 during rotation, each moving point of the limb was subjected to the Coriolis force (F_{cor} in the
161 following equation) acting perpendicularly to the limb displacement: $F_{\text{cor}} = -2m \times \omega \times v$, with
162 m the mass of the upper-limb segments in motion, ω the platform's angular velocity and v the
163 arm's linear velocity (Lackner & DiZio, 1994).

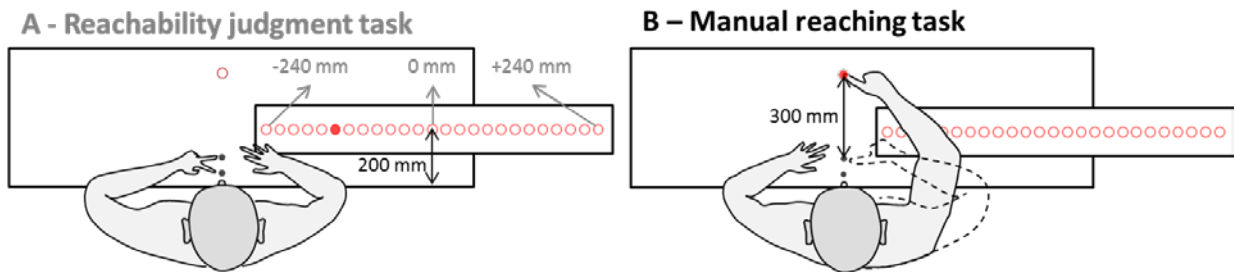
164 Several visual targets were positioned on a horizontal table placed in front of the subjects,
165 at waist level. All visual targets were low-intensity red light-emitting diodes (3 mm in
166 diameter) presented in an otherwise completely dark room, a condition which does not
167 preclude force-field adaptation (Lackner & DiZio, 1994, Lefumat et al., 2015).

168 Participants had to perform two tasks, each involving different visual targets (see Figure
169 1). In the manual reaching task, we used only one visual target, which was positioned 30 cm
170 directly ahead of the starting hand position along the mid-body sagittal axis. In the reachability
171 judgment task, 25 visual targets were aligned in a fronto-parallel plane and positioned in the
172 subject's right hemispace (with respect to the mid-body sagittal axis). The array of reachability
173 targets (inter-target distance was 20 mm; see details on Figure 1) was positioned according to
174 each subject's arm length (see Procedure). Reachability targets were positioned horizontally
175 in the right hemispace of participants in order to be in the same plane than the expected effect
176 of the perturbation, and the adaptation to it, namely orthogonal to the manual reaching
177 trajectory toward a straight-ahead visual target. On the horizontal table, two response buttons
178 were positioned close to the participant, one located 1 cm from the table's edge and the other
179 located 1 cm farther away. The participants operated these buttons with their left hand to
180 respond in the reachability judgment task (closer response button for reachable targets and
181 more distant response button for non-reachable targets). The more distant response button in
182 the reachability judgment task also served as the starting right hand position in the manual
183 reaching task, and could be illuminated with a light-emitting diode.

184 An infrared active marker was taped to the right index fingertip, whose position was
185 sampled at 350 Hz using an optical motion tracking system (Codamotion cx1 and MiniHub,
186 Charnwood Dynamics Ltd, Leicestershire, UK), to record hand movement kinematics during
187 the manual reaching task. Response buttons were sampled at 800 Hz to record reachability
188 estimates. The experimenter controlled the tracking system, the motorised platform and the

189 presentation of the visual targets from an adjacent room via customised software (Docometre)
190 governing a real-time acquisition system (ADwin-Pro, Jäger, Germany).

191



192 *Figure 1. Experimental setup. (A) Reachability judgment task: participants had to judge*
193 *whether a target illuminated on their right was reachable or not: they responded by pressing*
194 *the closer response button with their left index or the more distant button with their middle*
195 *finger, respectively. The 0 mm location, adjusted for each participant, corresponded to the*
196 *maximum physical distance reachable with the arm fully stretched. (B) Manual reaching task:*
197 *participants had to reach the visual target with their right index as accurately and as fast as*
198 *possible.*

199

200 2.3. Procedure

201 Once seated on the platform and before the experiment started, participants wore occluding
202 glasses to prevent them viewing the target array. They were then asked to fully stretch out their
203 right arm in the fronto-parallel plane: this allowed the experimenter to match the position of
204 each participant's index fingertip, with the arm fully stretched, with the position of the central
205 target in the array used for the reachability judgment task. The individually-adjusted position
206 of the central target thus corresponded to the actual maximum distance that was physically
207 reachable by each participant (Bourgeois et al., 2014; Valdès-Conroy et al., 2014; Patané et al.,
208 2017). After this personalized adjustment of the setup, the occluding glasses were removed and
209 participants were allowed to open their eyes in the dark room.

210 2.3.1. *Manual reaching task*

211 In the manual reaching task, each trial began with the right index positioned at the starting
212 hand location. The visual target was flashed for 200 ms, after a 100 ms auditory tone followed
213 by a random time of 500 to 1000 ms. As soon as the visual target was turned on, participants
214 had to reach towards it as fast and as accurately as possible with the right index. Participants
215 were asked to maintain their final hand position once the finger touched the horizontal board.
216 3.5 s after the start of the trial, the LED at starting hand location was turned on: this indicated
217 the end of the trial and signalled to participants that they should move their hand back to the
218 start position and prepare for the next trial. No explicit instructions were given with respect to
219 hand path.

220

221 2.3.2. *Reachability judgment task*

222 In the reachability judgment task, after a 100 ms auditory tone followed by a random time
223 of 500 to 1000 ms, one of the 25 visual targets was randomly presented in the participants'
224 right hemispace. Participants had to judge as fast and as accurately as possible, without
225 performing any reaching movement, whether the illuminated visual target was reachable or
226 not with their right index, from a stable trunk posture. This two-alternative forced choice was
227 recorded as participants pressed either the closer response button (“reachable”) with their left
228 index or the more distant response button (“unreachable”) with their middle finger. The target
229 disappeared as soon as the participant provided his/her response and, at the end of a fixed
230 period lasting 4 s from the 100 ms auditory tone, the next trial started with the same temporal
231 sequence.

232

233 All participants were familiarised with both tasks during a pre-experiment session. The
234 experiment involved five conditions, presented in successive blocks (see Figure 2):

235 - Manual reaching task / PRE-rotation (platform stationary). Participants executed a series
236 of thirty reaching movements towards the visual target to determine baseline sensori-motor
237 performance.

238 - Reachability judgment task / PRE-rotation (platform stationary). Participants performed
239 a series of one hundred reachability estimates (each of the 25 targets randomly presented 4
240 times) to determine baseline performance in the reachability judgment task. At the end of the
241 PRE-rotation stage, the platform was progressively accelerated, counterclockwise, for 80 s
242 (increase of $1.5^\circ/\text{s}^2$) to reach a constant velocity of $120^\circ/\text{s}$ (20 rpm).

243 - Manual reaching task / PER-rotation (platform rotating). Participants executed sixty
244 reaching movements towards the visual target. The platform's rotation generated Coriolis
245 force (F_{cor}) on the moving limb. Then, the platform was progressively decelerated for 80 s
246 (decrease of $1.5^\circ/\text{s}^2$) until stationarity.

247 - Reachability judgment task / POST-rotation (platform stationary). Participants performed
248 a new series of one hundred reachability estimates, as in PRE-rotation.

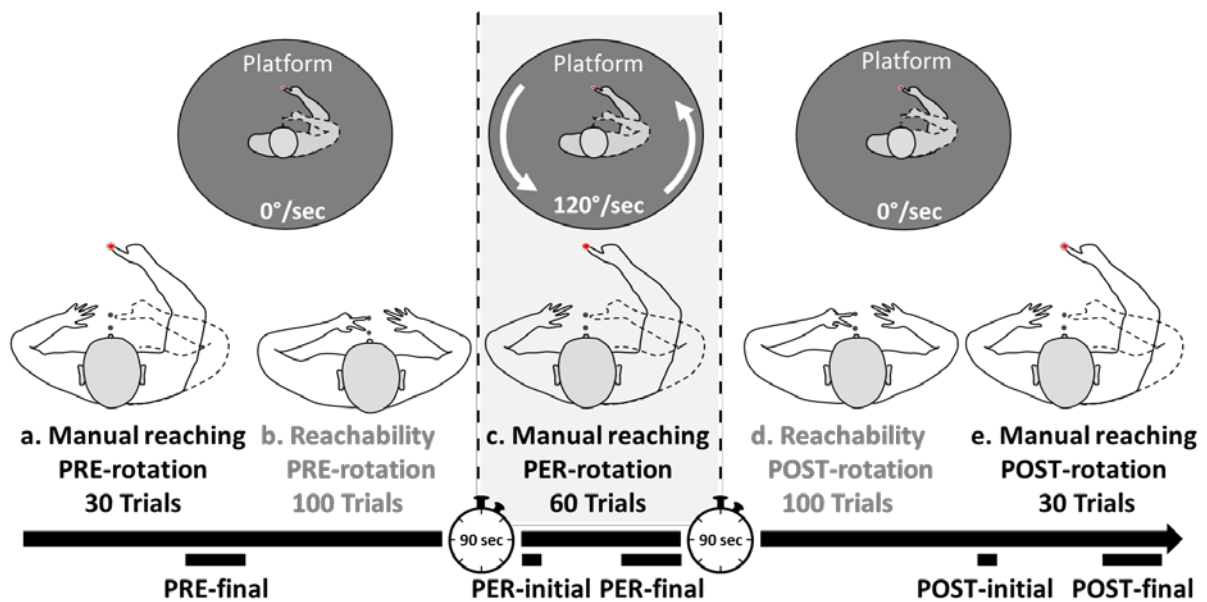
249 - Manual reaching task / POST-rotation (platform stationary). Participants ended the
250 experiment by performing a new series of thirty manual reaching movements.

251 A 90 s pause was included between the end of the platform rotation acceleration (or
252 deceleration) period and the ensuing task, to allow the vestibular semi-circular canals to return
253 to their resting discharge frequency (Goldberg & Fernandez, 1971). Subjects were instructed
254 not to move their opposite arm during the experiment (left arm during the manual reaching
255 task, right arm during the reachability judgment task).

256 The order of conditions was not counterbalanced, for two main reasons. First, the second
257 reachability judgment task (namely reachability POST-rotation in our manuscript) had to be

258 performed right after a reaching movement task, so the first reachability judgment task
 259 (reachability PRE-rotation) was also performed right after a reaching movement task; this
 260 way, a reachability judgment task was always preceded by a reaching movement task. Second,
 261 this experimental design allowed to compare the reachability judgment tasks performed just
 262 before and just after the sensorimotor adaptation phase, as has been done by Bourgeois &
 263 Coello (2012) (see also Ostry et al. (2010) for a similar design albeit with a different perceptual
 264 test).

265
 266



267

268 *Figure 2. Experimental procedure. Manual reaching movements were executed before (a),*
 269 *during (c) and after (e) platform rotation, while reachability was estimated before (b) and after*
 270 *(d) rotation. Under the black arrow of time, we specify the manual reaching trials used for*
 271 *statistical analyses: the ten last trials before the rotation (PRE-final), the first (PER-initial) and*
 272 *ten last trials during the rotation (PER-final), and the first (POST-initial) and ten last trials*
 273 *(POST-final) after the rotation.*

274

275 2.4. *Data recording and analysis*

276 In the manual reaching task, the (x, y, z) coordinates of the marker on the right index
277 fingertip were recorded and then analysed via customised Matlab software (Mathworks,
278 Natick, MA, USA). Raw data were low-pass filtered using a dual-pass, no-lag Butterworth
279 (cut-off frequency: 8Hz; order: 2). Velocity data were obtained from the filtered position data.
280 As in Lefumat et al. (2015), movement onset was defined as the first time hand velocity
281 reached 3 cm/s and movement offset was defined as the first time hand velocity dropped below
282 3 cm/s. These time markers were used to compute movement time.

283 Previous work showed that Coriolis force mainly influences the directional control of
284 movement (Lackner & DiZio, 1994; Coello et al., 1996; Bourdin et al., 2001; Sarlegna et al.,
285 2010). We therefore computed initial movement direction, as given by the angle between the
286 vector start position-to-target position and the vector start position-to-hand position at the
287 moment hand movement reached maximum velocity. Peak velocity was reached on average
288 217 ± 55 ms (mean \pm SD) after movement onset. We considered peak velocity to be of
289 particular interest in the present study because it coincided with the maximum effect of
290 Coriolis forces. We also analysed movement endpoint error as the angle between the vector
291 start position-to-target position and the vector start position-to-hand position at the end of the
292 reaching movement (Coello et al., 1996; Bourdin et al., 2001). In addition, we computed
293 maximum perpendicular deviation as the maximum distance between the hand and its
294 orthogonal projection on the straight line linking the hand starting position and its ending
295 position (Brown & al., 2007), assuming that subject's intended hand path would mainly be
296 directly ahead, unless instructed otherwise, particularly given the planar workspace (Morasso,
297 1981; Palluel et al., 2004). For all these variables, rightward trajectory deviations
298 corresponded to positive values, and leftward deviations to negative values.

299 Sensory-motor adaptation to the Coriolis force was characterised using a method similar to
300 that described by Lackner and DiZio (1994) and Lefumat et al. (2015). Data from the final ten
301 trials in the PRE-rotation phase (labelled PRE-final) were averaged for each participant and
302 used as baseline value. This baseline was then compared to the data of the first trial (PER-
303 initial) and the average of the final ten trials (PER-final) during the rotation of the platform,
304 and then to the first trial (POST-initial) and the average of the final ten trials (POST-final)
305 once rotation ceased. The analyses of initial direction, endpoint error and maximum amplitude
306 deviation were used to characterise adaptation to the perturbation. The PER-initial data (with
307 respect to baseline) reflected the effect of the velocity-dependent force field on the manual
308 reaching movements (perturbation), while the PER-final data and POST-initial data reflected
309 sensory-motor adaptation and after-effects of sensory-motor adaptation to the velocity-
310 dependent force field. In addition, we analysed peak acceleration, peak velocity and peak
311 deceleration amplitude in order to provide a detailed kinematic account of the reaching
312 movements throughout the experiment.

313 In the reachability judgment task, reachability judgments and response times were
314 registered through the participant's answers via the response buttons. As in Bourgeois &
315 Coello (2012), the estimated boundary of reachable space was determined using a maximum-
316 likelihood fit procedure based on the second-order derivatives (quasi-Newton method) to
317 obtain the logit regression model that best fitted the reachable/unreachable responses of the
318 participants. Taking into account the 25 positions of the target, the model relied on the
319 following equation: $y = e^{(\alpha+\beta x)} / (1+e^{(\alpha+\beta x)})$ in which y was the participant's response (0 for
320 unreachable and 1 for reachable), x the distance (in mm) between the presented target and the
321 target representing the physical limit of reachability, and $(-\alpha / \beta)$ the value of x at which the
322 transition from one type of response (reachable) to the other type of response (unreachable)
323 occurred (the probability p associated with the logit function was 0.50 for both responses).

324 This point of subjective equality (PSE) thus expresses the perceived boundary of reachable
325 space. Positive PSE values corresponded to an overestimation of the peripersonal space
326 boundary with respect to the physical one. We then calculated the difference between the PSE
327 in PRE-rotation and POST-rotation corresponding to the shift in peripersonal space
328 representation (Δ PSE) after the PER-rotation condition. In addition, we computed the
329 discrimination threshold, defined as the distance between the value of PSE (target distance at
330 $p = 0.50$) and the target distance at $p = 0.84$ (Ernst & Banks, 2002). The smaller the
331 discrimination threshold, the more accurate the participant was in distinguishing between
332 reachable and unreachable targets.

333 To analyse response time, defined as the time between the onset of stimulus presentation
334 and the onset of the button press, we divided the set of targets into three zones, corresponding
335 to (1) the three most reachable targets (Near), (2) the three targets around the boundary of
336 reachable space (adjusted for each participant) (Boundary) and (3) the three least reachable
337 targets (Far). Once the boundary was determined for each reachability phase, we selected the
338 closest target as well as the adjacent ones to determine response time in the boundary zone.
339 We calculated the mean response time for each region and verified that no targets were situated
340 in more than one zone (no overlap).

341

342 2.5. *Statistical analysis*

343 To assess sensori-motor adaptation in the manual reaching task, we conducted a repeated-
344 measure analysis of variance (ANOVA) with one factor, Phase (PRE-final, PER-initial, PER-
345 final, POST-initial, POST-final)], on the different variables. When there was a significant
346 main effect, a Tukey HSD post-hoc test was used for further analysis. In the reachability
347 judgment task, both perceived boundary of reachable space and discrimination threshold were
348 compared between reachability PRE- and POST-rotation conditions, using a t-test for related

349 samples. Level of significance was 0.05 for all analyses. Normality of data distribution was
350 verified in all experimental conditions, using the Kolmogorov-Smyrnov method.

351

352 **3. Results**

353 *3.1. Manual reaching task*

354 Since our aim was to assess the effect of sensori-motor adaptation on reachability judgment,
355 it was essential to confirm the presence of force-field adaptation in reaching arm movements.
356 We thus analysed both the spatial performance (initial direction, endpoint error, maximum
357 perpendicular deviation) and the temporal performance (movement time and time to peak
358 velocity) of the voluntary, unconstrained targeted movements.

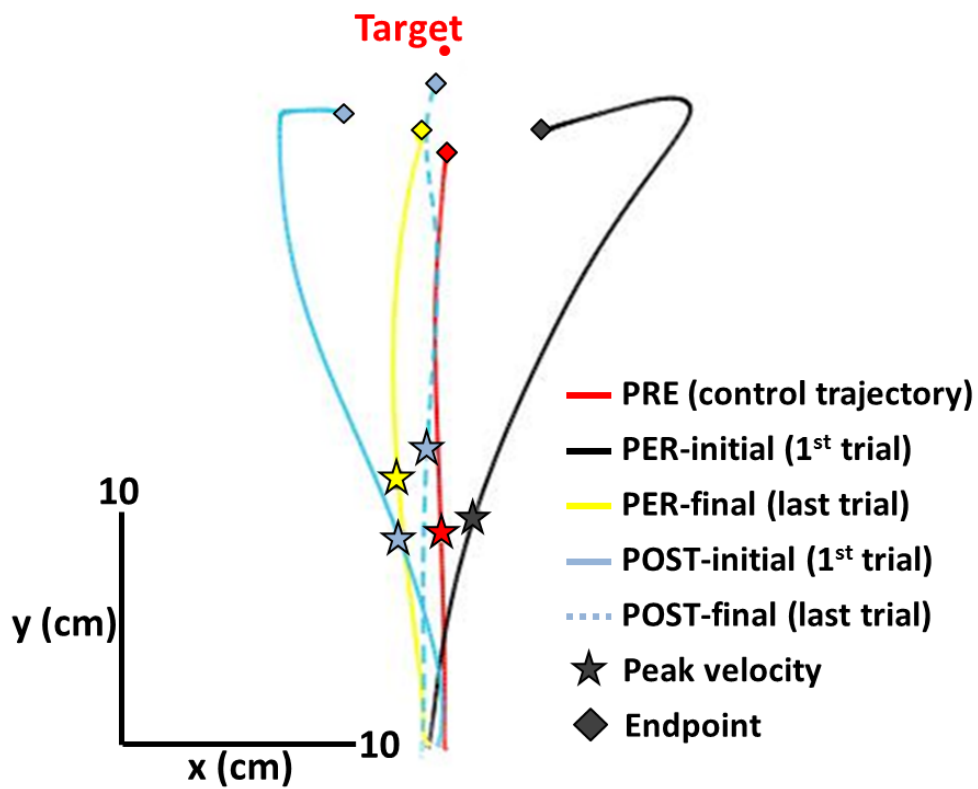
359

360 *3.1.1. Spatial performance*

361 The Coriolis force induced by platform rotation and limb movements influenced the spatial
362 performance of every participant, and sensori-motor adaptation was systematically observed.

363 *3.1.1.1. Hand trajectory*

364 Figure 3 shows that hand trajectories towards the visual target were quite straight during
365 baseline (PRE-rotation, average initial direction = $-2.3 \pm 3.5^\circ$; average endpoint error = $1.6 \pm$
366 2.2°). During counterclockwise platform rotation, Coriolis force initially altered the hand path,
367 as shown by the lateral deviation of the first reaching movement in the PER-rotation stage.
368 After 60 trials performed in rotation, the hand path was similar to baseline, suggesting
369 substantial force-field adaptation. After rotation was interrupted and the usual force field was
370 restored, there was a pronounced after-effect on the hand path of each participant, confirming
371 the presence of force-field adaptation. Indeed, the first movement in the POST-rotation
372 condition was clearly deviated to the left. Finally, at the end of the experiment, the last
373 movement in the POST-rotation condition was similar to the baseline.



374

375

Figure 3. Top view of the right index fingertip trajectories for a representative participant. Hand paths are shown for the last trial of the PRE-rotation (red line), the first trial of the PER-rotation (black line), the last trial of the PER-rotation (yellow line), the first trial of the POST-rotation (light blue line) and the last trial of the POST-rotation (light blue dotted line).

376

377

378

379 *3.1.1.2. Initial direction*

380 An ANOVA revealed a significant effect of Phase on initial direction ($F(4, 52) = 36.53$;
381 $p < 0.001$; $\eta^2 = 0.738$). HSD Tukey post-hoc comparison revealed that the initial direction of
382 the PER-rotation initial movement was significantly deviated to the right ($4.9 \pm 5^\circ$) compared
383 to PRE-final ($-2.3 \pm 3.5^\circ$), PER-final ($-2.6 \pm 3.1^\circ$), POST-initial ($-13.7 \pm 8.2^\circ$) and POST-final
384 ($-0.9 \pm 1.5^\circ$, all $p < 0.01$). Statistical analyses revealed that initial direction at the end of the
385 PER-rotation did not significantly differ from baseline ($p = 0.99$). The first movement in the
386 POST-rotation condition (POST-initial) was significantly deviated to the left: initial direction
387 (-13.6°) compared to PRE-final (-3.1°), PER-initial (4.9°), PER-final (-2.6°) and POST-final
388 (-0.9°) movements (all $p < 0.001$).

389

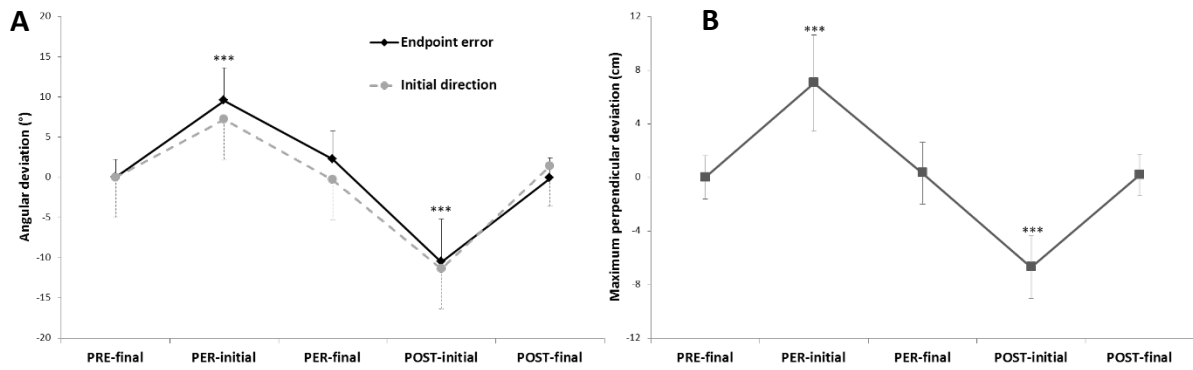
390 *3.1.1.3. Endpoint error*

391 An ANOVA revealed a significant effect of Phase on endpoint error ($F(4, 56) = 76.64$;
392 $p < 0.001$; $\eta^2 = 0.855$). HSD Tukey post-hoc comparison revealed that the PER-initial
393 endpoints were significantly deviated rightward ($11.3 \pm 4.1^\circ$) compared to PRE-final ($1.7 \pm$
394 2.2°), PER-final ($3.9 \pm 3.6^\circ$), POST-initial ($-8.9 \pm 5.3^\circ$) and POST-final ($1.6 \pm 2.6^\circ$, all
395 $p < 0.001$). Statistical analyses revealed that endpoint error at the end of the PER-rotation did
396 not significantly differ from baseline ($p = 0.35$). Once rotation stopped, the first movement
397 endpoint error in the POST-rotation condition (POST-initial) was significantly deviated to the
398 left (-13.6°) compared to PRE-final (-3.1°), PER-initial (4.9°), PER-final (-2.6°) and POST-
399 final (-0.9°) movements (all $p < 0.001$).

400

401

402



403
 404 *Figure 4. Behavioural adaptation to the force-field perturbation. (A) Mean angular endpoint*
 405 *error and initial direction of the first (PER-initial) and last ten trials (PER-final) of PER-*
 406 *rotation, and the first (POST-initial) and last ten trials (POST-final) of the POST-rotation*
 407 *phases, normalised with respect to the last ten trials of the PRE-rotation condition (PRE-final).*
 408 *(B) Mean maximum perpendicular distance of the hand trajectory from the straight line linking*
 409 *its starting and its final location as a function of the different phases and normalised with*
 410 *respect to PRE-final. Vertical bars represent the standard error of the mean. Asterisks*
 411 *correspond to statistically significant differences with respect to baseline (***: $p < 0.001$).*

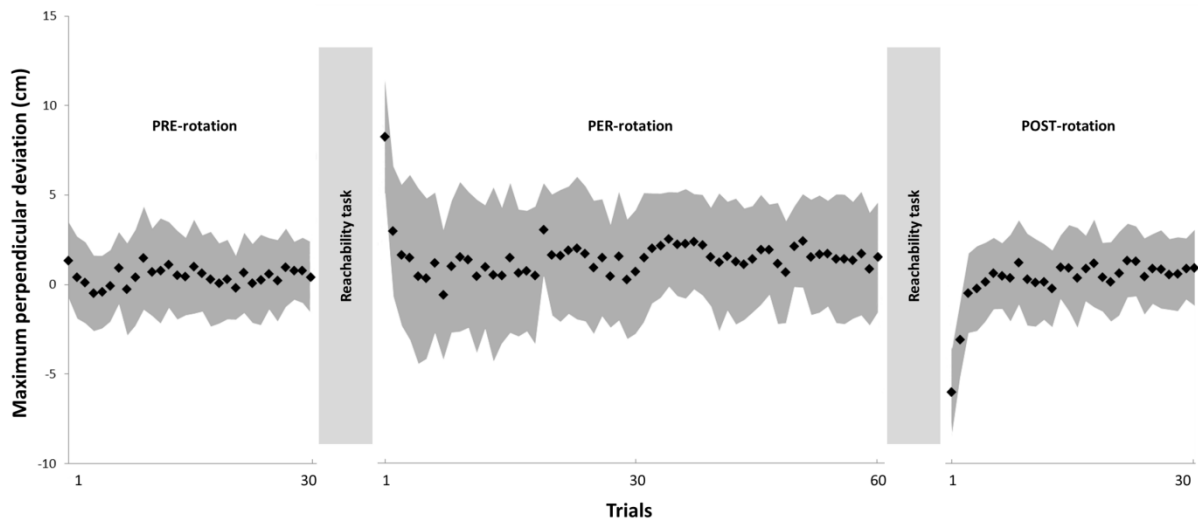
412

413 3.1.1.4. Maximum perpendicular deviation

414 An ANOVA on maximum perpendicular deviation revealed a main effect of Phase ($F_{(4, 52)}$
 415 $= 74.63$, $p < 0.001$; $\eta^2 = 0.852$) and post-hoc analysis revealed that deviations were
 416 significantly greater for the PER-initial trial (6.0 ± 3.6 cm) compared to the trials in PRE-final
 417 (1.1 ± 1.6 cm), PER-final (-0.8 ± 2.3 cm), POST-initial and POST-final (-0.9 ± 1.5 cm; all
 418 $p < 0.001$) phases. Figure 4 shows that data for the first trial after rotation ended (POST-
 419 initial: -7.8 ± 2.3 cm) differed from PRE-final data ($p < 0.001$), highlighting the after-effects
 420 of sensori-motor adaptation. As shown in Figure 5, participants corrected the deviation
 421 observed in the first trial of PER-rotation and POST-rotation phases such that, trial after trial,
 422 they recovered a straight hand path to the target.

423

424



425
 426 *Figure 5. Mean maximum perpendicular deviation across participants for all reaching*
 427 *movements throughout the experiment. The dark grey area surrounding black points represents*
 428 *the standard deviation of the mean. Participants progressively adapted to the Coriolis force*
 429 *that initially deviated their moving limb to the right when they performed manual reaching*
 430 *tasks during platform rotation (PER-rotation). After the perturbation ceased, participants'*
 431 *movements were deviated to the left during the first trials before recovering trajectories similar*
 432 *to the baseline (POST-rotation). Reachability judgment tasks (light grey vertical bars) were*
 433 *interleaved with platform rotation.*

434
 435 *3.1.2. Temporal performance and related kinematic data*

436 *3.1.2.1. Movement time*

437 Statistical analysis revealed an effect of Phase on the duration of reaching movements ($F_{(4, 52)} = 4.3$;
 438 $p = 0.004$; $\eta^2 = 0.249$). According to post-hoc analyses, movements were performed
 439 in a longer time in the POST-initial phase (mean = 485 ± 142 ms) compared to PRE-final (386
 440 ± 49 ms; $p < 0.05$) and POST-final (mean = 431 ± 54 ms; $p < 0.05$), and also in the PER-initial
 441 phase (mean = 497 ± 138 ms) compared to PRE-final ($p < 0.05$) and POST-final ($p < 0.05$).
 442 However, there was no significant difference between PRE- and PER-final trials (mean = 431
 443 ± 54 ms; $p = 0.5$). The percentage of movement time ($51 \pm 19\%$) taken to reach maximum
 444 velocity was not significantly altered by Phase ($F_{(4, 52)} = 1.45$; $p = 0.22$; $\eta^2 = 0.101$), suggesting
 445 that the overall temporal organisation of the movement was preserved.

446

447 *3.1.2.2. Acceleration, velocity and deceleration peaks amplitude*

448 We conducted a repeated-measure, one-way analysis of variance with one factor Phase (PRE-
449 final, PER-initial, PER-final, POST-initial, POST-final) for peak velocity, peak acceleration
450 and peak deceleration. There was no significant effect for peak acceleration ($F_{(4, 52)} = 0.2987$;
451 $p = 0.88$; $\eta^2 = 0.022$) and peak deceleration ($F_{(4, 52)} = 2.34$; $p = 0.07$; $\eta^2 = 0.153$). For peak
452 velocity, the ANOVA revealed a significant main effect ($F_{(4, 52)} = 3.18$; $p = 0.02$; $\eta^2 = 0.196$).
453 Post-hoc analysis (HSD Tukey test) only showed a greater peak velocity in the PER-initial
454 trial (mean = 227 ± 59 cm/s) compared with the POST-initial trial (mean = 195 ± 51 cm/s;
455 $p < 0.05$). However, there was no significant difference between either PRE-final (mean = 229
456 ± 44 cm/s) and PER-final trials (mean = 218 ± 54 cm/s; $p = 0.72$), PRE-final and PER-initial
457 trials ($p = 0.24$) or PER-initial and PER-final trials ($p = 0.91$). There was also no significant
458 difference between either PRE-final and POST-final trials (mean = 210 ± 49 cm/s; $p = 0.99$),
459 PRE-final and POST-initial trials (mean = 195 ± 51 cm/s; $p = 0.74$), or POST-initial and
460 POST-final trials ($p = 0.52$).

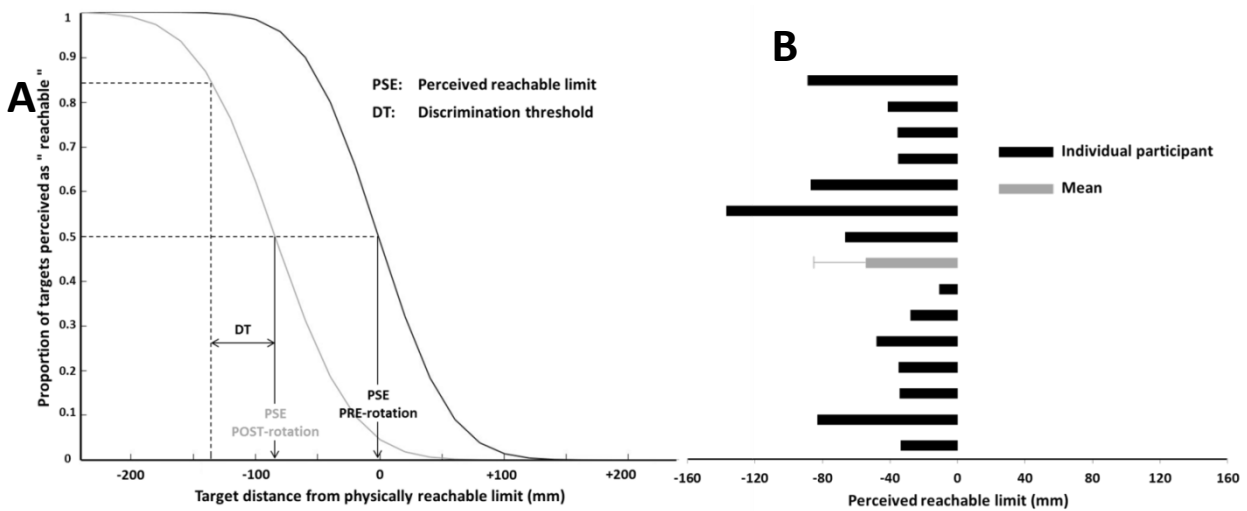
461

462 *3.2. Reachability judgment task*

463 *3.2.1. Reachability judgments*

464 We performed a paired t-test to compare the perceived boundary of reachability between
465 the POST-rotation and the PRE-rotation stages. The shift (mean Δ PSE = 55 ± 34 mm) in
466 perceived reachable space was statistically significant: a t-test showed that the perceived
467 boundary of reachability in POST-rotation (mean PSE = -13 mm ± 89 mm) was significantly
468 reduced compared to the PRE-rotation (mean PSE = 42 mm ± 75 mm; $t(13) = 6.06$; $p < 0.001$;
469 $\eta^2 = 0.674$). Figure 6 illustrates the finding that, on average, participants overestimated the
470 boundary of reachable space by 45 mm in baseline, before being subjected to the rotating

471 platform. Figure 6 also illustrates the main finding of the present study, i.e. that following
 472 exposure to the rotation (POST-rotation), reachability was shifted compared to PRE-rotation.
 473 By contrast with the perceived boundary of reachability, the discrimination threshold in the
 474 PRE-rotation (116 ± 53 mm) and POST-rotation (115 ± 64 mm) conditions did not
 475 significantly differ ($t(13) = 0.4$; $p = 0.7$). Thus, after force-field adaptation, the perceptual
 476 reachability estimates shifted with respect to baseline, in the direction of the compensatory
 477 reach response (opposite to the perturbation).
 478



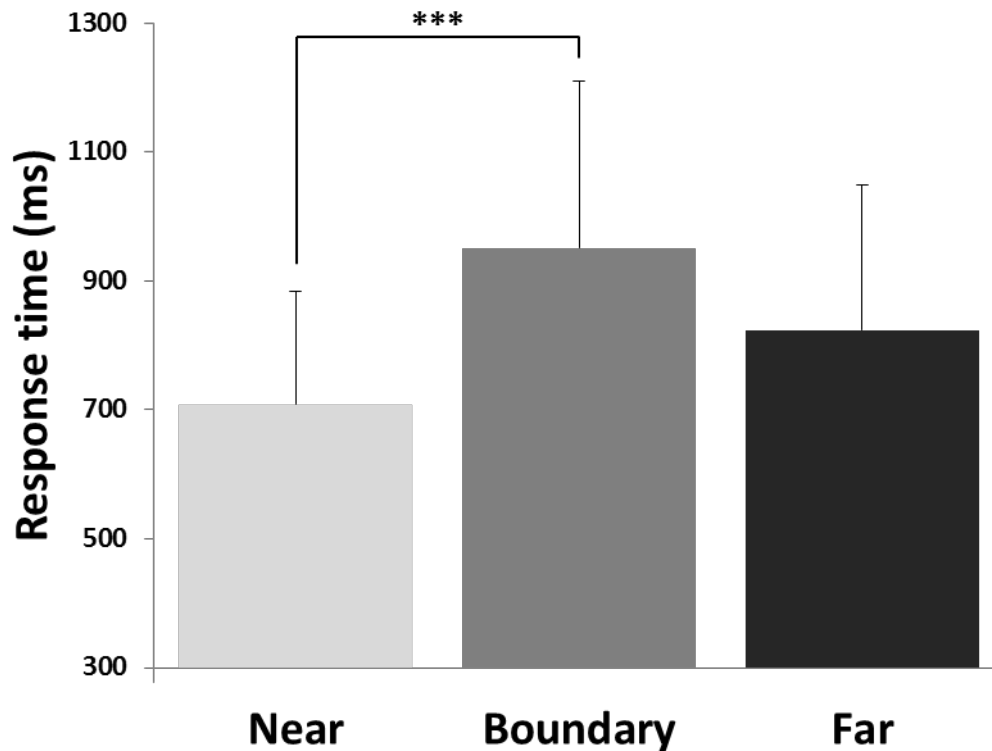
479
 480 *Figure 6. Systematic shift in reachability judgment. (A) Results of logit regression analysis for*
 481 *a representative participant during reachability PRE-rotation (dark line) and POST-rotation*
 482 *(grey line) conditions. (B) Individual shift in the limit of perceived reachable space [POST-*
 483 *rotation - PRE-rotation] for each participant (in black) and mean perceived reachable limit (in*
 484 *grey).*

486 3.2.2. Response time

487 An ANOVA with repeated measures on RT (mean for the Near zone = 708 ± 176 ms; mean
 488 Boundary = 917 ± 286 ms; mean Far = 824 ± 225 ms) confirmed the significant effect of Target
 489 zone ($F_{(2, 26)} = 11.28$; $p < 0.001$; $\eta^2 = 0.465$) but did not show a significant effect of Condition
 490 ($F_{(1, 13)} = 2.1$; $p = 0.12$; $\eta^2 = 0.172$) or interaction ($F_{(2, 26)} = 0.119$; $p = 0.89$; $\eta^2 = 0.009$). Post-

491 hoc analysis of the Target zone effect showed that RTs for targets in the Near zone were
492 significantly lower than for those in the Boundary zone ($p < 0.001$). Figure 7 illustrates the
493 finding that response time (RT) was greater for targets at the boundary of reachable space.

494



495

496 *Figure 7. Mean response time for three different sets of targets in the reachability judgment*
497 *task across both conditions of rotation. The three zones (Near, Boundary and Far)*
498 *corresponded to the 3 most reachable (closest) targets, 3 targets around the boundary of*
499 *reachable space and the 3 least reachable (farthest) targets, respectively. Vertical bars*
500 *represent the standard deviation of the mean. Statistically significant differences between zones*
501 *were tested using Tukey's HSD post-hoc test (***: $p < 0.001$).*

502

503 3.3. Correlation analyses

504 We performed correlation analyses (Pearson's correlation coefficient) to test the link
505 between the shift in peripersonal space representation (Δ PSE) and movement parameters in
506 the POST-initial trial which reflect sensorimotor adaptation. Results showed no significant

507 correlation between Δ PSE and initial direction ($r = 0.50$; $p = 0.07$), maximal perpendicular
508 deviation ($r = 0.47$; $p = 0.09$) and endpoint error ($r = 0.48$; $p = 0.08$).

509 In summary, the present study suggests that the estimated boundary of reachable space is
510 shifted as the result of sensori-motor adaptation to a novel force field. However, the possibility
511 that the change in peripersonal space perception observed here could also be due to the
512 movement repetition itself (Verstynen & Sabes, 2010; Marinovic et al., 2017; Mawase et al.,
513 2017) and/or to the platform rotation (Pfeiffer et al., 2018), rather than to sensori-motor
514 adaptation, cannot be ruled out. To test our hypothesis on the role of sensori-motor adaptation,
515 we separately investigated the effect of movement repetition and platform rotation, without
516 sensori-motor adaptation. Based on the results from the main experiment, we conducted a
517 post-hoc power analysis (paired-samples t test, effect-size = 1.07, $\alpha = .05$, two-tailed)
518 indicating a minimum of 9 participants to reach a power of 0.8. 10 participants were thus
519 enrolled for each of the following control experiments.

520

521 **Control experiment 1**

522 To assess whether the observed change in peripersonal space could be due to the nature of
523 the manual reaching task itself (rather than to sensori-motor adaptation), a control experiment
524 was run using the same experimental setup and the same protocol as in the main experiment
525 but without platform rotation.

526 Ten new healthy participants (4 females and 6 males, age = 23.7 ± 2.7 years) took part in
527 this experiment. They gave their prior informed consent in accordance with the ethical
528 standards set out in the 1964 Declaration of Helsinki. All participants were self-declared right-
529 handed and had normal or corrected-to-normal vision. No significant difference in reachability
530 judgments ($t(9) = 1.83$; $p = 0.1$) was found between PRE- (mean PSE = 18 ± 78 mm) and
531 POST-tests (mean PSE = -3 ± 82 mm). No significant difference was found between
532 discrimination thresholds in PRE- and POST-tests (mean = 85 ± 23 mm; $t(8) = 0.18$; $p = 0.86$).
533 These results support the hypothesis that neither the boundary of estimated reachable space
534 nor the precision of this judgment were affected by the movement repetition in the main
535 experiment.

536 RTs were also analysed for the three zones, using the same methods as in the main
537 experiment. A 2x3 ANOVA with repeated measures (2 Conditions: PRE-, POST-rotation x 3
538 Target zones: Near, Boundary, Far) showed the significance of the effect of Target zone on
539 RT ($F(2, 18) = 6.93$; $p = 0.006$; $\eta^2 = 0.052$) but there was no significant effect of Condition
540 (mean PRE-rotation = 389 ± 142 ms; mean POST-rotation = 335 ± 122 ms) ($F(2, 18) = 1.98$;
541 $p = 0.19$; $\eta^2 = 0.243$) and no significant interaction between Target zone and Condition ($F(2,$
542 $18) = 1.49$; $p = 0.25$; $\eta^2 = 0.076$). RT varied according to whether targets were in the Near
543 (mean = 318 ± 115 ms), Boundary (424 ± 163 ms) or the Far zone (374 ± 149 ms) but post-
544 hoc analysis only showed that RT for the Near zone was lower than for the Boundary zone (p
545 = 0.004).

546 Overall, the results of the first control experiment indicated that when reaching arm
547 movements were repeated in the absence of platform rotation, there was no significant change
548 in reachability estimates (see also Bourgeois & Coello 2012). In the second control
549 experiment, new participants underwent the same experiment but without manual reaching
550 during the rotation, to assess the effect of platform rotation without adaptation on reachability
551 judgments.

552

553 **Control experiment 2**

554 Ten new healthy participants (3 females and 7 males, mean age = 20.9 ± 2.4 years) took
555 part in this experiment. They gave their prior informed consent in accordance with the ethical
556 standards set out in the 1964 Declaration of Helsinki. All participants were self-declared right-
557 handed and had normal or corrected-to-normal vision. The participants were required to
558 perform the reachability judgment task (identical to experiment 1) before (PRE-rotation),
559 during (PER-rotation) and after (POST-rotation) platform rotation, but without any manual
560 reaching. A one-way analysis of variance with repeated measures was used to compare the
561 perceived boundary of reachable space and the discrimination threshold in the PRE- (mean
562 PSE = 36 ± 60 mm), PER- (mean PSE = 12 ± 75 mm) and POST-rotation (mean PSE = $32 \pm$
563 71 mm) conditions.

564 No significant effect of the rotation on perceived boundary of reachable space (mean PSE
565 = 27 ± 67 mm) was found ($F(2, 18) = 2.54$; $p = 0.11$; $\eta^2 = 0.22$). In addition, analysis of the
566 discrimination threshold (85 ± 23 mm) showed no significant effect of the rotation ($F(2, 18)$
567 = 0.191 ; $p = 0.83$; $\eta^2 = 0.021$).

568 RTs were also analysed. A 3x3 ANOVA with repeated measures (3 Conditions: PRE-,
569 PER-, POST-rotation x 3 Target zones: Near, Boundary, Far) on response time showed an
570 effect of Target zone ($F(2, 18) = 7.53$; $p = 0.004$; $\eta^2 = 0.455$) but not of Condition ($F(2, 18) =$

571 3.36; $p = 0.057$) and no significant interaction ($F_{(2, 18)} = 0.83$; $p = 0.52$; $\eta^2 = 0.084$). RT varied
572 according to whether participants judged targets to be the most reachable (Near zone: mean
573 $RT = 491 \pm 192$ ms) around the boundary of reachable space (Boundary zone: 781 ± 326 ms)
574 or the least reachable (Far zone: 599 ± 216 ms). However, post hoc analysis only pinpointed
575 a lower RT for the Near zone than for the Boundary zone ($p = 0.003$). Overall, the results of
576 the second control experiment indicate that when movements were not performed during
577 platform rotation, i.e. in the absence of sensori-motor adaptation, there was no significant
578 change in reachability estimates.

579

580 Thus, the two control experiments show that neither the boundary of reachable space nor
581 the accuracy of reachability judgment was significantly affected by the rotation of the platform
582 or the repetition of 60 reaching movements. This is consistent with the hypothesis that the
583 shift in boundary of reachable space observed in the main experiment was related to sensori-
584 motor adaptation, and not merely due to the rotation of the platform.

585 4. Discussion

586 The aim of the present study was to investigate whether sensori-motor adaptation to a
587 change in limb dynamics alters the representation of peripersonal space, as in the case of
588 geometrical changes due to tool use (for a review see: Làdavas & Serino, 2008; Cléry et al.
589 2015; di Pellegrino & Làdavas, 2015). By assessing perception of peripersonal space before
590 and after force-field adaptation, we found that peripersonal space was systematically
591 perceived as being closer to the body after sensori-motor adaptation.

592

593 4.1. *Confirmation of sensori-motor adaptation: a prerequisite*

594 A rotating platform can be used to study sensori-motor adaptation to a perturbed force field
595 (Lackner & DiZio, 1994; Coello et al., 1996; DiZio & Lackner, 2000; Sarlegna et al., 2010;
596 Lefumat et al., 2015). In our study, participants had to deal with the Coriolis force acting on
597 their active, unconstrained arm during the rotation. Participants exhibited the classic pattern
598 of motor response to this kind of novel dynamics: deviation of the movement trajectory during
599 the first PER-rotation trials in the direction of the perturbation, followed by a rapid recovery
600 of unperturbed kinematic performance, i.e. reaching straight ahead towards the target.
601 Moreover, once the rotation has stopped, the trajectories were deviated in the opposite
602 direction from the perturbation, which is typical of the after-effects of sensori-motor
603 adaptation. This was systematically observed for each participant. Moreover the after-effect
604 was statistically significant when analysing endpoint error, initial movement direction and
605 maximum perpendicular deviation. These are clear markers of sensorimotor adaptation, which
606 is classically considered as arising from an updating of the arm's internal model to take
607 account of new limb dynamics (Ghez & Sainburg, 1995; Ostry et al., 2010; Shadmehr, 2017).
608 It is noteworthy that the period between the first modification in limb dynamics at the very
609 beginning of the rotation and the first movement after the rotation stop lasted about ten

610 minutes. We were thus able to investigate whether this sensori-motor adaptation had an effect
611 on peripersonal space representation by comparing judgments before and after the adaptation
612 phase.

613

614 4.2. *Reproduction of reachability judgment task features*

615 Perception of peripersonal space was investigated through a widely used reachability
616 judgment task (Grade et al., 2015; Bartolo et al., 2018; Cartaud et al., 2018). However, we
617 slightly modified this perceptive task to match the direction of the force-field perturbation
618 (Coriolis force applied orthogonally to the main direction of movement). Our participants had
619 thus to judge the reachability of targets aligned in the frontal plane (rather than in the more
620 commonly used sagittal plane) and in their right hemisphere (rather than aligned with the
621 cyclopean eye). We made these modifications to assess the hypothesised lateral effect of
622 sensori-motor adaptation, while verifying that the task was feasible in such a configuration
623 with subjects and platform still. Interestingly, our results share numerous characteristics with
624 the results generally observed in the literature. For example, participants overestimated their
625 reachable limit, as frequently reported for reachability judgment tasks (Carello et al., 1989;
626 Rochat & Wraga, 1997; Gabbard et al. 2007; Bourgeois & Coello, 2014; Coello et al., 2012;
627 Wamain et al., 2016; Gouzien et al., 2017). Another important common feature concerned the
628 increase in response time around the boundary of reachability compared to the nearest targets.
629 Several studies have reported the same results (Valdès-Conroy et al. 2012; Bourgeois &
630 Coello, 2012; Bartolo et al., 2014; Grade et al., 2015; Wamain et al., 2016), which could be
631 due to participants experiencing difficulty responding around the more uncertain reachable
632 space boundary.

633 Specifically for the Near and Far zones, where judgment can be assumed to be less
634 uncertain, response time tended to be lower for the close, most reachable targets than for the

635 far, less reachable targets. While this was not statistically significant, this is consistent with
636 psychophysics findings which usually show a longer response time for a negative answer ('Not
637 reachable' in our study) than for a positive one (Coltheart et al., 2001; Brouillet et al., 2010).
638 However, in our experimental design, the eccentric peripheral position of the more distant
639 targets may also have induced higher latency in detecting them (Fuler, 1996; Gruber et al.,
640 2014; Bartolo et al., 2017). Given that studies using reachability judgment tasks in the sagittal
641 plan did not show a difference in response time between the nearest and the farthest targets
642 (Bourgeois & Coello, 2014; Coello et al., 2012), the differences here are likely due to the
643 varying target eccentricity in our experimental protocol. Overall, our results are consistent
644 with the literature and therefore support the reliability of our method to assess reachability
645 judgments.

646

647 4.3. *Sensori-motor adaptation and reachability judgment are linked*

648 The core concern of this study was to examine the relationships between sensori-motor
649 adaptation to changes in limb dynamics and peripersonal space representation. Our results
650 strongly suggest that the perceived boundary of reachable space, used as proxy for the
651 representation of peripersonal space, systematically moved towards the body after sensori-
652 motor adaptation. In other words, participants perceived the boundary of their peripersonal
653 space as being closer after sensori-motor adaptation compared to before. Whereas plasticity
654 of peripersonal space has previously been shown to depend on the geometrical properties of
655 the body-environment relationship, which change when using a tool (Maravita & Iriki, 2004;
656 Witt et al., 2005; Cardinali et al., 2009; Martel et al., 2016) or when artificially modifying
657 current visuomotor calibration (Bourgeois & Coello, 2012), our study is the first to indicate
658 that the representation of limb dynamics may play a major role in the representation of the
659 peripersonal space.

660 We did not find any significant correlation between the shift in the perception of
661 reachability and motor behavior measures of force-field adaptation. We considered that the
662 systematic effect we observed on peripersonal space representation could have two
663 explanations other than an influence of the new force field, hence the new limb dynamics.
664 Firstly, our main experimental procedure involved rotating the platform, which could have
665 been sufficient to influence perception of the surrounding space. Indeed, the vestibular
666 stimulation induced by whole-body rotation can have an effect on peripersonal space
667 representation, as shown in particular for the peri-head space (Pfeiffer et al., 2018). Our
668 control experiment, however, dismisses this possible interpretation, showing that the platform
669 rotation alone does not induce any significant effect on reachability judgments, in contrast to
670 the main experiment. The absence of significant effect may not be surprising given that
671 participants performed the reachability judgment tasks either without rotation or when the
672 platform's angular velocity was constant. During rotation at constant velocity, vestibular semi-
673 circular canals remain in a resting state (Goldberg & Fernandez, 1971) and thus do not appear
674 to modulate the representation of peripersonal space. Secondly, the repetition of the
675 movements during the sensori-motor adaptation phase might have had an effect. Participants
676 had to perform several manual reaching movements during rotation in order to adapt.
677 However, another control experiment enabled us to exclude the possibility that reaching
678 movement repetition influences peripersonal space representation. Both control experiments
679 proved essential to our conclusions on the effect of sensori-motor adaptation to a new force
680 field on the representation of peripersonal space. Furthermore, throughout our experiments,
681 the discrimination threshold related to the accuracy of reachability judgments in the perceptual
682 task did not differ before and after sensori-motor adaptation, indicating that the observed effect
683 cannot be explained by a different (lesser or greater) difficulty of the reachability judgment
684 task after the adaptation stage.

685

686 One question remains: was the observed effect of sensori-motor adaptation specifically
687 anchored to peripersonal space or more generally related to a modification of the space
688 representation? In other words, perception could be shifted after the experience of the force
689 field such that the whole external space underwent an overall rotation, indirectly leading to a
690 shift in the peripersonal space representation. Although our study did not settle this question,
691 a recent study by Michel et al. (2018) investigated the relationship between adaptation to new
692 limb dynamics and space perception. In their study, participants had to perform a perceptual
693 task before and after adaptation to a velocity-dependent perturbation generated by a robotic
694 device. Unlike the reachability judgement task, their perceptive task (line bisection) likely did
695 not imply action simulation. Their results did not show any significant difference between
696 participants' performances in the two line bisection tasks. In the light of our results, adaptation
697 to new limb dynamics may thus have a specific effect on peripersonal space representation, as
698 a space directly related to our motor experience, but does not appear to influence the line
699 bisection task.

700 Bufacchi & Iannetti (2018) recently conceptualized the peripersonal space as a functional
701 space around the body whose measures can “reflect the relevance of potential actions that aim
702 to either create or avoid contact between a stimulus and a body part”. In agreement with the
703 interactive view of Cisek and Kalaska (2010), Bufacchi & Iannetti (2018) refer to the
704 importance of the prediction of potential actions consequences to act appropriately in the
705 peripersonal space. Such predictions which are updated during sensori-motor adaptation may
706 be the key factor leading to the modification of peripersonal space representation.

707 4.4. *Somatosensory modifications may contribute to perceived peripersonal space*
708 *changes*

709 In our study, reaching movement kinematics before and at the end of the sensori-motor
710 adaptation phase, i.e. preceding each reachability judgement task, shared the same features.
711 This means that the trajectories of reaching movements after sensori-motor adaptation were
712 strictly comparable under force-field perturbation and under a normal gravity force field. As
713 previously discussed, sensori-motor adaptation to novel limb dynamics can be explained by
714 an update of the arm's internal models (Ghez & Sainburg, 1995; Shadmehr et al., 2010).
715 Reaching a visual target requires the sensori-motor system to map the limb's desired motion
716 with the predicted acting forces. If these forces change, as during platform rotation, motor
717 commands and expected sensory consequences are modified so as to adapt to the new
718 properties of the environment (Shadmehr & Mussa-Ivaldi, 1994). Representing peripersonal
719 space and its boundaries does not require an actual motor command to be performed but after
720 sensori-motor adaptation to novel limb dynamics, the predicted sensory consequences of the
721 reaching movement are modified, and this modification may have induced a change in
722 peripersonal space representation. The after-effects observed in movement trajectories once
723 the rotation stopped suggest that the internal model was no longer appropriate to the novel
724 force-field environment (namely, the normal force field) and we eventually observed similar
725 modifications of motor performance and perception in the peripersonal space.

726 An alternative explanation may be rooted in the influence of sensori-motor adaptation on
727 the spatial representation of the limb. Studies have shown that the arm reaching adaptation to
728 a perturbed force field can lead to modifications in the somatosensory perception of the
729 adapted limb's location in space (Ostry & Gribble, 2016). Ostry et al. (2010) studied the effect
730 of exposure to a force field generated by a robotic device on the active hand's position. Their
731 results showed that after sensori-motor adaptation to novel limb dynamics, perception of the

732 altered limb position is changed in the opposite direction of the perturbation. In our study,
733 modifications of peripersonal space perception after the sensori-motor adaptation to novel
734 limb dynamics could also arise from the modified felt position of the participant's right hand.
735 In line with this idea, Fischer (2000) showed that reachable judgement is linked to the body
736 configuration. We thus could speculate that a modified arm's localization (concurrently with
737 sensori-motor adaptation) could have an effect on peripersonal space perception. It would be
738 interesting to further study this issue and measure the perceived arm's position before and
739 after exposure to a novel force field created by means of a platform rotation.

740 Besides the representation of arm's position, an interesting approach to probe the
741 representation of the arm's length is to analyse kinematic parameters of movement before and
742 after the sensori-motor adaptation phase (Cardinali et al., 2009). In the present study, peak
743 velocity, peak acceleration and peak deceleration did not significantly differ between reaching
744 movements in PRE- and POST-tests. Subtle changes in movement time were found, but they
745 likely reflect the additional time that was necessary to correct for the substantial movement
746 errors in the initial trials of PER- and POST-rotation. Overall, our findings may suggest that
747 the body schema, or the representation of arm length, was not modified by the change in limb
748 dynamics. Other paradigms such as tool-use directly modify the length of the segment used to
749 act on the environment: this methodological difference may explain the difference between
750 our results and those of Cardinali et al. (2009) for instance.

751 It would be interesting in future studies to assess whether the effect reported on peripersonal
752 space representation can be generalised to different target directions, and to investigate any
753 relationships between this effect and the reference systems used by the organism to interact
754 with the environment (Dupierrix et al., 2009; Herlihey et al., 2013).

755

756

757 **5. Conclusion**

758 The present study provided the first demonstration that sensori-motor adaptation to altered
759 limb dynamics leads to a modification of the representation of peripersonal space. Overall,
760 our findings are consistent with the idea that force-field adaptation does not only influence
761 sensori-motor mechanisms, but can also affect the perception and possibly the representational
762 level of peripersonal space. This insight should prove valuable for future studies exploring
763 sensori-motor plasticity and its potential consequences on cognitive processes. A way to
764 further investigate the nature of the effect of sensori-motor adaptation on the representation of
765 peripersonal space would be to perform new experiments with a clockwise rotation of the
766 platform (opposite to the rotation used in our study) or with reachability targets in the opposite
767 hemispace. An inverse effect on peripersonal space (rightward shift) would strengthen the
768 hypothesis of a specific link between sensori-motor adaptation to novel dynamics and
769 peripersonal space representation. In a wider perspective, the influence of the sensori-motor
770 adaptation to novel limb dynamics on space perception and categorization may be important
771 to understand how to accurately perform and coordinate movements in microgravity. In
772 spaceflight for example, alterations of spatial representation could be crippling for crew safety
773 and mission success in addition to other critical alterations of oculomotor control, eye-hand
774 coordination, spatial orientation, and time perception (Clement, 2018).

775 **Acknowledgements**

776 The authors wish to thank Hannah Lefumat for developing the script on which we based
777 our kinematic analyses, Alain Donneaud for technical development, Frank Buloup for
778 software development and technological expertise and Marjorie Sweetko for correcting and
779 improving the English in the manuscript. This work was supported by the AUTON program
780 of the CNRS.

781 **Reference list**

- 782 Aimola, L., Schindler, I., Simone, A.M., Venneri, A., 2012. Near and far space neglect: Task
783 sensitivity and anatomical substrates. *Neuropsychologia* 50, 1115–1123.
784 <https://doi.org/10.1016/j.neuropsychologia.2012.01.022>
- 785 *Ambrosini, E., Costantini, M., 2013. Handles lost in non-reachable space. Exp Brain Res* 229,
786 197–202. <https://doi.org/10.1007/s00221-013-3607-0>
- 787 Babiloni, C., Carducci, F., Cincotti, F., Rossini, P.M., Neuper, C., Pfurtscheller, G., Babiloni, F.,
788 1999. Human Movement-Related Potentials vs Desynchronization of EEG Alpha Rhythm: A
789 High-Resolution EEG Study. *NeuroImage* 10, 658–665.
790 <https://doi.org/10.1006/nimg.1999.0504>
- 791 Bartolo, A., Coello, Y., Edwards, M.G., Delepouille, S., Endo, S., Wing, A.M., 2014.
792 Contribution of the motor system to the perception of reachable space: an fMRI study. *European*
793 *Journal of Neuroscience* 40, 3807–3817. <https://doi.org/10.1111/ejn.12742>
- 794 Bartolo, A., Rossetti, Y., Revol, P., Urquizar, C., Pisella, L., Coello, Y., 2018. Reachability
795 judgement in optic ataxia: Effect of peripheral vision on hand and target perception in depth.
796 *Cortex* 98, 102–113. <https://doi.org/10.1016/j.cortex.2017.05.013>
- 797 Berti, A., Frassinetti, F., 2000. When far becomes near: Remapping of space by tool use. *Journal*
798 *of cognitive neuroscience* 12, 415–420. <https://doi.org/10.1162/089892900562237>
- 799 Bourdin, C., Bringoux, L., Gauthier, G.M., Vercher, J.L., 2006. Vision of the hand prior to
800 movement onset allows full motor adaptation to a multi-force environment. *Brain Research*
801 *Bulletin* 71, 101–110. <https://doi.org/10.1016/j.brainresbull.2006.08.007>
- 802 Bourdin, C., Gauthier, G., Blouin, J., Vercher, J.-L., 2001. Visual feedback of the moving arm
803 allows complete adaptation of pointing movements to centrifugal and Coriolis forces in human
804 subjects. *Neuroscience letters* 301, 25–28. [https://doi.org/10.1016/S0304-3940\(01\)01584-1](https://doi.org/10.1016/S0304-3940(01)01584-1)
- 805 Bourgeois, J., Coello, Y., 2012. Effect of visuomotor calibration and uncertainty on the
806 perception of peripersonal space. *Attention, Perception, & Psychophysics* 74, 1268–1283.
807 <https://doi.org/10.3758/s13414-012-0316-x>
- 808 Bourgeois, J., Farnè, A., Coello, Y., 2014. Costs and benefits of tool-use on the perception of
809 reachable space. *Acta Psychol (Amst)* 148, 91–95. <https://doi.org/10.1016/j.actpsy.2014.01.008>
- 810 Brown, L.E., Wilson, E.T., Goodale, M.A., Gribble, P.L., 2007. Motor Force Field Learning
811 Influences Visual Processing of Target Motion. *Journal of Neuroscience* 27, 9975–9983.
812 <https://doi.org/10.1523/JNEUROSCI.1245-07.2007>
- 813 Brozzoli, C., Cardinali, L., Pavani, F., Farnè, A., 2010. Action-specific remapping of
814 peripersonal space. *Neuropsychologia, The Sense of Body* 48, 796–802.
815 <https://doi.org/10.1016/j.neuropsychologia.2009.10.009>
- 816 Bufacchi, R.J., Iannetti, G.D., 2018. An Action Field Theory of Peripersonal Space. *Trends in*
817 *Cognitive Sciences* 22, 1076–1090. <https://doi.org/10.1016/j.tics.2018.09.004>
- 818 Bursztyn, L.L.C.D., Ganesh, G., Imamizu, H., Kawato, M., Flanagan, J.R., 2006. Neural
819 Correlates of Internal-Model Loading. *Current Biology* 16, 2440–2445.
820 <https://doi.org/10.1016/j.cub.2006.10.051>
- 821 Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., Casile, A., 2009. Mirror neurons differentially
822 encode the peripersonal and extrapersonal space of monkeys. *Science* 324, 403–406.
823 <https://doi.org/10.1126/science.1166818>
- 824 Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use
825 reshapes the boundaries of body and peripersonal space representations. *Exp Brain Res* 228,
826 25–42. <https://doi.org/10.1007/s00221-013-3532-2>
- 827 Cardellicchio, P., Sinigaglia, C., Costantini, M., 2011. The space of affordances: A TMS study.
828 *Neuropsychologia* 49, 1369–1372. <https://doi.org/10.1016/j.neuropsychologia.2011.01.021>

829 Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009. Tool-use
830 induces morphological updating of the body schema. *Current Biology* 19, R478–R479.
831 <https://doi.org/10.1016/j.cub.2009.05.009>

832 Carello, C., Groszofsky, A., Reichel, F.D., Solomon, H.Y., Turvey, M.T., 1989. Visually
833 Perceiving What is Reachable. *Ecological Psychology* 1, 27–54.
834 https://doi.org/10.1207/s15326969eco0101_3

835 Cartaud, A., Ruggiero, G., Ott, L., Iachini, T., Coello, Y., 2018. Physiological Response to Facial
836 Expressions in Peripersonal Space Determines Interpersonal Distance in a Social Interaction
837 Context. *Front. Psychol.* 9. <https://doi.org/10.3389/fpsyg.2018.00657>

838 Chao, L.L., Martin, A., 2000. Representation of Manipulable Man-Made Objects in the Dorsal
839 Stream. *NeuroImage* 12, 478–484. <https://doi.org/10.1006/nimg.2000.0635>

840 Chao, L.L., Weisberg, J., Martin, A., 2002. Experience-dependent modulation of category-
841 related cortical activity. *Cereb. Cortex* 12, 545–551. <https://doi.org/10.1093/cercor/12.5.545>

842 Cisek, P., Kalaska, J.F., 2010. Neural mechanisms for interacting with a world full of action
843 choices. *Annu. Rev. Neurosci.* 33, 269–298.
844 <https://doi.org/10.1146/annurev.neuro.051508.135409>

845 Clément, G., 2018. Perception of time in microgravity and hypergravity during parabolic flight.
846 *NeuroReport* 29, 247. <https://doi.org/10.1097/WNR.0000000000000923>

847 Cléry, J., Guipponi, O., Wardak, C., Ben Hamed, S., 2015. Neuronal bases of peripersonal and
848 extrapersonal spaces, their plasticity and their dynamics: Knowns and unknowns.
849 *Neuropsychologia* 70, 313–326. <https://doi.org/10.1016/j.neuropsychologia.2014.10.022>

850 Cochin, S., Barthelemy, C., Roux, S., Martineau, J., 1999. Observation and execution of
851 movement: similarities demonstrated by quantified electroencephalography. *Eur. J. Neurosci.*
852 11, 1839–1842. <https://doi.org/10.1046/j.1460-9568.1999.00598.x>

853 Coello, Y., Bartolo, A., Amiri, B., Devanne, H., Houdayer, E., Derambure, P., 2008. Perceiving
854 what is reachable depends on motor representations: evidence from a Transcranial Magnetic
855 Stimulation study. *PLoS ONE* 3, e2862. <https://doi.org/10.1371/journal.pone.0002862>

856 Coello, Y., Bourgeois, J., Iachini, T., 2012. Embodied perception of reachable space: how do we
857 manage threatening objects? *Cognitive Processing* 13, 131–135.
858 <https://doi.org/10.1007/s10339-012-0470-z>

859 Coello, Y., Orliaguet, J.P., Prablanc, C., 1996. Pointing movement in an artificial perturbing
860 inertial field: A prospective paradigm for motor control study. *Neuropsychologia* 34, 879–892.
861 [https://doi.org/10.1016/0028-3932\(96\)00003-6](https://doi.org/10.1016/0028-3932(96)00003-6)

862 Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., Committeri, G., 2010. Where does an
863 object trigger an action? An investigation about affordances in space. *Exp Brain Res* 207, 95–
864 103. <https://doi.org/10.1007/s00221-010-2435-8>

865 Creem-Regehr, S.H., Lee, J.N., 2005. Neural representations of graspable objects: are tools
866 special? *Brain Res Cogn Brain Res* 22, 457–469.
867 <https://doi.org/10.1016/j.cogbrainres.2004.10.006>

868 Cullen, K.E., Brooks, J.X., 2015. Neural Correlates of sensory prediction errors in monkeys:
869 Evidence for internal models of voluntary self-motion in the cerebellum. *Cerebellum* 14, 31–
870 34. <https://doi.org/10.1007/s12311-014-0608-x>

871 de Vignemont, F., 2010. Body schema and body image—Pros and cons. *Neuropsychologia* 48,
872 669–680. <https://doi.org/10.1016/j.neuropsychologia.2009.09.022>

873 de Vignemont, F., Iannetti, G.D., 2014. How many peripersonal spaces? *Neuropsychologia* 70.
874 <https://doi.org/10.1016/j.neuropsychologia.2014.11.018>

875 di Pellegrino, G., Làdavas, E., 2015. Peripersonal space in the brain. *Neuropsychologia* 66, 126–
876 133. <https://doi.org/10.1016/j.neuropsychologia.2014.11.011>

877 di Pellegrino, G., Làdavas, E., Farnè, A., 1997. Seeing where your hands are. *Nature* 388, 730.
878 <https://doi.org/10.1038/41921>

879 DiZio, P., Lackner, J.R., 2000. Congenitally blind individuals rapidly adapt to coriolis force
880 perturbations of their reaching movements. *J. Neurophysiol.* 84, 2175–2180.
881 <https://doi.org/10.1152/jn.2000.84.4.2175>

882 Donchin, O., Rabe, K., Diedrichsen, J., Lally, N., Schoch, B., Gizewski, E.R., Timmann, D.,
883 2012. Cerebellar regions involved in adaptation to force field and visuomotor perturbation.
884 *Journal of Neurophysiology* 107, 134–147. <https://doi.org/10.1152/jn.00007.2011>

885 Dupierriex, E., Gresty, M., Ohlmann, T., Chokron, S., 2009. Long Lasting Egocentric
886 Disorientation Induced by Normal Sensori-Motor Spatial Interaction. *PLOS ONE* 4, e4465.
887 <https://doi.org/10.1371/journal.pone.0004465>

888 Fischer, M.H., 2000. Estimating reachability: Whole body engagement or postural stability?
889 *Human movement science* 19, 297–318. [https://doi.org/10.1016/S0167-9457\(00\)00016-6](https://doi.org/10.1016/S0167-9457(00)00016-6)

890 Fuller, J.H., 1996. Eye position and target amplitude effects on human visual saccadic latencies.
891 *Exp Brain Res* 109, 457–466. <https://doi.org/10.1007/BF00229630>

892 Gabbard, C., Cordova, A., Lee, S., 2007. Examining the effects of postural constraints on
893 estimating reach. *Journal of Motor Behavior* 39, 242–246.
894 <https://doi.org/10.3200/JMBR.39.4.242-246>

895 Gallivan, J.P., Cavina-Pratesi, C., Culham, J.C., 2009. Is That within Reach? fMRI Reveals That
896 the Human Superior Parieto-Occipital Cortex Encodes Objects Reachable by the Hand. *Journal*
897 *of Neuroscience* 29, 4381–4391. <https://doi.org/10.1523/JNEUROSCI.0377-09.2009>

898 Gallivan, J.P., McLean, A., Culham, J.C., 2011. Neuroimaging reveals enhanced activation in a
899 reach-selective brain area for objects located within participants' typical hand workspaces.
900 *Neuropsychologia* 49, 3710–3721. <https://doi.org/10.1016/j.neuropsychologia.2011.09.027>

901 Ghez, C., Sainburg, R., 1995. Proprioceptive control of interjoint coordination. *Canadian Journal*
902 *of Physiology and Pharmacology* 73, 273–284. <https://doi.org/10.1139/y95-038>

903 Goldberg, J.M., Fernandez, C., 1971. Physiology of peripheral neurons innervating semicircular
904 canals of the squirrel monkey. I. Resting discharge and response to constant angular
905 accelerations. *Journal of Neurophysiology* 34, 635–660.
906 <https://doi.org/10.1152/jn.1971.34.4.635>

907 Gouzien, A., Vignemont, F. de, Touillet, A., Martinet, N., Graaf, J.D., Jarrassé, N., Roby-Brami,
908 A., 2017. Reachability and the sense of embodiment in amputees using prostheses. *Scientific*
909 *Reports* 7, 4999. <https://doi.org/10.1038/s41598-017-05094-6>

910 Grade, S., Pesenti, M., Edwards, M.G., 2015. Evidence for the embodiment of space perception:
911 concurrent hand but not arm action moderates reachability and egocentric distance perception.
912 *Frontiers in Psychology* 6. <https://doi.org/10.3389/fpsyg.2015.00862>

913 Grafton, S.T., Fadiga, L., Arbib, M.A., Rizzolatti, G., 1997. Premotor Cortex Activation during
914 Observation and Naming of Familiar Tools. *NeuroImage* 6, 231–236.
915 <https://doi.org/10.1006/nimg.1997.0293>

916 Graziano, M.S., Gandhi, S., 2000. Location of the polysensory zone in the precentral gyrus of
917 anesthetized monkeys. *Exp Brain Res* 135, 259–266. <https://doi.org/10.1007/s002210000518>

918 Gruber, N., Müri, R.M., Mosimann, U.P., Bieri, R., Aeschimann, A., Zito, G.A., Urwyler, P.,
919 Nyffeler, T., Nef, T., 2014. Effects of age and eccentricity on visual target detection. *Front*
920 *Aging Neurosci* 5, 101. <https://doi.org/10.3389/fnagi.2013.00101>

921 Haggard, P., M. Wolpert, D., 2005. Disorders of Body Scheme. In J. Freund, M. Jeannerod, M.
922 Hallett, R. Leiguarda (Eds.), *High-Order Motor Disorders: From Neuroanatomy and*
923 *Neurobiology to Clinical Neurology*. Oxford: Oxford University Press, pp. 261–271.

924 Haith, A., Vijayakumar, S., 2009. Implications of different classes of sensorimotor disturbance
925 for cerebellar-based motor learning models. *Biol Cybern* 100, 81–95.
926 <https://doi.org/10.1007/s00422-008-0266-5>

927 Herlihey, T.A., Black, S.E., Ferber, S., 2013. Action modulated cognition: the influence of
928 sensori-motor experience on the global processing bias. *Neuropsychologia* 51, 1973–1979.
929 <https://doi.org/10.1016/j.neuropsychologia.2013.06.014>

930 Hommel, B., Pratt, J., Colzato, L., Godijn, R., 2001. Symbolic control of visual attention. *Psychol*
931 *Sci* 12, 360–365. <https://doi.org/10.1111/1467-9280.00367>

932 Iachini, T., Coello, Y., 2016. Embodied perception of objects and people in space: Towards a
933 unified theoretical framework. In Y. Coello, & M. Fischer (Eds.), *Foundations of embodied*
934 *cognition* (pp. 198-219). New York: Psychology Press. pp. 198–219.

935 Iachini, T., Ruggiero, G., Ruotolo, F., Vinciguerra, M., 2014. Motor resources in peripersonal
936 space are intrinsic to spatial encoding: Evidence from motor interference. *Acta Psychologica*
937 153, 20–27. <https://doi.org/10.1016/j.actpsy.2014.09.001>

938 Kan, I.P., Kable, J.W., Van Scoyoc, A., Chatterjee, A., Thompson-Schill, S.L., 2006.
939 Fractionating the left frontal response to tools: Dissociable effects of motor experience and
940 lexical competition. *J. Cogn. Neurosci.* 18, 267–277.
941 <https://doi.org/10.1162/jocn.2006.18.2.267>

942 Kawato, M., 1999. Internal models for motor control and trajectory planning. *Current Opinion*
943 *in Neurobiology* 9, 718–727. [https://doi.org/10.1016/S0959-4388\(99\)00028-8](https://doi.org/10.1016/S0959-4388(99)00028-8)

944 Lackner, J.R., Dizio, P., 1994. Rapid adaptation to Coriolis force perturbations of arm trajectory.
945 *J. Neurophysiol.* 72, 299–313. <https://doi.org/10.1152/jn.1994.72.1.299>

946 Làdavas, E., Serino, A., 2008. Action-dependent plasticity in peripersonal space representations.
947 *Cognitive Neuropsychology* 25, 1099–1113. <https://doi.org/10.1080/02643290802359113>

948 Lefumat, H.Z., Vercher, J.-L., Miall, R.C., Cole, J., Buloup, F., Bringoux, L., Bourdin, C.,
949 Sarlegna, F.R., 2015. To transfer or not to transfer? Kinematics and laterality quotient predict
950 interlimb transfer of motor learning. *Journal of Neurophysiology* jn.00749.2015.
951 <https://doi.org/10.1152/jn.00749.2015>

952 Llanos, C., Rodriguez, M., Rodriguez-Sabate, C., Morales, I., Sabate, M., 2013. Mu-rhythm
953 changes during the planning of motor and motor imagery actions. *Neuropsychologia* 51, 1019–
954 1026. <https://doi.org/10.1016/j.neuropsychologia.2013.02.008>

955 Makin, T.R., Holmes, N.P., Ehrsson, H.H., 2008. On the other hand: Dummy hands and
956 peripersonal space. *Behavioural Brain Research* 191, 1–10.
957 <https://doi.org/10.1016/j.bbr.2008.02.041>

958 Maravita, A., Iriki, A., 2004. Tools for the body (schema). *Trends Cogn. Sci. (Regul. Ed.)* 8, 79–
959 86. <https://doi.org/10.1016/j.tics.2003.12.008>

960 Marinovic, W., Poh, E., de Rugy, A., Carroll, T.J., n.d. Action history influences subsequent
961 movement via two distinct processes. *eLife* 6. <https://doi.org/10.7554/eLife.26713>

962 Mark, L.S., Nemeth, K., Gardner, D., Dainoff, M.J., Paasche, J., Duffy, M., Grandt, K., 1997.
963 Postural dynamics and the preferred critical boundary for visually guided reaching. *J. Exp.*
964 *Psychol.-Hum. Percept. Perform.* 23, 1365–1379. <https://doi.org/10.1037/0096-1523.23.5.1365>

965 Martel, M., Cardinali, L., Roy, A.C., Farnè, A., 2016. Tool-use: An open window into body
966 representation and its plasticity. *Cogn Neuropsychol* 33, 82–101.
967 <https://doi.org/10.1080/02643294.2016.1167678>

968 Martin, A., 2007. The representation of object concepts in the brain, in: *Annual Review of*
969 *Psychology*. Annual Reviews, Palo Alto, pp. 25–45.

970 Matelli, M., Luppino, G., Rizzolatti, G., 1985. Patterns of cytochrome oxidase activity in the
971 frontal agranular cortex of the macaque monkey. *Behav. Brain Res.* 18, 125–136.
972 [https://doi.org/10.1016/0166-4328\(85\)90068-3](https://doi.org/10.1016/0166-4328(85)90068-3)

973 Mawase, F., Lopez, D., Celnik, P.A., Haith, A.M., 2018. Movement Repetition Facilitates
974 Response Preparation. *Cell Reports* 24, 801–808. <https://doi.org/10.1016/j.celrep.2018.06.097>

975 Medina, J., Coslett, H.B., 2010. From maps to form to space: Touch and the body schema.
976 *Neuropsychologia* 48, 645–654. <https://doi.org/10.1016/j.neuropsychologia.2009.08.017>

977 Michel, C., Bonnetain, L., Amoura, S., White, O., 2018. Force field adaptation does not alter
978 space representation. *Scientific Reports* 8, 10982. <https://doi.org/10.1038/s41598-018-29283-z>

979 Morasso, P., 1981. Spatial control of arm movements. *Exp Brain Res* 42, 223–227.
980 <https://doi.org/10.1007/BF00236911>

981 Morasso, P., Casadio, M., Mohan, V., Rea, F., Zenzeri, J., 2015. Revisiting the body-schema
982 concept in the context of whole-body postural-focal dynamics. *Front Hum Neurosci* 9, 83.
983 <https://doi.org/10.3389/fnhum.2015.00083>

984 Noppeney, U., 2008. The neural systems of tool and action semantics: a perspective from
985 functional imaging. *J. Physiol. Paris* 102, 40–49.
986 <https://doi.org/10.1016/j.jphysparis.2008.03.009>

987 Ostry, D.J., Darainy, M., Mattar, A.A.G., Wong, J., Gribble, P.L., 2010. Somatosensory
988 Plasticity and Motor Learning. *Journal of Neuroscience* 30, 5384–5393.
989 <https://doi.org/10.1523/JNEUROSCI.4571-09.2010>

990 Ostry, D.J., Gribble, P.L., 2016. Sensory Plasticity in Human Motor Learning. *Trends in*
991 *Neurosciences* 39, 114–123. <https://doi.org/10.1016/j.tins.2015.12.006>

992 Palluel-Germain, R., Boy, F., Orliaguet, J.P., Coello, Y., 2004. Visual and motor constraints on
993 trajectory planning in pointing movements. *Neurosci. Lett.* 372, 235–239.
994 <https://doi.org/10.1016/j.neulet.2004.09.045>

995 Patané, I., Farnè, A., Frassinetti, F., 2017. Cooperative tool-use reveals peripersonal and
996 interpersonal spaces are dissociable. *Cognition* 166, 13–22.
997 <https://doi.org/10.1016/j.cognition.2017.04.013>

998 Pfeiffer, C., Noel, J.-P., Serino, A., Blanke, O., 2018. Vestibular modulation of peripersonal
999 space boundaries. *European Journal of Neuroscience* 47, 800–811.
1000 <https://doi.org/10.1111/ejn.13872>

1001 Pickering, M.J., Clark, A., 2014. Getting ahead: forward models and their place in cognitive
1002 architecture. *Trends Cogn. Sci. (Regul. Ed.)* 18, 451–456.
1003 <https://doi.org/10.1016/j.tics.2014.05.006>

1004 Pipereit, K., Bock, O., Vercher, J.-L., 2006. The contribution of proprioceptive feedback to
1005 sensorimotor adaptation. *Exp Brain Res* 174, 45. <https://doi.org/10.1007/s00221-006-0417-7>

1006 Poincaré, H., Maitland, F., 2003. *Science and Method*. Courier Corporation.

1007 Previc, F.H., 1998. The neuropsychology of 3-D space. *Psychol Bull* 124, 123–164.
1008 <https://doi.org/10.1037//0033-2909.124.2.123>

1009 Proverbio, A.M., 2012. Tool perception suppresses 10–12Hz μ rhythm of EEG over the
1010 somatosensory area. *Biological Psychology* 91, 1–7.
1011 <https://doi.org/10.1016/j.biopsycho.2012.04.003>

1012 Rizzolatti, G., Scandolara, C., Matelli, M., Gentilucci, M., 1981. Afferent properties of
1013 periarculate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2, 147–163.
1014 [https://doi.org/10.1016/0166-4328\(81\)90053-X](https://doi.org/10.1016/0166-4328(81)90053-X)

1015 Rochat, P., Wraga, M., 1997. An account of the systematic error in judging what is reachable. *J*
1016 *Exp Psychol Hum Percept Perform* 23, 199–212. <https://doi.org/10.1037/0096-1523.23.1.199>

1017 Salenius, S., Schnitzler, A., Salmelin, R., Jousmäki, V., Hari, R., 1997. Modulation of human
1018 cortical rolandic rhythms during natural sensorimotor tasks. *Neuroimage* 5, 221–228.
1019 <https://doi.org/10.1006/nimg.1997.0261>

1020 Salmelin, R., Hari, R., 1994. Characterization of spontaneous MEG rhythms in healthy adults.
1021 *Electroencephalogr Clin Neurophysiol* 91, 237–248. [https://doi.org/10.1016/0013-4694\(94\)90187-2](https://doi.org/10.1016/0013-4694(94)90187-2)

1022

1023 Sarlegna, F.R., Malfait, N., Bringoux, L., Bourdin, C., Vercher, J.-L., 2010. Force-field
1024 adaptation without proprioception: Can vision be used to model limb dynamics?
1025 *Neuropsychologia* 48, 60–67. <https://doi.org/10.1016/j.neuropsychologia.2009.08.011>

1026 Shadmehr, R., 2017. Learning to Predict and Control the Physics of Our Movements. *J. Neurosci.*
1027 37, 1663–1671. <https://doi.org/10.1523/JNEUROSCI.1675-16.2016>

1028 Shadmehr, R., Mussa-Ivaldi, F.A., 1994. Adaptive representation of dynamics during learning of
1029 a motor task. *J. Neurosci.* 14, 3208–3224. [https://doi.org/10.1523/JNEUROSCI.14-05-](https://doi.org/10.1523/JNEUROSCI.14-05-03208.1994)
1030 [03208.1994](https://doi.org/10.1523/JNEUROSCI.14-05-03208.1994)

1031 Shadmehr, R., Smith, M.A., Krakauer, J.W., 2010. Error correction, sensory prediction, and
1032 adaptation in motor control. *Annual Review of Neuroscience* 33, 89–108.
1033 <https://doi.org/10.1146/annurev-neuro-060909-153135>

1034 Tanaka, H., Sejnowski, T.J., 2013. Computing reaching dynamics in motor cortex with Cartesian
1035 spatial coordinates. *J. Neurophysiol.* 109, 1182–1201. <https://doi.org/10.1152/jn.00279.2012>

1036 Valdés-Conroy, B., Román, F.J., Hinojosa, J.A., Shorkey, S.P., 2012. So Far So Good: Emotion
1037 in the Peripersonal/Extrapersonal Space. *PLOS ONE* 7, e49162.
1038 <https://doi.org/10.1371/journal.pone.0049162>

1039 Verstynen, T., Sabes, P.N., 2011. How Each Movement Changes the Next: An Experimental and
1040 Theoretical Study of Fast Adaptive Priors in Reaching. *J. Neurosci.* 31, 10050–10059.
1041 <https://doi.org/10.1523/JNEUROSCI.6525-10.2011>

1042 Wamain, Y., Gabrielli, F., Coello, Y., 2016. EEG μ rhythm in virtual reality reveals that motor
1043 coding of visual objects in peripersonal space is task dependent.
1044 <https://doi.org/10.1016/j.cortex.2015.10.006>

1045 Weiss, P.H., 2000. Neural consequences of acting in near versus far space: a physiological basis
1046 for clinical dissociations. *Brain* 123, 2531–2541. <https://doi.org/10.1093/brain/123.12.2531>

1047 Witt, J.K., Proffitt, D.R., Epstein, W., 2005. Tool Use Affects Perceived Distance, But Only
1048 When You Intend to Use It. *Journal of Experimental Psychology: Human Perception and*
1049 *Performance* 31, 880–888. <https://doi.org/10.1037/0096-1523.31.5.880>

1050 Wolpert, D., Ghahramani, Z., Jordan, M., 1995. An internal model for sensorimotor integration.
1051 *Science* 269, 1880–1882. <https://doi.org/10.1126/science.7569931>

1052 Wolpert, D.M., Ghahramani, Z., Flanagan, J.R., 2001. Perspectives and problems in motor
1053 learning. *Trends in Cognitive Sciences* 5, 487–494. [https://doi.org/10.1016/S1364-](https://doi.org/10.1016/S1364-6613(00)01773-3)
1054 [6613\(00\)01773-3](https://doi.org/10.1016/S1364-6613(00)01773-3)

1055 Wolpert, D.M., Kawato, M., 1998. Multiple paired forward and inverse models for motor control.
1056 *Neural Networks* 11, 1317–1329. [https://doi.org/10.1016/S0893-6080\(98\)00066-5](https://doi.org/10.1016/S0893-6080(98)00066-5)

1057 Wolpert, D.M., Miall, R.C., 1996. Forward Models for Physiological Motor Control. *Neural*
1058 *Netw* 9, 1265–1279. [https://doi.org/10.1016/S0893-6080\(96\)00035-4](https://doi.org/10.1016/S0893-6080(96)00035-4)

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