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# **Opposing force fields induce direction-specific sensorimotor adaptation but a non-specific perceptual shift consistent with a contraction of peripersonal space representation**

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**Abstract**

Most of our daily interactions with objects occur in the space immediately surrounding the body, i.e. the peripersonal space. The peripersonal space is characterized by multisensory processing of objects which are coded in terms of potential actions, specifying for instance whether objects are within reach or not. Our recent work suggested a link between exposure to a new force field, which changed the effector dynamics, and the representation of peripersonal space. To better understand the interplay between the plasticity of the motor system and peripersonal space representation, the present study examined whether changing the direction of the force field specifically modified the perception of action boundaries. Participants seated at the centre of an experimental platform estimated visual targets' reachability before and after adapting upper-limb reaching movements to the Coriolis force generated by either clockwise or counterclockwise rotation of the platform (120°/s). Opposite spatial after-effects were observed, showing that force-field adaptation depends on the direction of the rotation. In contrast, perceived action boundaries shifted leftward following exposure to the new force field, regardless of the direction of the rotation. Overall, these findings support the idea that abrupt exposure to a new force field results in a direction-specific updating of the central sensorimotor representations underlying the control of arm movements. Abrupt exposure to a new force field also results in a nonspecific shift in the perception of action boundaries which is consistent with a contraction of the peripersonal space and could be related to its protective role. Such effect, which does not appear to be related to state anxiety, ~~and~~ could be related to ~~the~~ its protective role of the peripersonal space in response to the uncertainty of the sensorimotor system induced by the abrupt modification of the environment.

**Keywords:** motor control, force-field adaptation, manual reaching, reachability judgment, peripersonal space representation

## **Declarations**

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### **Conflicts of interest/Competing interests (include appropriate disclosures)**

The authors declare that they have no conflicts of interest/competing interests.

### **Ethics approval (include appropriate approvals or waivers)**

The study was approved by the institutional review board of the Institute of Movement Sciences and was performed in accordance with the Code of Ethics of the World Medical Association (1964 Declaration of Helsinki).

### **Consent to participate (include appropriate statements)**

All participants gave their written informed consent prior to inclusion in the study.

### **Consent for publication (include appropriate statements)**

All authors read and approved the final manuscript.

### **Availability of data and material (data transparency)**

Data are available upon reasonable request.

### **Code availability (software application or custom code)**

Code is available upon reasonable request.

### **Authors' contributions (optional: please review the submission guidelines from the journal whether statements are mandatory)**

Conceptualization: Christophe Bourdin, Yann Coello, Nicolas X. Leclere, Fabrice Sarlegna; Methodology: Christophe Bourdin, Yann Coello, Nicolas X. Leclere, Fabrice Sarlegna; Formal analysis and investigation: Nicolas X. Leclere; Writing - original draft preparation: Nicolas X. Leclere; Writing - review and editing: Christophe Bourdin, Yann Coello, Nicolas X. Leclere, Fabrice Sarlegna; Supervision: Christophe Bourdin, Fabrice Sarlegna.

## Introduction

Most of our daily interactions with the environment occur in the space closely surrounding our body, for instance when we shake somebody's hand or grasp a cup of tea. The portion of space where we can directly interact with objects is usually referred to as the peripersonal space (De Vignemont and Iannetti 2015; Cléry et al. 2015; Di Pellegrino and Ladavas 2015; Coello et al. 2018). Peripersonal space delimits action boundaries and is conceived as a multisensory interface between the body and the environment where objects can be reached and are coded in terms of potential actions (Rizzolatti et al. 1997; Previc 1998; Berti and Frassinetti 2000; Holmes and Spence 2004; Cardellicchio et al. 2011; Wamain et al. 2016; Bufacchi and Iannetti 2018). Several behavioural studies showed that perception of action boundaries is linked to anticipation of deployable actions in the environment (Fischer 2000; Coello and Delevoye 2007; Gabbard et al. 2007; Iachini et al. 2014). In support of this view, it was found that modifying arm length in the body schema through tool use (Holmes et al. 2004; Farnè et al. 2005; Witt and Proffitt 2005; Costantini et al. 2011; Cardinali et al. 2012; Bourgeois et al. 2014) or biasing the visuospatial outcome of a manual reaching action (Bourgeois and Coello 2012) modifies perception of action boundaries. In the same vein, transient immobilisation of the dominant arm induces a concurrent reduction of the activity of the brain motor areas (Facchini et al. 2002; Huber et al. 2006; Avanzino et al. 2011) and the distance at which visual objects are perceived as within reach (Toussaint et al. 2020). Likewise, neurological patients with lesioned brain motor regions have an abnormally reduced perception of their action boundaries (Bartolo et al. 2014a). However, despite the wealth of studies highlighting the contribution of the motor system to the coding of objects in the peripersonal space, the underlying mechanisms remain unclear. To shed further light on these mechanisms, the present study assessed the putative link between the processes underlying sensorimotor adaptation and the perception of action boundaries.

One way to better understand the interplay between the plasticity of the motor system and peripersonal space representation is to induce a modification in the control of object-directed actions and to assess the resulting effects on perception of action boundaries. The plasticity of sensorimotor control processes is currently described as a trial-by-trial iterative updating of motor commands based on sensory feedback, which allows individuals to adapt to a wide range of environmental constraints (for reviews, Shadmehr et al. 2010; Wolpert et al. 2011; McDougle et al. 2016). For instance, manual reaching involves adaptation to a new force field, in which a set of motor commands has different consequences on arm motion, and thus on associated sensory feedback, compared to the usual force field. This process is commonly explained as relying on updating internal models of limb dynamics (Gandolfo et al. 1996; Sainburg et al. 1999; Lackner and DiZio 2005; Heald et al. 2018; Shadmehr 2018). Thus, when a new force field sustainably alters limb dynamics, the control processes subtending the execution of upper-limb movements are recalibrated to restore optimal performance (Coello et al. 1996; Kurtzer et al. 2003; Bourdin et al. 2006; Ostry et al. 2010; Sarlegna et al. 2010; Franklin and Wolpert 2011).

In a recent study (Leclere et al. 2019), we tested how exposure to a new force field may affect perception of action boundaries. Participants seated at the centre of an experimental platform were requested to perform manual acquisitions of visual targets. The rotation of the platform generated Coriolis forces on the moving limb, thus altering its accuracy. The originality of the study consisted in testing perception of action boundaries before and after exposure to the new Coriolis forces. In addition to the classically observed sensorimotor adaptation of reaching movements (Lackner and DiZio 1994; Bourdin et al. 2001; Lefumat et al. 2015), we observed a systematic bias in the perception of action boundaries: the rotation-induced Coriolis forces were oriented rightward, triggering a sensorimotor adaptation oriented leftward. The perception of action boundaries shifted leftward too, suggesting a relationship

between perception of action boundaries and updating of internal models for motor control. Moreover, we carried out two control experiments to test whether platform rotation per se (without reaching movements) or repetition of reaching movements (without platform rotation) had an effect on action boundaries perception (Leclere et al. 2019). No significant shift in reachability estimation was found in both control studies, and the shift was only observed when subjects adapted to the perturbation.

While our previous work ~~which~~ led us to suggest a link between action space perception and sensorimotor adaptation, there is an alternative explanation for the link between exposure to a new force field and modified perception of action boundaries. Modified perception of action boundaries following exposure to the new force field could ~~also~~ result from the perceived incongruence between expected and actual sensorimotor performances in the new inertial field. Indeed, lack of congruency could lead to a conservative strategy for perceiving action boundaries (Rochat and Wraga 1997; Fischer 2000). Supporting this latter interpretation, Bourgeois and Coello (2012) reported a contraction of perceived action boundaries after exposure to randomly altered visual feedback presented at the movement end point. The perception of action boundaries may also be influenced by anxiety, as the distance perceived as reachable seems to be reduced with a higher level of anxiety (Pijpers et al. 2006; Graydon et al. 2012; Daviaux et al. 2016). The abrupt exposure to the new force field may thus increase state anxiety of participants and therefore induce a contraction of perceived action boundaries.

The present study thus aimed at determining whether modified perception of action boundaries after exposure to a new force field results from sensorimotor adaptation, or from a conservative strategy triggered by suddenly experiencing a new force field. To disentangle these alternative interpretations, we replicated the design used in our previous study (Leclere et al. 2019), but modified the direction of the force field and assessed its consequences on reach

adaptation and perception of action boundaries. In addition, we measured the potential effect of state anxiety on peripersonal space perception by measuring it at the beginning and at the end of the experiment. We hypothesised that force-field adaptation specifically drives perception of action boundaries and that exposure to opposing force fields would induce perceptual changes in opposite directions. This led us to predict that exposure to a clockwise rotation would result in a rightward shift of the sensorimotor performance as well as the perception of action boundaries.

## **Methods**

### *Participants*

Fourteen right-handed adults (3 females and 11 males, mean age  $\pm$  standard deviation of the mean =  $20.4 \pm 1.7$  years) participated in this experiment. Their performance was compared with the performance of another group of 14 healthy right-handed adults (3 females, mean age =  $21.9 \pm 2.1$  years) reported previously (Leclere et al. 2019). A power analysis on expected statistical analyses (within-between subjects ANOVA with repeated measures, medium effect-size = 0.5 (Cohen 1988),  $\alpha = 0.05$ ) necessitated a sample size of at least 8 participants to reach a power of 0.80. None of the participants declared any sensorimotor or neurological deficit. 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 Code of Ethics of the World Medical Association (1964 Declaration of Helsinki). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment.



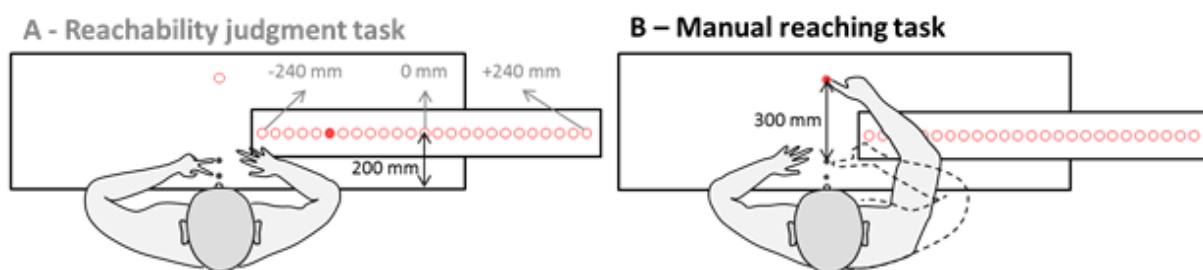
### *Experimental set-up*

The experimental setup described hereafter is identical to the setup described previously for a totally different pool of participants (Leclere et al. 2019). Participants sat at the centre of a motorised rotating platform and were strapped in with a seat belt to constrain trunk movement. 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 inertial forces on the head during platform rotation. When the upper limb was voluntarily moved toward the target during rotation, each moving point of the limb was subjected to the Coriolis force ( $F_{\text{cor}}$  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,  $\omega$  the platform's angular velocity and  $v$  the arm's linear velocity (Lackner and DiZio 1994).

Figure 1 shows that several visual targets were positioned on a horizontal table placed in front of the participants, at waist level. All visual targets were low-intensity red light-emitting diodes (3 mm in diameter) presented in a dark room, a condition which does not preclude force-field adaptation (Lackner and DiZio 1994; Lefumat et al. 2015). Participants had to perform two tasks, each involving different visual targets: a manual reaching task to assess sensorimotor adaptation to a new force field and a reachability judgment task to assess resulting changes in the perception of action boundaries (see Figure 1). In the manual reaching task, participants had to reach toward one visual target, 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, in the participant's right hemisphere (with respect to the mid-body sagittal axis). The array of reachability targets was positioned according to each participant's arm length (see Procedure), with an inter-target distance of 20 mm. Reachability targets were positioned horizontally in such a way as to be in the same plane as the expected effect of the perturbation and the ensuing 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 used their left hand to respond to the question 'Is the target reachable with your right hand?' by pressing the closer response button for 'Reachable' or the more distant response button for 'Unreachable'. 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 judgments. 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).



**Fig. 1** Experimental setup. (A) Reachability judgment task: participants had to judge whether a target illuminated on their right was reachable or not with their right hand: they responded by pressing the closer response button with their left index ('Reachable') or the more distant button with their left middle finger ('Unreachable'). 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 toward the visual target with their right index as accurately and as fast as possible.

## *Procedure*

Before the experiment started, participants were required to fill a test to evaluate their state anxiety (see details below). The target array was hidden from participants, being draped in a black opaque sheet. Wearing occluding glasses, participants were then asked to fully stretch out their right arm in the fronto-parallel plane, so that the experimenter could match the position of each participant's index fingertip, arm fully stretched, with the position of the central target (0 mm location) in the array. The individually-adjusted position of the central target thus corresponded to the actual maximum distance that was physically reachable by each participant (Valdès-Conroy et al. 2012; Bourgeois et al. 2014; Patané et al. 2017). After this personalised adjustment of the setup, the room lights were switched off, the occluding glasses and the black sheet were removed, and participants were allowed to open their eyes in the dark room. Once the experiment ended, participants were required to fill an anxiety test for the second time.

### *a. Manual reaching task*

In the manual reaching task, each trial lasted 4.5 s and 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 pause of 500 to 1000 ms. As soon as the visual target was turned on, participants had to reach toward it as fast and as accurately as possible with the right index. Movements were not constrained in the horizontal table plane: participants were instructed to lift their finger off the table during the reaching movement. They had to maintain their final hand position once their finger touched the table. 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 signaled to participants that they should move their hand back to the start position and prepare for the next

trial, which started automatically. No explicit instructions were given with respect to the hand path.

*b. Reachability judgment task*

In the reachability judgment task, after a 100 ms auditory tone followed by a random pause 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 left middle finger. The target disappeared as soon as participants provided their response and, at the end of a fixed period lasting 4 s from the 100 ms auditory tone, the next trial started automatically with the same temporal sequence.

*c. State anxiety test*

In order to investigate a possible effect of the anxiety on the reachability judgments, we used a validated french version (Bruchon-Schweitzer and Paulhan 1993) of the State-Trait Anxiety Inventory (STAI, Spielberger et al. 1983). The test was a 20-item self-report scale that measures state anxiety, characterized by subjective feelings of tension, apprehension, nervousness, and worry, and by activation or arousal of the autonomic nervous system related to an event. Each item presented a description (e.g. "I feel calm" or "I am tense"), and participants were asked to indicate the extent to which each item felt appropriate on a 4-point scale (e.g., from "Not at all" to "Very much so"). The score range for the test is 20-80, the

higher score indicating higher anxiety. State anxiety was measured just before (anxiety-PRE) and immediately after (anxiety-POST) the first and the last manual reaching tests, respectively.

### *Experimental design*

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 toward the visual target to determine baseline sensorimotor performance.

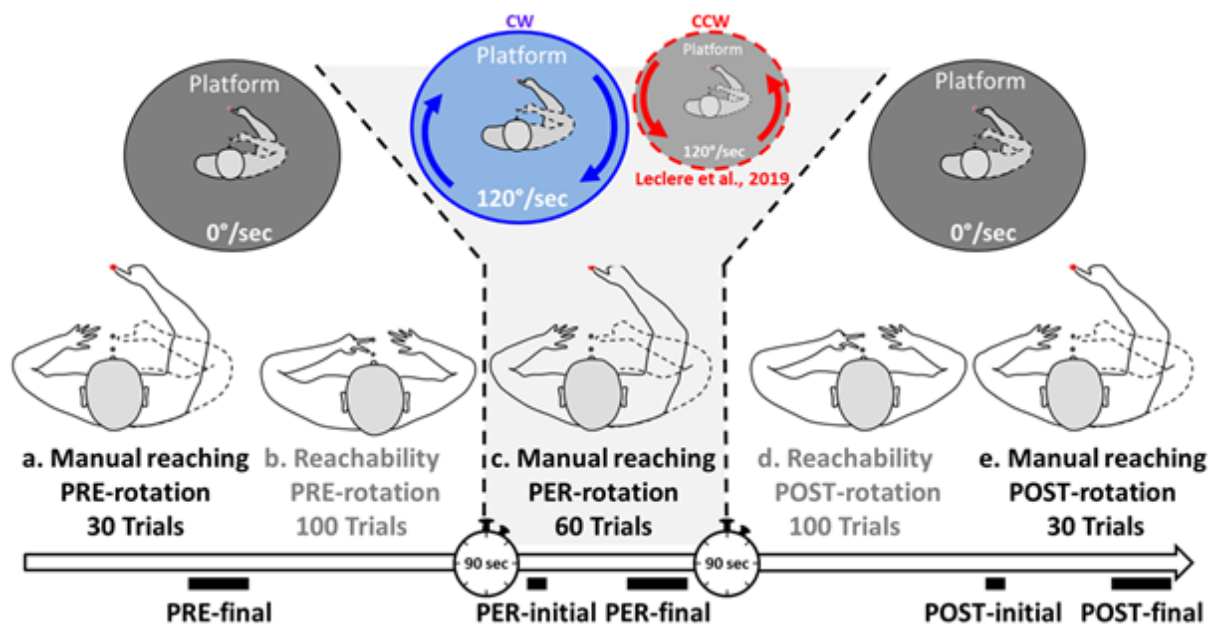
- Reachability judgment task / PRE-rotation (platform stationary). Participants performed a series of one hundred reachability judgments (each of the 25 targets randomly presented 4 times) to determine baseline performance in the reachability judgment task. At the end of this condition, the platform was progressively accelerated 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 toward the visual target. The platform's rotation generated Coriolis force ( $F_{cor}$ ) on the moving limb. In this experiment, the platform rotated clockwise (CW), thus resulting in leftward forces on the participant's limb moved toward the central target. In a previous study (Leclere et al. 2019), a different set of participants performed an identical experiment, the only difference being that they were exposed to a counterclockwise (CCW) rotation, thus resulting in rightward forces on the limb moved toward the central target. Both groups of participants therefore faced a perturbation of the same magnitude but in opposite directions. Once the sixty reaching movements were completed during platform rotation, the platform was progressively decelerated for 80 s (decrease of  $1.5^{\circ}/s^2$ ) until stationary.

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

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

A 90 s pause was included between the end of the platform rotation acceleration (and deceleration) period and the ensuing task, to allow the vestibular semicircular canals to return to their resting discharge frequency (Goldberg and Fernandez 1971). Participants 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).



**Fig. 2** Experimental procedure. Manual reaching movements were executed before (a), during (c) and after (e) platform rotation (c), while reachability was estimated just before (b) and after (d) rotation. Under the arrow indicating time, at the bottom of the figure, thick black lines show the manual reaching trials used for statistical analyses: the ten last trials to assess baseline performance (PRE-final), the first (PER-initial) and ten last (PER-final) trials during the rotation to assess adaptation, and the first (POST-initial) and ten last (POST-final) trials after the rotation to assess after-effect and de-adaptation. In the present study, participants were rotated clockwise (CW) in PER-rotation. Their results were compared with those from the previous study of Leclere et al. (2019) where participants were rotated counterclockwise (CCW) in PER-rotation.

### *Data analysis*

Data analysis was identical to that in Leclere et al. (2019). In the manual reaching task, the marker coordinates ( $x$ ,  $y$ ,  $z$ ) 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. 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 and DiZio 1994; Coello et al. 1996; Bourdin et al. 2001; Sarlegna et al. 2010). We 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). For this variable, rightward trajectory deviations corresponded to positive values, and leftward deviations to negative values.

Sensorimotor 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 condition (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) after rotation ceased. The analysis of endpoint error was used to characterise sensorimotor 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 sensorimotor

adaptation and after-effects of sensorimotor adaptation to the velocity-dependent force field. In addition, we analysed movement time and peak velocity to provide a detailed kinematic account of the reaching movements throughout the experiment. In order to compare the results obtained with participants performing clockwise vs counterclockwise rotation, we inverted the sign of kinematic data from the previous study (Leclere et al. 2019) in PER-initial, PER-final and POST-initial.

In the reachability judgment task, reachability judgments and response times were registered through the participant's answers via the response buttons. As in Bourgeois and Coello (2012), perception of action boundaries was determined using a maximum-likelihood procedure 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 probability  $p$  associated with the logit function was 0.50 for both responses. This point of subjective equality (PSE) can be used as a proxy for perception of action boundaries (Bourgeois and Coello 2012; Leclere et al. 2019). Positive PSE values corresponded to an overestimated perception of action boundaries with respect to actual physical boundaries. We then calculated the difference between the PSE in PRE-rotation and POST-rotation to determine the shift in perception of action boundaries ( $\Delta$ PSE). In addition, we computed the discrimination threshold, defined as the distance between the target distance at  $p = 0.50$  (PSE) and the target distance at  $p = 0.84$  (Ernst and Banks 2002). The smaller the discrimination threshold, the more accurate the participant was in distinguishing between reachable and unreachable targets.



We defined response time (RT) as the time between the onset of stimulus presentation and the onset of the button press. We calculated the mean RT for each target position, which yielded 25 mean RTs per condition (PRE-rotation and POST-rotation) for each participant. Only individual RTs around the mean of plus or minus 2.5 times the corresponding standard deviation were included in subsequent analysis (3.1% of data omitted in PRE- and 3.3% in POST-rotation condition). We then fitted RTs as a function of target position with a Gaussian regression model to estimate the distance at which maximum RT (RT max) occurred for each participant in each condition. Because computations for 4 participants in each group yielded a maximum RT distance beyond the range of the targets, we considered aberrant values as an exclusion criterion and conducted RT analyses on 10 participants in each group. Previous studies showed that RT should be greatest for stimuli that can be judged as either reachable or unreachable (Hirose et al. 2010; Bourgeois and Coello 2012; Stone 2014). Therefore, maximum RT should occur for targets presented near perceived action boundaries. Finally, we calculated the Pearson coefficient ( $r$ ) of the correlation between the target distance corresponding to the PSE and the target distance corresponding to the maximum RT on the Gaussian fit.

### *Statistical analysis*

To assess sensorimotor adaptation in the manual reaching task, we used a mixed design analysis of variance (5x2 ANOVA) with one repeated-measure factor Phase (PRE-final, PER-initial, PER-final, POST-initial, POST-final), and a Group factor (CW or CCW rotation) on the different reach variables. In the reachability judgment task, we used a 2x2 ANOVA to compare the perception of action boundaries, discrimination threshold and response time with one repeated-measure Condition factor (PRE- and POST-rotation) and a Group factor (CW

and CCW rotation). When there was a significant main effect or interaction, a Tukey honestly significant difference (HSD) post-hoc test was used for further analysis. State anxiety scores obtained at the beginning (Anxiety-PRE) and at the end (Anxiety-POST) of the experiment were compared using a paired t-test and we performed Pearson correlations to assess the link between the change in state anxiety and the shift in the perception of action boundaries. Level of significance was 0.05 for all analyses. The Kolmogorov-Smirnov method revealed that data distribution did not significantly differ from a normal distribution for all data in all experimental conditions.

## Results

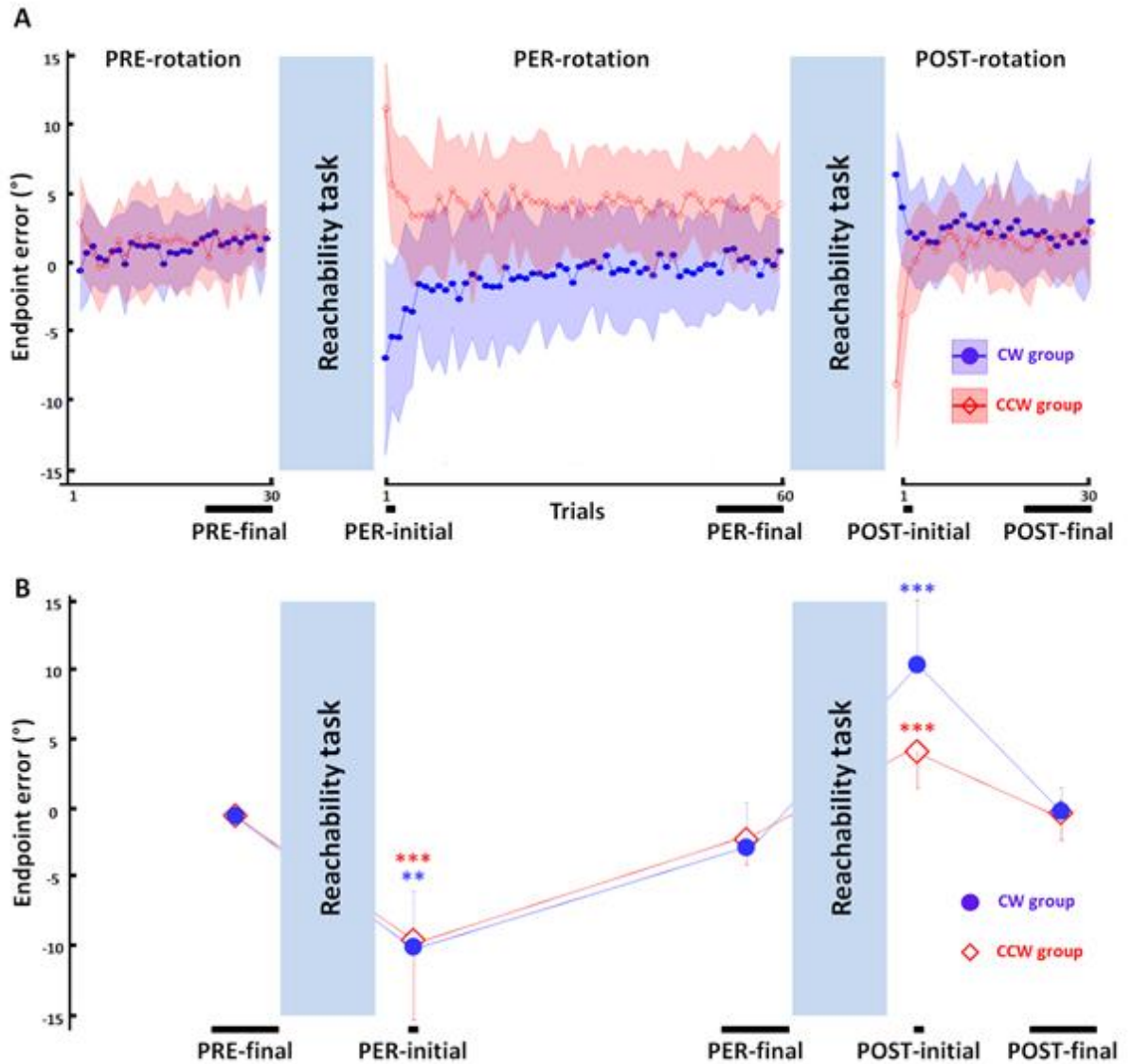
Presented below are the results for the group of fourteen participants in the current study who performed the manual reaching task before, during and after a clockwise (CW) platform rotation. These are compared to those of fourteen age-matched subjects who performed the same task in an earlier study where the rotation was counterclockwise (CCW, see Leclere et al. 2019). First, the analyses of both spatial and temporal performances in the reaching movements demonstrate that sensorimotor adaptation occurred during the experiment.

### *a. Manual reaching*

#### *Endpoint error*

For both groups, at the end of the PRE-rotation phase, hand paths toward the target were quite straight and accurate, as illustrated by the low endpoint error shown in Figure 3. Once the experimental platform was rotated either clockwise or counterclockwise, the first movement was deviated to the left or the right, respectively, reflecting the effect of Coriolis forces on the moving arm. At the end of the PER-rotation phase, endpoint error decreased toward baseline values, suggesting force-field adaptation. Once the rotation stopped, and after POST-rotation reachability judgments, endpoint errors were deviated to the right for the CW group and to the left for the CCW group, an after-effect that demonstrated the presence of force-field adaptation. Finally, endpoint errors at the end of the experiment were similar to those at baseline for each group.

A 2x5 ANOVA showed a significant effect of Phase ( $F(4, 104) = 66.28, p < 0.001, \eta^2 = 0.72$ ) but no significant effect of Group ( $F(1, 26) = 2.21, p = 0.15, \eta^2 = 0.08$ ). Moreover, results showed a significant interaction between Phase and Group factors ( $F(4, 104) = 4.01, p < 0.01, \eta^2 = 0.13$ ). Post-hoc analyses revealed that POST-initial endpoint error for both groups significantly differed from endpoint error in all other phases ( $p < 0.001$ ), but did not significantly differ between groups ( $p = 0.78$ ). Similarly, PER-initial endpoint error for both groups significantly differed from endpoint error in all other phases ( $p < 0.01$ ), but did not significantly differ between groups ( $p = 0.30$ ). The interaction was due to the fact that PER-initial endpoint error for the CCW group ( $11.0 \pm 4.1^\circ$ ) differed from PER-final endpoint error for the CW group ( $1.7 \pm 0.5^\circ; p < 0.001$ ), but not vice-versa, as PER-initial endpoint error for the CW group ( $6.9 \pm 7.0^\circ$ ) did not significantly differ from PER-final endpoint error for the CCW group ( $4.1 \pm 3.7^\circ; p = 0.41$ ). Overall, our results demonstrated a sensorimotor adaptation to the new force field for the two groups.



**Fig. 3** Reach adaptation to the force-field perturbation. (A) Mean movement endpoint error for CW (filled blue circle) and CCW (empty red diamond) groups over the course of the experiment. (B) Mean movement endpoint error of both CW and CCW groups during each phase of the experiment, normalised with respect to the ten last trials of the PRE-rotation condition (PRE-final). In PER-rotation, the two groups performed reaching movements rotated in two opposite directions: clockwise (CW) or counterclockwise (CCW). To compare endpoint error of CW and CCW groups, the sign of PER-initial, PER-final and POST-initial trial values was inverted for the CCW group. Error bars represent the standard deviation of the mean. Stars indicate significant differences between a given condition and its respective baseline for each group (\*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ).

### *Movement time and peak velocity*

A 2x5 ANOVA showed an effect of Phase ( $F(4, 104) = 4.89, p < 0.01, \eta^2 = 0.16$ ) on movement time but no significant effect of Group ( $p = 0.39$ ) or interaction between the two factors ( $p = 0.11$ ). Post-hoc analyses revealed that PER-initial movements (mean =  $472 \pm 134$ ms) lasted longer than PRE- (mean =  $397 \pm 54$ ms;  $p < 0.01$ ) and POST-final (mean =  $413 \pm 57$ ms;  $p < 0.05$ ) movements. In addition, POST-initial movements (mean =  $455 \pm 127$ ms) lasted longer than PRE-final movements ( $p < 0.05$ ).

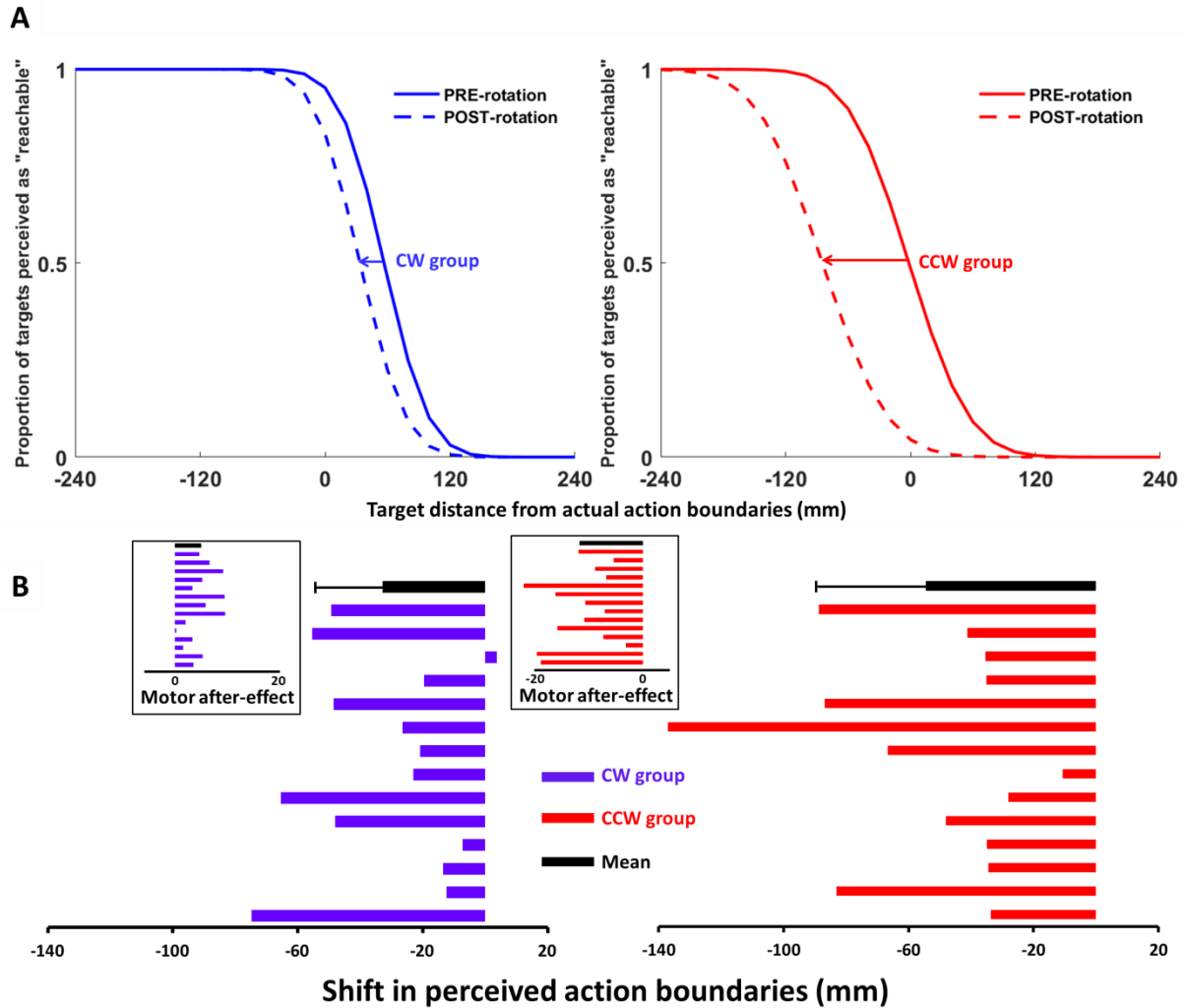
A 2x5 ANOVA showed an interaction between Phase and Group factors on peak velocity ( $F(4, 104) = 4.79; p < 0.01; \eta^2 = 0.16$ ) but no significant effect of Phase ( $F(4, 104) = 0.57, p = 0.69, \eta^2 = 0.02$ ) or Group ( $F(1, 26) = 1.45, p = 0.24, \eta^2 = 0.06$ ) factors. Post-hoc tests revealed that participants reached a higher peak velocity in PER-initial (mean =  $228 \pm 62$ cm/s) than in POST-initial (mean =  $199 \pm 50$ cm/s;  $p < 0.05$ ) movement for the CCW group but not for the CW group (mean PER-initial =  $187 \pm 52$ cm/s; mean POST-initial =  $203 \pm 48$ cm/s;  $p = 0.59$ ). Overall, we did not find substantial differences in temporal performance between groups or across experimental phases.

### *b. Reachability judgment task*

#### *Perceived action boundaries*

Participants had to judge targets' reachability through a forced-choice task as a function of target distance, leading to the psychophysical curve illustrated in Figure 4A. A 2 Group (CW and CCW) x 2 Condition (PRE- and POST-rotation) ANOVA on perceived action boundaries showed a significant effect of Condition ( $F(1, 26) = 62.96, p < 0.001, \eta^2 = 0.71$ ). Post-hoc analyses revealed that perceived action boundaries were farther away in PRE- (mean =  $48 \pm$

71mm) than in POST-rotation (mean =  $4 \pm 79$ mm;  $p < 0.001$ ). There was no significant effect of Group ( $p = 0.42$ ) and the interaction between the two factors was close to but did not reach statistical significance (mean CW =  $38 \pm 68$ mm; mean CCW =  $15 \pm 85$ mm;  $p = 0.06$ ), indicating some variability in the magnitude of the shift in perceived action boundaries. In contrast, the 2x2 ANOVA on the discrimination threshold did not show any significant effect of Condition ( $p = 0.33$ ) or Group ( $p = 0.38$ ), and no significant interaction between the two factors (mean PRE- =  $112 \pm 51$ mm; mean POST- =  $102 \pm 52$ mm;  $p = 0.15$ ). Thus, after force-field adaptation, perceived action boundaries shifted by 44 mm on average with respect to baseline. The key finding here is that the direction of the shift was the same for both experimental CW and CCW groups (and all participants but one).



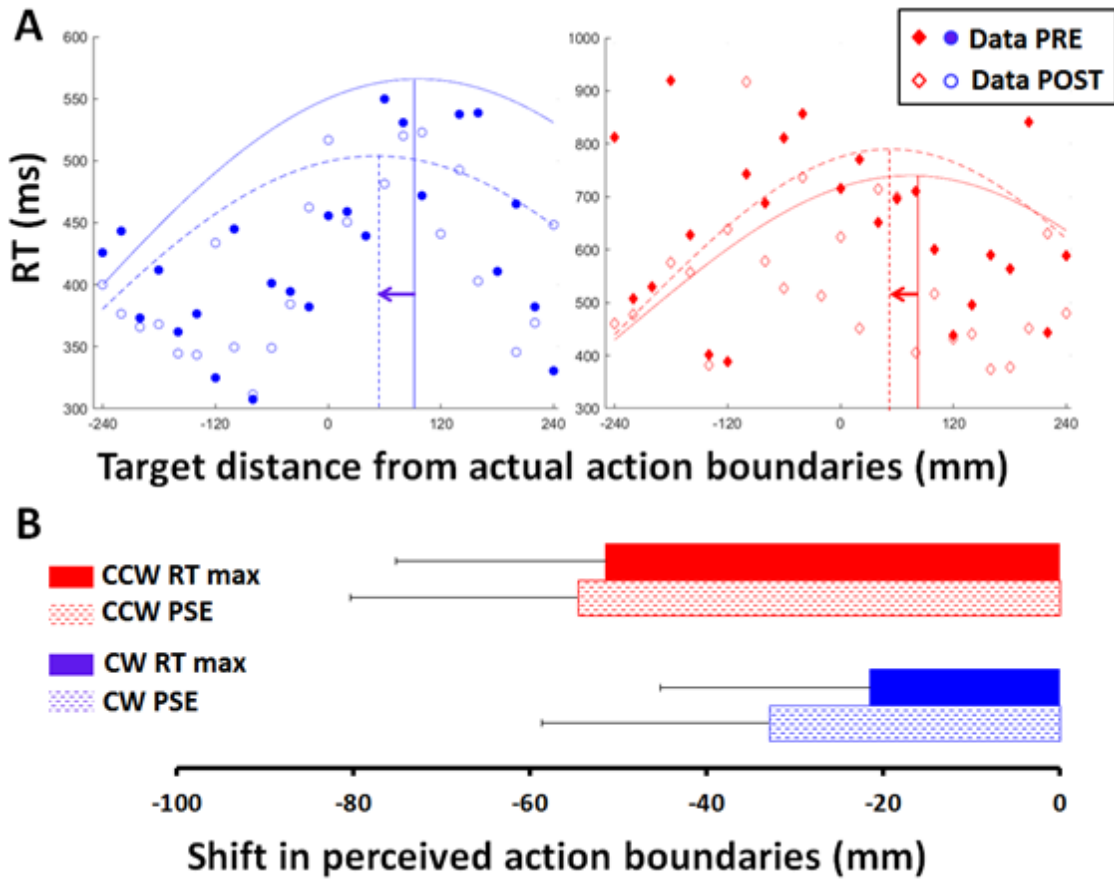
**Fig. 4** Systematic shift of perceived action boundaries. (A) Mean sigmoid fit across participants for CW (left blue panel) and CCW groups (right red panel) before (solid line) and after (dotted line) the platform rotation. The shift is highlighted by horizontal arrows. (B) Mean (in black) and individual shift in perceived action boundaries [POST-rotation - PRE-rotation] for each participant (in blue for the CW group (left panel) and in red for the CCW group (right panel)). Manual reaching after-effects (POST-initial error normalised according to PRE-final error) are represented inside black boxes in the same order as perceived action boundaries; positive and negative values correspond to right and left deviations, respectively. Error bars represent the standard deviation of the mean.



### *Response time*

Another way of assessing change in perception of action boundaries is by analysing response time (RT) as a function of target position. Response time is generally greatest under greatest uncertainty, i.e. when both responses “reachable” and “not reachable” feel equally right (PSE). When fitting RT as a function of target location with a Gaussian regression model (see Figure 5A), we found that the CCW group’s maximum RT occurred on average at a distance of  $61 \pm 124\text{mm}$  in PRE-rotation and at a distance of  $10 \pm 111\text{mm}$  in POST-rotation, while the CW group showed their maximum RT at a distance of  $73 \pm 62\text{mm}$  in PRE-rotation and at a distance of  $51 \pm 64\text{mm}$  in POST-rotation. Figure 5B shows that the mean shift computed with this maximum RT method for both groups was thus negative (mean=-36mm), as with the PSE method (mean=-44 mm). In addition, both groups’ maximum RT distance was found to correlate with the distance of perceived action boundaries both before and after the rotation, as revealed by the significant correlation in PRE- ( $p<0.001$ ;  $r=0.67$ ;  $\text{PSE}=37.1+0.85 \times \text{RT max}$ ) and in POST-rotation ( $p<0.001$ ;  $r=0.83$ ;  $\text{PSE}=40+0.94 \times \text{RT max}$ ).

A 2 Group (CW and CCW) x 2 Condition (PRE- and POST-rotation) ANOVA on maximum RT distance showed a significant effect of Condition ( $F(1, 18) = 12.92$ ,  $p<0.01$ ,  $\eta^2 = 0.42$ ) but no significant effect of Group ( $p=0.53$ ) or interaction ( $p=0.16$ ). Post-hoc analyses revealed that maximum RT occurred at a closer target distance in POST- (mean =  $31 \pm 91\text{mm}$ ) than in PRE-rotation (mean =  $67 \pm 96\text{mm}$ ;  $p<0.01$ ), showing a mean shift of 36 mm.



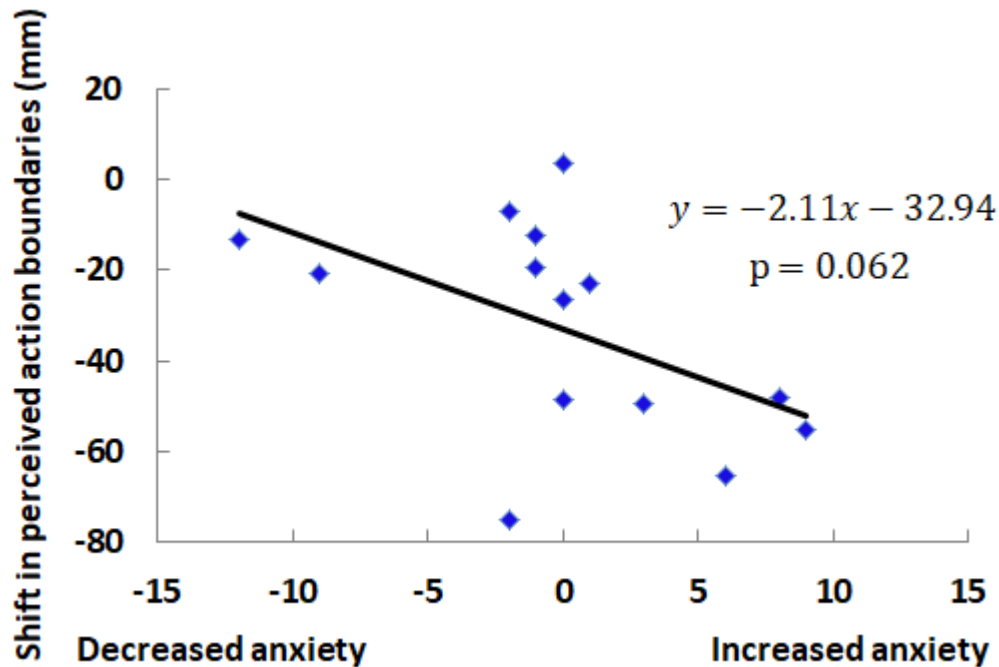
*Fig. 5 Shift in perceived action boundaries associated with a CW or CCW rotation. (A) Response time of a representative participant from CW group (left panel) and CCW group (right panel) as a function of target distance. Data points represent mean response times for each target position in PRE- (filled circles) and POST-rotation (empty diamonds), and curves illustrate the Gaussian fit of PRE-rotation (solid line) and POST-rotation (dotted line) data. (B) Mean shift between target distances corresponding to maximum response time (solid bars) and PSE (striped bars) in PRE- and POST-rotation, for CW group (blue) and CCW group (red). Error bars represent the standard deviation of the mean.*

*c. State anxiety test*

State anxiety scores of participants of the CW group ranged between 20 and 37 in anxiety-PRE, and ranged between 20 and 35 in anxiety-POST, indicating that state anxiety was low throughout the experiment for all participants. A paired t-test between state anxiety scores

in anxiety-PRE ( $27.7 \pm 5.6$ ) and anxiety-POST ( $27.7 \pm 4.7$ ) revealed no significant difference between the two conditions ( $t(13)=0.00$ ;  $p=1.0$ ). While there was little variation in state anxiety across PRE- and POST-tests, we performed correlation analyses (Pearson's correlation coefficient) to test the link between individual anxiety and individual shifts in perceived action boundaries. Results showed that state anxiety in the PRE-test was not significantly correlated with the  $\Delta$ PSE ( $r=0.14$ ;  $p=0.62$ ) and shift in maximum RT distance ( $r=0.60$ ;  $p=0.072$ ). Although the increase of state anxiety tended to correlate with an increase in the PSE shift, as illustrated in Figure 6, there was no significant correlation between anxiety changes and shift in maximum RT distance ( $r=0.60$ ;  $p=0.067$ ) or  $\Delta$ PSE ( $r=0.51$ ;  $p=0.062$ ). To further analyse this possible effect, we compared the shift in perceived action boundaries in the seven participants with the largest increase in state anxiety versus the other seven participants (small increase or decreased state anxiety). An independent t-test between  $\Delta$ PSE in the two groups did not reveal a significant difference ( $t(12)=0.58$ ;  $p=0.57$ )

To assess whether state anxiety was linked to action boundaries perception in the present study, we also conducted correlation analyses between state anxiety scores in PRE and POST-condition ( $27.7 \pm 4.6$ ) and PSE in PRE- and POST-rotation. We found no significant correlation between mean anxiety score and PSE in PRE- ( $r=0.15$ ;  $p=0.61$ ) or in POST-rotation ( $r=0.10$ ;  $p=0.73$ ), between anxiety-PRE scores and PSE in PRE-rotation ( $r=0.11$ ;  $p=0.72$ ) or between anxiety-POST scores and PSE in POST-rotation ( $r=0.01$ ;  $p=0.98$ ). We found no significant correlation between mean anxiety score and maximum RT distance in PRE- ( $r=0.15$ ;  $p=0.61$ ) or in POST-rotation ( $r=0.10$ ;  $p=0.73$ ), between anxiety-PRE scores and maximum RT distance in PRE-rotation ( $r=0.51$ ;  $p=0.13$ ) or between anxiety-POST scores and maximum RT distance in POST-rotation ( $r=0.23$ ;  $p=0.53$ ).



**Fig. 6** Evolution of state anxiety level through the experiment as a function of the shift in perceived action boundaries, for the CW group. Data points represent each participant in the CW group and the solid line illustrates the linear regression.

## Discussion

Our previous work showed a link between exposure to modified limb dynamics and change in perception of action boundaries, suggesting that the representation of peripersonal space is partly subtended by internal models for motor control (Leclere et al. 2019). To further explore the plasticity of peripersonal space representation, in the present study we reversed the direction of the new force field and analysed its effect on perception of action boundaries. Overall, our results show that participants perceive action boundaries closer to their body following exposure to new limb dynamics, irrespective of the direction of the inertial perturbation. This finding supports the idea that although exposure to new limb dynamics results in specific updating of internal models, it generates a nonspecific leftward shift of the

representation of peripersonal space. We now consider certain mechanisms through which exposure to an inertial perturbation, and associated motor errors, may influence perception of action boundaries and thus peripersonal space representation.

*Sensorimotor adaptation as a function of the direction of the perturbation*

We used a rotating platform to study sensorimotor adaptation in participants who had to move their hand toward a visual target in a perturbed force field. Our results were consistent with findings from many previous studies using a similar short-term adaptation paradigm (Lackner and DiZio 1994; Coello et al. 1996; Bourdin et al. 2001; Sarlegna et al. 2010). Our participants exhibited a typical pattern of motor responses when moving their arm in a perturbed force-field. Once the platform rotation began, reaching movements were deviated in the direction of the perturbation before rapidly recovering a performance similar to that observed in the usual force field. Then, in the first movements after the rotation ended, trajectories were deviated opposite to the perturbation, a well-known after-effect from sensorimotor adaptation. Finally, arm reaching movements at the end of the experiment were as accurate as in baseline.

Critically, the present study compared the performance of two groups of participants performing arm reaching movements during opposite rotations: clockwise (CW) vs counterclockwise (CCW). Coriolis forces deviated the arm counterclockwise (leftward for straight-ahead movements) for participants in the CW group and clockwise (rightward) for the CCW group. Rightward adaptation was observed in the CW group, as reflected by the rightward after-effects. Leftward adaptation and thus leftward after-effects were observed in the CCW group, consistent with other reach adaptation studies performed during platform rotation, mainly counterclockwise, since the pioneer work of Lackner and DiZio (1994) and

Coello and Orliaguet (1994) (see also Coello et al. 1996; Bourdin et al. 2001; Sarlegna et al. 2010; Lefumat et al. 2016).

Reach adaptation to a new force field is currently explained in the mainstream literature on motor control as related to the updating of the forward and inverse internal models of limb dynamics (Wolpert and Kawato 1998; Sainburg et al. 1999; Shadmehr 2018). In our study, the new limb dynamics during rotation were likely taken into account by the inverse model to formulate the motor commands generating arm displacement to the target, while the forward model also took into account the new limb dynamics to update prediction of the sensory consequences of the motor commands. Updating of such central representations may thus underlie the adaptation process observed in the present study, and the specific adaptation to each force field is consistent with several studies reporting after-effects of sensorimotor adaptation in the opposite direction to the perturbation (Diedrichsen et al. 2010; Ostry et al. 2010; Michel et al. 2018; Ohashi et al. 2019).

The force field remained the same during the exposure phase and the large errors made in the initial trials with the new force field likely influenced the sensorimotor adaptation process. A fast process is known to lead to rapid changes in movement control at the beginning of sensorimotor adaptation, while a slow process gradually sets in and induces changes in movement control (Smith et al. 2006; Shadmehr et al. 2010; Wolpert et al. 2011; McDougle et al. 2016). Some studies suggest that the fast process corresponds to an explicit adaptation linked with declarative memory (Keisler and Shadmehr 2010; McDougle et al. 2015), while the slow process may correspond to a more implicit adaptation (McDougle et al. 2015). Mazzoni and Krakauer (2006) clearly showed the importance of implicit mechanisms in sensorimotor adaptation and McDougle et al. (2016) suggested that sensory prediction errors, the mismatch between predicted and actual feedback, may drive implicit adaptation, while the making of

errors may drive explicit adaptation. In the context of the present study, implicit and explicit processes could be seen as contributing differently to the updating of sensorimotor control processes and reachability judgments, an issue that should be specifically investigated in further work.

*Change in perceived action boundaries is unrelated to the direction of the perturbation*

The novel finding from the present study concerns the direction of the shift in perception of action boundaries following exposure to a new force field. Indeed, our results combined with those from a previous study (Leclere et al. 2019) show that, regardless of the direction of the force-field perturbation and sensorimotor adaptation, the distance at which participants judged themselves able to reach objects was shifted to the left after exposure to the perturbation than before. In other words, two groups that had specifically adapted to two opposing force fields exhibited a similar leftward shift of their perceived action boundaries. Moreover, the non-significant effect of the inertial perturbation on their discrimination threshold suggests that changes in perceived action boundaries were not due to any between-condition differences in difficulty of the reachability judgment task. In addition, the distance generating the maximum response time was shifted leftward after adaptation to the rotation than before, and was positively correlated with perceived action boundaries. The observation of a response time maximum around perceived action boundaries corroborates findings from previous studies (Coello et al. 2008; Hirose et al. 2010; Bartolo et al. 2014b), and the shifts revealed by analysis of response time and by the reachability judgement itself support the idea of an undifferentiated leftward shift of peripersonal space representation following exposure to new limb dynamics.

This leftward shift could reflect a displacement of the entire peripersonal space perception to the left as well as a contraction of the perceptual judgements. Although our results cannot rule out the first alternative, a displacement of the peripersonal space appears to be unlikely in view of previous work in the field. Indeed, several studies highlighted a modification of the peripersonal space perception getting closer to the body, after wearing a wrist weight (Longo and Lourenco 2009), being adapted to a biased visual feedback (Bourgeois and Coello 2012) or moving a shortened virtual arm (Yang et al. 2020). All these studies concluded to a reduction of the peripersonal space related to the independent variable they manipulated. Although a leftward shift represents an alternative interpretation, it seems unlikely due to the fact that, in contrast to our study, opposite sensorimotor adaptations usually lead to opposite shifts of the spatial frame of reference, as indicated by the straight-ahead for instance (Harris 1963; McLaughlin 1967; Girardi et al. 2004) and that gaze directed to lateral targets implying eye rotation does not induce shift in subjective straight ahead (Newport et al. 2008).

This undifferentiated contraction of perceived action boundaries contrasts with findings elsewhere on the representation of the hand position following exposure to a new force field. Ostry et al. (2010) showed that hand position was perceived to be displaced in the opposite direction to the perturbation its movements had previously adapted to. The nonspecific effect of force-field perturbation on perception of action boundaries also appears to contrast with the effect of visuomotor perturbation (Linkenauger et al. 2015; Bourgeois and Coello 2012). For instance, Bourgeois and Coello (2012) manipulated the relationship between visual and actual movement amplitude and showed that visuomotor adaptation in two groups with opposite changes of visual gain was associated with opposite variations in perception of action boundaries. However, a key difference between their study and ours is that Bourgeois and Coello (2012) induced a kinematic bias in the relationship between motor commands and their



visual spatial consequences, whereas we induced a dynamic bias in the relationship between motor commands and their somatosensory spatial consequences. The well-documented differences between visuomotor and force-field adaptation (Krakauer et al. 1999; Haith and Vijayakumar 2009; Sarlegna and Bernier 2010; Donchin et al. 2012) may explain why the change in perceived action boundaries was not dependent on the direction of the perturbation in the present study.

#### *Consequence of sensorimotor uncertainty on perceived action boundaries*

In the present study, perturbation of the force field systematically resulted in a direction-specific updating of the central representation of limb dynamics and, contrary to our expectations, in an undifferentiated modification of perceived action boundaries regardless of the direction of the perturbation. We must point out that an ordinal interaction between groups and conditions on the action boundaries perception was close to significance. However, the direction of the shift in reachability was the same whether the perturbation was in one direction or the opposite, and even though results in motor performance clearly showed after-effects opposite to the direction of the perturbation. Therefore, the hypothetical difference in the magnitude of the perceptual effect between the two groups does not alter the main conclusion of our study, that the direction of the perceptual shift is similar despite changes in the direction of the new force field. This key result thus sheds new light on the interplay between the plasticity of the motor system and peripersonal space representation.

Previous studies showed that the representation of peripersonal space can be influenced by context, shrinking in the presence of dangerous objects (Bourgeois et al. 2012) or when anxiety increases (Graydon et al. 2012). We did not assess participants' anxiety for the CCW group in our previous study (Leclere et al. 2019), but assessed state anxiety of participants in

the CW group in the present study. State anxiety of participants remained quite low throughout the experimental procedure, corroborating the fact that no explicit feeling of anxiety was reported by participants during or after the experiment, for instance due to the platform rotation. Such potential source of anxiety for the participants was shown to not significantly influence their perception of action boundaries (Leclere et al. 2019). The perception of action boundaries was not significantly correlated with state-anxiety level, although a trend was observed. Future work will be necessary to further assess the influence of anxiety on reachability judgments, which has been shown by Iachini et al. (2015) as state anxiety was correlated with perceived distance of action boundaries (although not greatly:  $r=0.297$ ;  $p<0.05$ ). Changes in peripersonal space representation are thus more likely to stem from the initial altered reaching performance in the novel force-field environment, which may have induced uncertainty about sensorimotor performance. While Bourgeois and Coello (2012) showed that perception of action boundaries was modified eventually according to the direction of biased visual feedback, they also reported that initial exposure to distorted visual feedback resulted in a contraction of perceived action boundaries, irrespective of the visuomotor bias. In a second experiment, Bourgeois and Coello (2012) showed that increasing uncertainty about sensorimotor performance by providing random visual feedback produced the same contraction of perceived action boundaries (without any visuomotor adaptation). They interpreted this contraction as due to the sudden experience of lack of sensorimotor system reliability, the uncertainty as to motor performance thus reducing subjects' confidence in their action capabilities. In the same vein, the modification of perceived action boundaries observed in the present study could be due to a "conservative" response of the nervous system, i.e. a contraction of peripersonal space representation linked to the perturbation context.

Our participants made large reaching errors in trials immediately following the platform rotation. These initial performance errors may have been associated with an explicit

“conservative” strategy (McDougle et al. 2015, 2016). The conservative strategy observed on reachability judgments could also result from participants attributing the large errors at the beginning of the exposure phase to the fact that the platform rotation was changed from 0 to 120 deg/s (Lefumat et al. 2015). When the rotation of the platform was changed again, this time from 120 to 0 deg/s, participants may have predicted large motor errors based on those experienced before (Herzfeld et al. 2014) and their peripersonal space representation may have contracted conservatively, consistent with its protective role (Dosey et al. 1969; De Vignemont and Iannetti 2015; Graziano 2018; Noel et al. 2018; Coello and Iachini in press). In other words, even though participants were not explicitly informed about changes in limb dynamics due to the platform rotation, the platform deceleration could have triggered the recall of large movement errors following a change in platform rotation. Since in our study, participants were explicitly informed about the forthcoming modification of the platform state (i.e., platform acceleration or deceleration), we speculate that large movement errors may have generated sensorimotor adaptation and modification of perceived action boundaries through two distinct mechanisms relying on implicit and explicit processes. Further investigations could contribute to determining, for instance, whether gradual exposure to new limb dynamics, which is known to result in sensorimotor adaptation without large errors (Ingram et al. 2000; Klassen et al. 2005; Mattar et al. 2013), also induces contraction of peripersonal space representation. Moreover, we did not assess perception of action boundaries after the de-adaptation phase as this was not crucial to determine if the observed perceptual shift was specific to the direction of the perturbation. However, adjusting the experimental design in future studies will allow a better characterization of the temporal dynamics of the shift in the perception of peripersonal space after exposure to a new force field.

## *Conclusion*

In conclusion, the present study showed that the representation of peripersonal space changed after exposure to new limb dynamics, and that this change was not dependent on the direction of the perturbation encountered. In particular, participants judged action boundaries to be reduced after reach adaptation, suggesting that their peripersonal space representation contracted after exposure to new limb dynamics. This may have been due to uncertainty about their action capabilities and sensorimotor predictions, which could have influenced the perception of action boundaries. Overall, our results highlight the plasticity of the representation of peripersonal space, and support its interdependence with the sensorimotor control system.

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