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Sensori-motor adaptation to novel limb dynamics influences the representation of peripersonal space

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Abstract

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

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

1. Introduction

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

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

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

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

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

2. Material and methods

2.1. Participants

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

2.2. Experimental set up

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

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

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

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

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

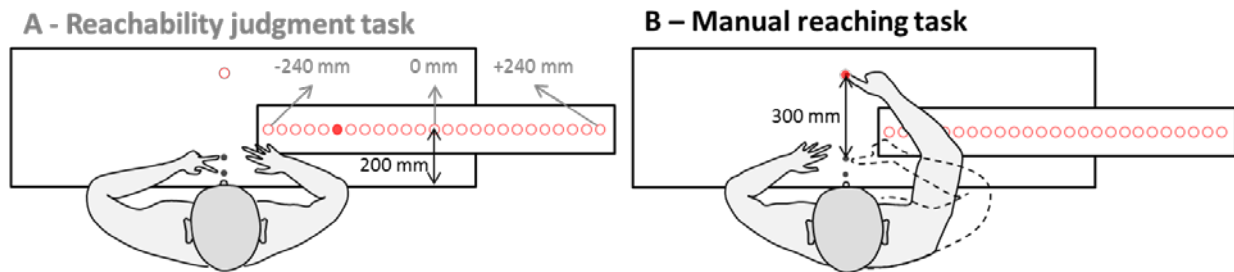


Figure 1. Experimental setup. (A) Reachability judgment task: participants had to judge whether a target illuminated on their right was reachable or not: they responded by pressing the closer response button with their left index or the more distant button with their middle finger, respectively. The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

2.3. Procedure

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

2.3.1. *Manual reaching task*

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

2.3.2. *Reachability judgment task*

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

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

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

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

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

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

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

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

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

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

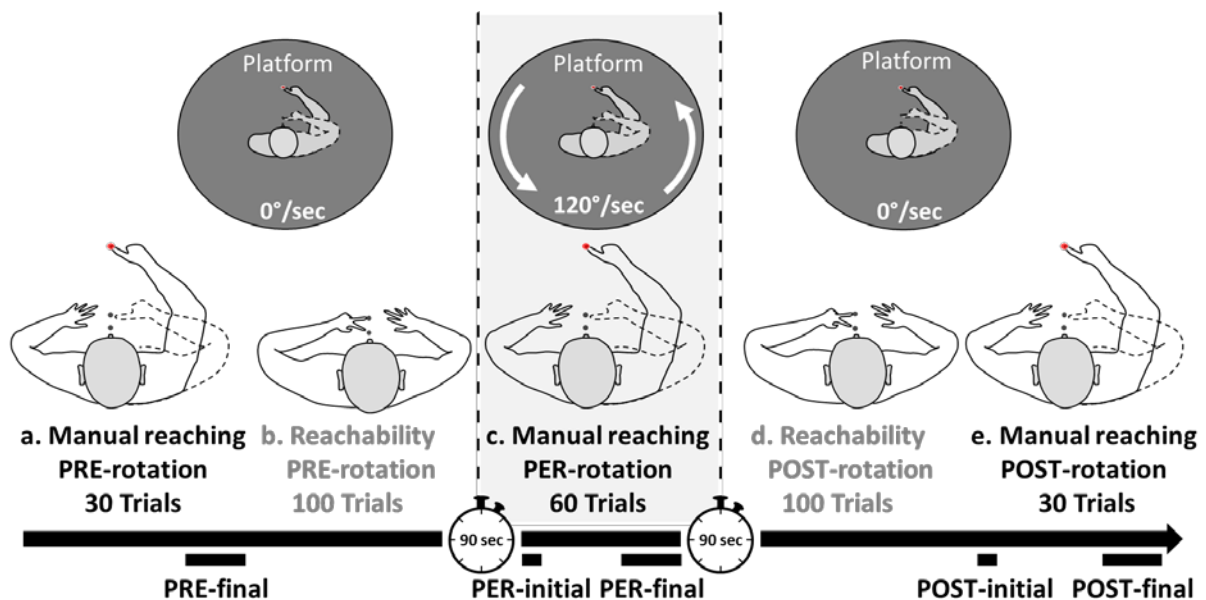


Figure 2. Experimental procedure. Manual reaching movements were executed before (a), during (c) and after (e) platform rotation, while reachability was estimated before (b) and after (d) rotation. Under the black arrow of time, we specify the manual reaching trials used for statistical analyses: the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

2.4. *Data recording and analysis*

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

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

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

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

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

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

2.5. Statistical analysis

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

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

3. Results

3.1. Manual reaching task

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

3.1.1. Spatial performance

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

3.1.1.1. Hand trajectory

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

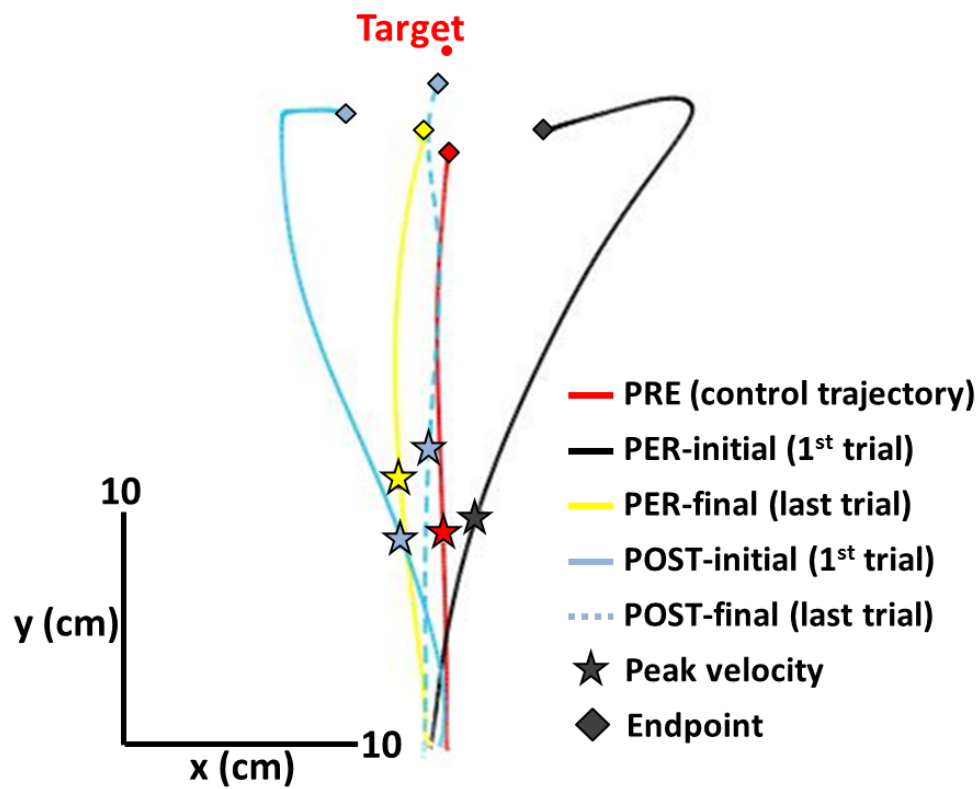


Figure 3. Top view of the right index fingertip trajectories for a representative participant. Hand paths are shown for the last trial of the PRE-rotation (red line), the first trial of the PER-rotation (black line), the last trial of the PER-rotation (yellow line), the first trial of the POST-rotation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

3.1.1.2. Initial direction

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

3.1.1.3. Endpoint error

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

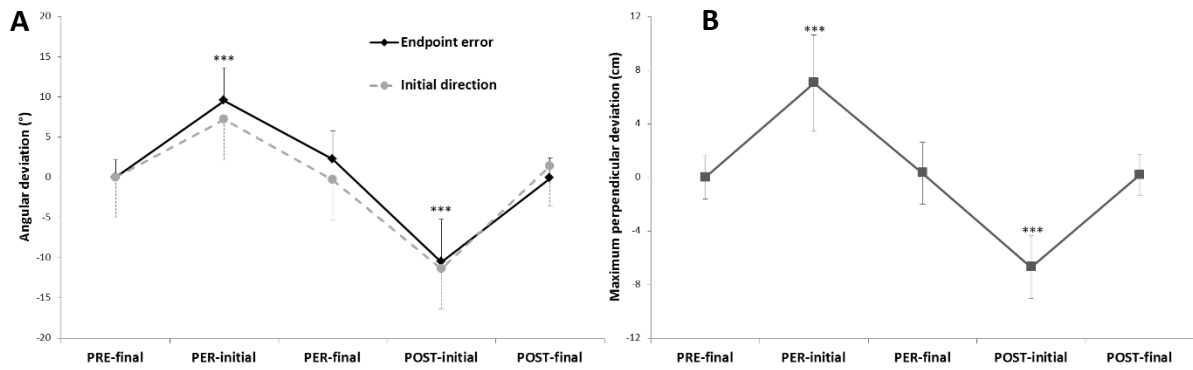


Figure 4. Behavioural adaptation to the force-field perturbation. (A) Mean angular endpoint error and initial direction of the first (PER-initial) and last ten trials (PER-final) of PER-rotation, and the first (POST-initial) and last ten trials (POST-final) of the POST-rotation phases, normalised with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

3.1.1.4. Maximum perpendicular deviation

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

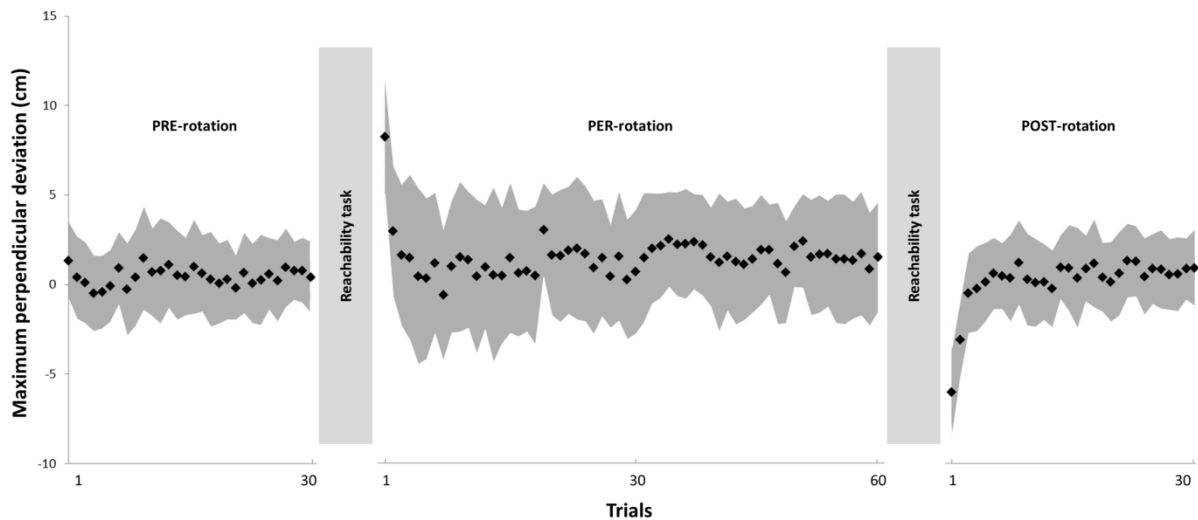


Figure 5. Mean maximum perpendicular deviation across participants for all reaching movements throughout the experiment. The dark grey area surrounding black points represents the standard deviation of the mean. Participants progressively adapted to the Coriolis force that initially deviated their moving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

3.1.2. Temporal performance and related kinematic data

3.1.2.1. Movement time

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

3.1.2.2. Acceleration, velocity and deceleration peaks amplitude

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

3.2. Reachability judgment task

3.2.1. Reachability judgments

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

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

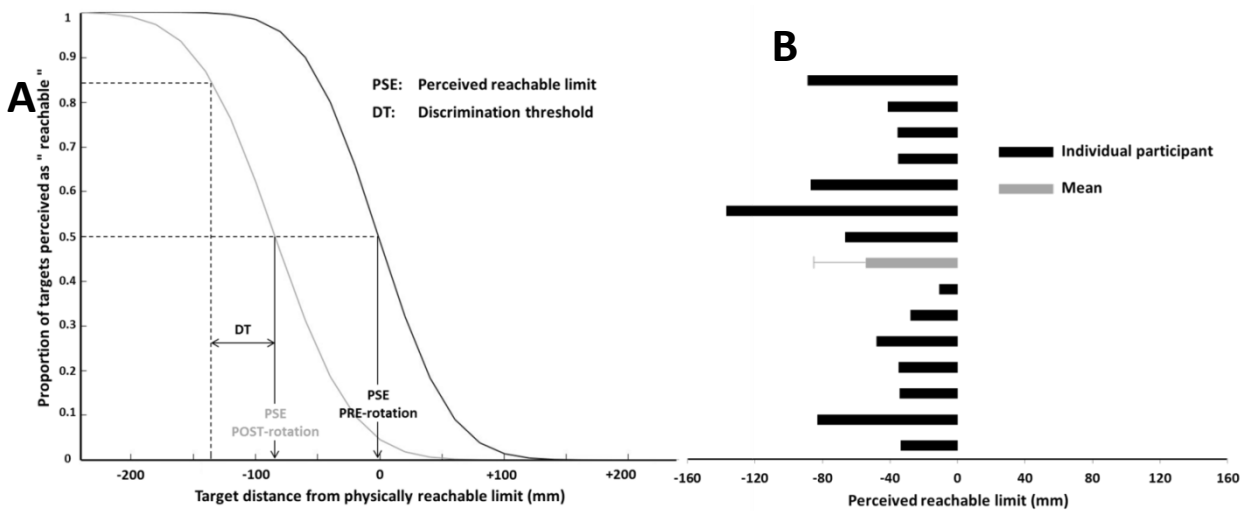


Figure 6. Systematic shift in reachability judgment. (A) Results of logit regression analysis for a representative participant during reachability PRE-rotation (dark line) and POST-rotation (grey line) conditions. (B) Individual shift in the limit of perceived reachable space [POST-rotation - PRE-rotation]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

3.2.2. Response time

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

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

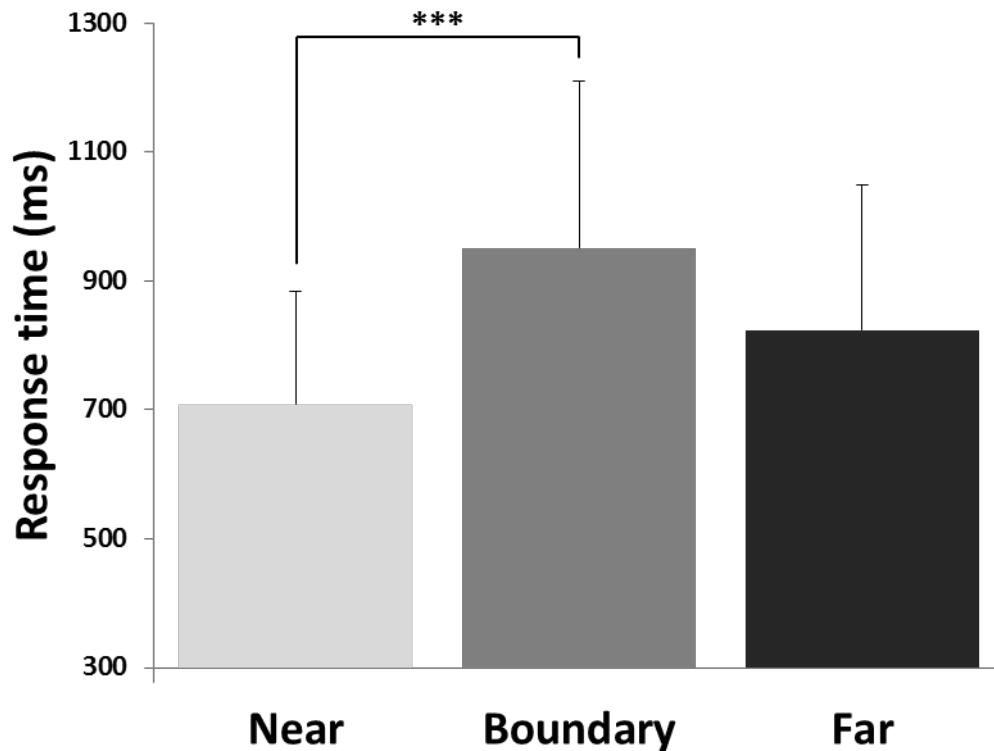


Figure 7. Mean response time for three different sets of targets in the reachability judgment task across both conditions of rotation. The three zones (Near, Boundary and Far) corresponded to the 3 most reachable (closest) targets, 3 targets around the boundary of reachable space and the 3 least reachable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

3.3. Correlation analyses

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

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

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

Control experiment 1

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

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

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

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

Control experiment 2

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

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

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

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

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

4. Discussion

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

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

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

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

4.2. *Reproduction of reachability judgment task features*

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

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

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

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

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

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

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

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

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

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

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

5. Conclusion

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

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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., Delepoulle, 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., Comitteri, 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., Farné, 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 Dupierri, 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., Aeschmann, 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)
 1059