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Right-left hand asymmetry in manual tracking: when poorer control is associated with better adaptation and interlimb transfer

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Abstract

To date, interlimb transfer following visuomotor adaptation has been mainly investigated through discrete reaching movements. Here we explored this issue in the context of continuous manual tracking, a task in which the contribution of online feedback mechanisms is crucial, and in which there is a well-established right (dominant) hand advantage under baseline conditions. We had two objectives 1) to determine whether this preexisting hand asymmetry would persist under visuomotor rotation, 2) to examine interlimb transfer by assessing whether prior experience with the rotation by one hand benefit to the other hand. To address these, 44 right-handed participants were asked to move a joystick and to track a visual target following a rather unpredictable trajectory. Visuomotor adaptation was elicited by introducing a 90° rotation between the joystick motion and the cursor motion. Half of the participants adapted to the rotation first with the right hand, and then with the left, while the other half performed the opposite protocol. As expected during baseline trials, the left hand was less accurate while also exhibiting more variable and exploratory behavior. However, participants exhibited a left hand advantage during first exposure to the rotation. Moreover, interlimb transfer was observed albeit more strongly from the left to the right hand. We suggest that the less effective and more variable/exploratory control strategy of the left hand promoted its adaptation, which incidentally favored transfer from left to right hand. Altogether, this study speaks for further attention to the dominant/non-dominant asymmetry during baseline before examining interlimb transfer of adaptation.

Introduction

Understanding how humans adapt hand movements when confronted to a visuomotor perturbation has relied primarily on discrete reaching movements performed towards a stationary target (Carroll et al., 2014; Henriques & Cressman, 2012; Krakauer et al., 2000; Krakauer, 2009; Seidler, 2006; Wang & Sainburg, 2006). Although considerable knowledge has been brought by these studies, this body of research does not necessarily account for the adaptation of continuous movements (Cohen et al., 2019; Coudiere et al., 2022). First, the contribution of online visual feedback control (i.e. the ability to exploit ongoing visual information for updating hand motor command) is expected to increase for continuous tasks, especially when tracking a target that follows an unpredictable path (Coudiere et al., 2022; Lam & Zénon, 2021). Second, when visuomotor adaptation is required, the use of continuous tasks minimizes the implication of cognitive strategies as time pressure inherent to these tasks imposes fast deliberation to ongoing actions (Yang et al., 2021; Yoo et al., 2021). Third, asymmetrical transfer of visuomotor adaptation between discrete and continuous tasks confirms that these types of movement are driven by (at least partly) distinct neural mechanisms (Abeele & Bock, 2003; Coudiere et al., 2022; Ikegami et al., 2010). The overarching goal of the current study is to help filling this gap by assessing interlimb differences and transfer in visuomotor adaptation during manual tracking, a task in which a hand dominance effect at baseline (i.e. without adaptation) has been consistently reported (Aoki et al., 2006; Carey et al., 2003; Mathew et al., 2019, 2020; Peña-Pérez et al., 2023; Simon et al., 1952).

The first objective is to compare the adaptation of manual tracking by right (dominant) and left (non-dominant) hands to a visuomotor rotation. Various results have been found in the context of discrete reaching movements. While some studies report that visuomotor adaptation is facilitated in the right hand (Chase & Seidler, 2008; Taylor et al., 2011), others found no advantage from either hand (Balitsky Thompson & Henriques, 2010; Kumar et al., 2020;

Sainburg, 2002; Yamagami et al., 2021). Even more contrasting findings were obtained when comparing the acquisition of new motor skills, with sometimes a left hand advantage (Perelle et al., 1981; Wang et al., 2020; Yadav & Mutha, 2020), a right hand advantage (Cho et al., 2006; McGrath & Katak, 2016), or no advantage (Garry et al., 2004; Schulze et al., 2002). Interestingly, few studies paid attention to possible preexisting right-left hand asymmetries before the launch of adaptation/acquisition protocols. As stated above, there is accumulated evidence that the left (non-dominant) hand has poorer tracking performance (Aoki et al., 2006; Carey et al., 2003; Mathew et al., 2019, 2020; Simon et al., 1952). Whether this right hand advantage persists or not under rotated feedback has not been addressed yet. Indeed, although several studies have already investigated the adaptation of manual tracking under rotated feedback, to our knowledge, all of them were conducted exclusively on the dominant hand (Abeele & Bock, 2001; Gouirand et al., 2019; Mathew et al., 2018; Ogawa & Imamizu, 2013; Tong & Flanagan, 2003). In this context, we formulate two opposite hypotheses. Assuming that the right (dominant) hand/left hemisphere has an advantage for visual feedback processing (Apolinário-Souza et al., 2023; Elliott et al., 1999; Flowers, 1975; Goble & Brown, 2008; Roy & Elliott, 1986), one possibility is that the right hand will exhibit better performance than the left hand when it is first confronted to visual errors induced by the rotated feedback. Conversely, it is possible that the left (non-dominant) hand will exhibit better performance because the control processes driving this hand may be less reticent to changes imposed by the visual perturbation. Such possibility is grounded upon the observation that movement variability, task exploration and lower state estimation during baseline condition could induce faster adaptation (Dhawale et al., 2017; Wei & Koerding, 2010; Wu et al., 2014; although see He et al., 2016).

The second objective is to investigate interlimb transfer following the adaptation of manual tracking. Interlimb transfer refers to the ability of one limb to benefit from prior learning/adaptation acquired with the other limb. Again, interlimb transfer of sensorimotor

adaptation has essentially focused on reaching movements, and reports can vary substantially across studies (Lefumat et al., 2015). First, the magnitude of interlimb transfer can range from zero (Harris, 1963; Kitazawa et al., 1997; Martin et al., 1996) to nearly full transfer (Imamizu & Shimojo, 1995; Poh et al., 2016). Second, when interlimb transfer is observed, it is often described as asymmetric (Balitsky Thompson & Henriques, 2010; Carroll et al., 2014; Wang & Sainburg, 2004), but the direction of this asymmetry vary across studies. Indeed, although some studies argue for greater transfer from the left to the right hand (Chase & Seidler, 2008; Sainburg, 2002; Wang & Sainburg, 2004), contrary findings have been reported elsewhere (Balitsky Thompson & Henriques, 2010; Imamizu & Shimojo, 1995). Notably, this asymmetry could depend on the task and on the variable of interest (Sainburg & Wang, 2002), but also on individual movement characteristics (Renault et al., 2020). At this stage, we are only aware of four studies that investigated interlimb transfer following visuomotor adaptation during continuous tasks (Latash, 1999; Parlow & Kinsbourne, 1989; Thut et al., 1996; Yamagami et al., 2021). In the former study, Latash (1999) showed that adaptation to mirror writing with the dominant hand transfers to the non-dominant hand (transfer in the opposite direction was not addressed). In the next two studies that either required drawing meaningless figures or printing letters (Parlow & Kinsbourne, 1989; Thut et al., 1996), training of the left hand benefited more to the right hand than the other way around. In the last one, adaptation of visuomotor tracking to second-order machine dynamics resulted in large and symmetrical interlimb transfer (Yamagami et al., 2021). Still, despite growing interest for the adaptation of manual tracking to a visuomotor rotation (Abeele & Bock, 2003; Coudiere et al., 2022; Mathew et al., 2018; Ogawa & Imamizu, 2013; Snyder et al., 2014; Yang et al., 2021), the issue of interlimb transfer has not been explored yet in this particular context. Here, we reason that interlimb generalization is more likely to occur from the hand that exhibited greater learning (Chase & Seidler, 2008), and/or that acquired the highest level of implicit adaptation (Kumar et al., 2020).

Namely, if a right hand advantage is observed under rotated feedback, we predict greater transfer from right to left than the other way around, and vice versa if a left hand advantage is observed under rotated feedback.

In short, the current experiment focused on visuomotor adaptation of continuous pursuit movements in right-handers with the two following issues in mind: 1) Does the right hand advantage observed under baseline condition persists during adaptation to a visuomotor rotation? 2) Is there interlimb transfer of adaptation, and if any, is it asymmetrical? To address these questions, we used a between-group design (Coudiere et al., 2022; Mathew et al., 2018) in which we compared the tracking performance of two right-handed groups that successively adapted each hand to a 90° visuomotor rotation, with one group adapting first with the right hand, and the other adapting first with the left hand (Sainburg & Wang, 2002; Wang et al., 2011). Group comparisons allowed to assess possible differences in right/left hand learning, as well as in the extent of interlimb transfer.

Methods

Participants

Two groups of 22 healthy right-handed volunteers were recruited (Group 1: 24.0 ± 3.8 yrs, 11 females; Group 2: 22.7 ± 3.4 yrs, 11 females). Handedness of participants was verified using the Oldfield Handedness Inventory (Oldfield, 1971) with a mean laterality index of 81.7 ± 15.1 for Group 1, and 82.3 ± 15.2 for Group 2. All participants gave written consent prior to participation. The experimental paradigm was approved by the local ethics committee (comité d'éthique pour la recherche en sciences et techniques des activités physiques et sportives) and complied with the Declaration of Helsinki.

Data Acquisition

Figure 1 shows the experimental set up. Participants were seated comfortably in a dark room facing a screen (BENQ, 1920×1080, 27 inch, 144Hz) positioned on the frontal plane 57 cm away from the participant's eye. Participants' head movements were restrained by a chin rest and a padded forehead rest so that the eyes in primary position were directed toward the center of the screen. To block the vision of their hands, a mask was positioned under the participants' chin. They were required to hold with the hand a joystick (Serie 812, Megatron, France, with ± 25 degrees of rotation along X-Y axes) positioned horizontally on a table in front of the participant, in line with the central sagittal plane. Note that there was no restoring force to bring back the joystick at the central position. Both the right and left forearms were resting on the table. The output of the joystick was fed into a data acquisition system (Keithley ADwin Real-Time, Tektronix) and sampled at 1000 Hz.

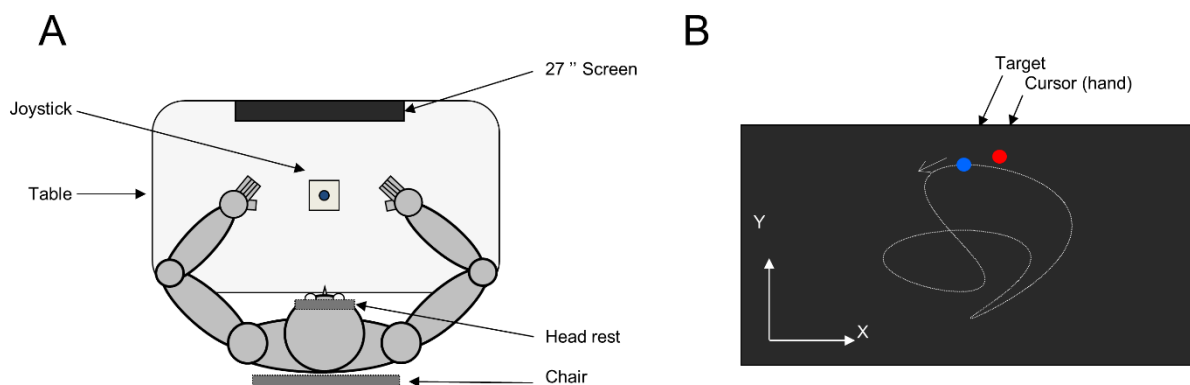


Fig. 1 Schematic drawing of the experimental setup. A. Top view of the participant sitting in the experimental setup. B. Schematic view of the screen during the tracking task (see Methods for more details).

Experimental design

During the tracking task, participants were instructed to minimize the distance between a red cursor (0.5° in diameter) driven by a joystick and a blue target (0.5° in diameter). The

delay between the joystick (hand) and the cursor was only slightly longer than the time needed to render and display the cursor on the screen (on the order of 7-8 ms). The motion of the target resulted from the combination of sinusoids: two along the frontal axis, and two others along the sagittal axis. This technique was used to generate pseudo-random 2D pattern while preserving smooth changes in velocity and direction (Mrotek & Soechting, 2007; Soechting et al., 2010). We used the same equations and parameter setting as those employed in Mathew et al. (2018). This led to a total of 5 different patterns that were randomized across trials. Mean target eccentricity measured in all directions with respect to the center of the screen was 6.0 ± 2.7 cm, with values ranging from 0.4 up to 11.8 cm. The time necessary to complete a full revolution of each pattern was 5 s. Given that all trials had a duration of 10 s, each movement pattern was repeated twice during each trial.

Under baseline condition, the relation between the joystick motion and its visual consequences on the screen was very intuitive, mimicking the behavior of a computer mouse. Under adaptive condition, the previous mapping was rotated by 90° counter-clockwise (Ogawa & Imamizu, 2013).

Participants were split into two groups that both performed the tracking task under the regular and rotated mapping, using successively the right and left hands. The experimental session consisted of 3 phases (see Fig. 2). During the initial phase (Baseline, 0°), the first group of participants (Group RL) performed one block of 10 trials with the right hand followed by one block of 10 trials with the left hand, both under the regular mapping. Subsequently, during the adaptation phase (90°), this group performed one block of 40 trials with the right hand followed by one block of 40 trials with the left hand, both under the rotated mapping. During the final phase, the initial mapping was restored (0°), allowing to test for after-effects with 2 trials with the left hand followed by 2 trials with the right hand. The second group of participants (Group LR) followed the same protocol (baseline, adaptation to rotation, and after-effects)

except that the order of hand was reversed for each phase. This experimental design was selected to assess possible interlimb asymmetries in adaptation and its transfer by means of group comparisons.

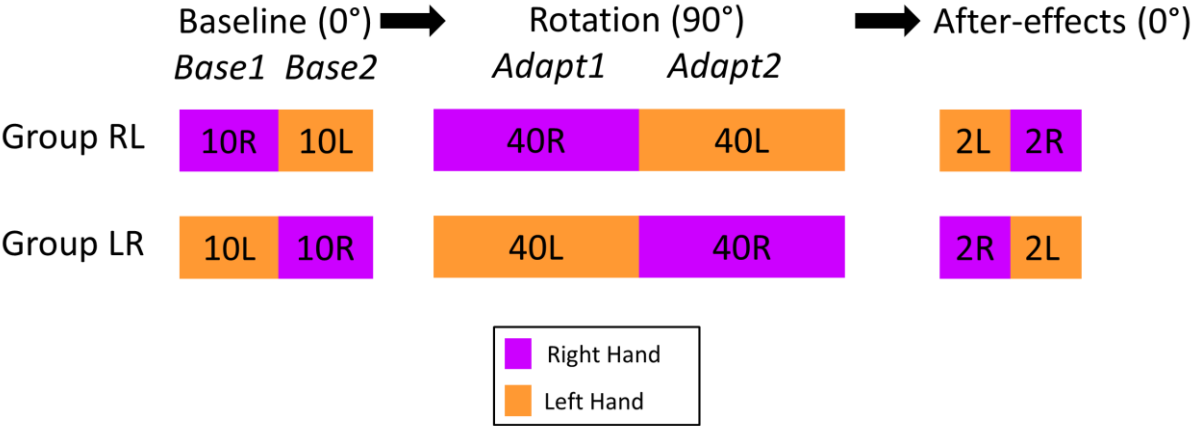


Fig. 2 Experimental design for each group of participants (see Methods for further information).

Data analysis

Data were analyzed using Matlab R2022b. To assess tracking performance in each trial, we measured the mean Euclidian distance between the cursor (moved by the hand) and the target while discarding the first second of each trial (to minimize transients due to initial cursor positioning). To assess cursor variability across baseline trials, we took advantage of the fact that each participant performed two trials with each of the 5 target patterns. For each pair of trials, we evaluated the gap between the two cursor trajectories with the procedure illustrated in Figure 3. Practically we measured for each data point the Euclidian distance between the cursor’s position during the first and second trial. In line with the assessment of tracking performance, the resulting distances were averaged over the last 9 seconds of tracking. Finally, those distances were averaged across patterns while analyzing each hand separately. As an attempt to capture the extent of task exploration during baseline, we conducted a second analysis in which we estimated the total area visited by the cursor around the target during each

trial. This estimation was obtained by means of a 10 by 10 grid (100 squares of 1cm² each) centered on the current target position. We then measured the total number of squares that were visited at least once by the cursor. We reasoned that a greater surface was indicative of greater task exploration.

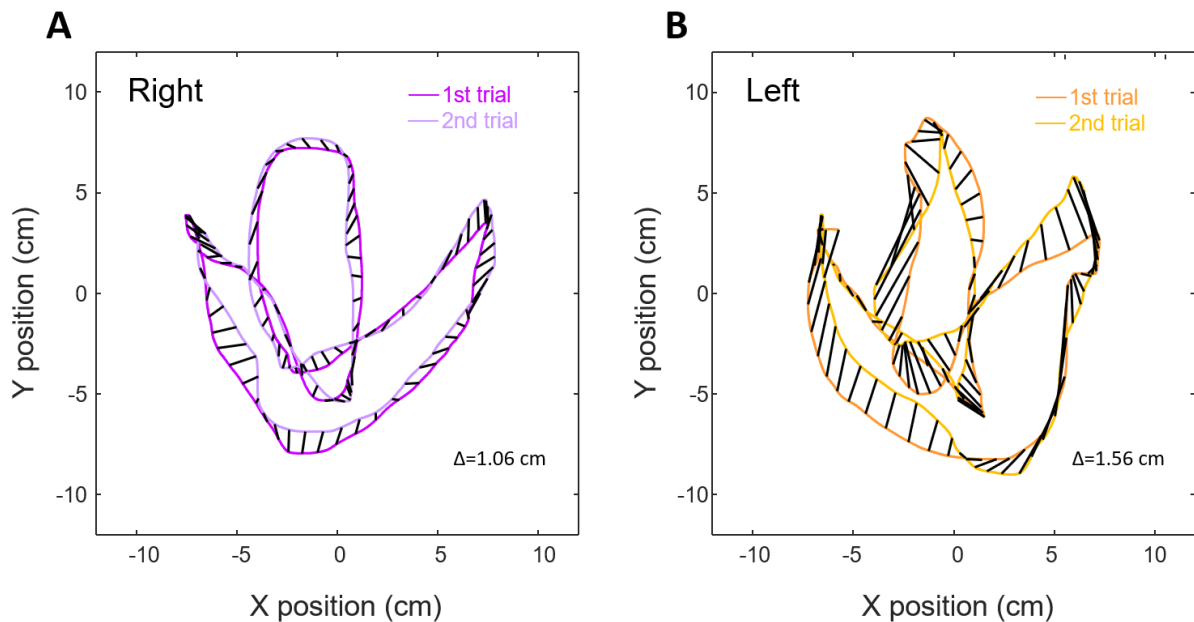


Fig. 3 Method used to assess between-trials variability in hand movement trajectory. Black segments represent the instantaneous Euclidian distance between cursor positions across the two baseline trials that employed the same target pattern. Cursor variability (Δ) was obtained by averaging the length of all the black segments. We display 2 typical trials performed by the right (A) and left hand (B) of the same participant (only 5 s of signals are displayed for clarity). Note the larger variability of the left hand compared to the right hand (see Methods for further information).

Using Statistica (version 13), repeated measures ANOVAs were used as the main tool for statistical analyses. Depending on the comparison, we assessed the effect of HAND (Right vs. Left), GROUP (RL vs. LR) and TRIAL (2 first vs. 4 last trials); initial tracking error was assessed using only 2 trials as it decreased rapidly, whereas more stable final tracking error allowed its assessment using a larger set of trials. To remain consistent with the procedure used for baseline tracking performance, final tracking error was assessed by averaging errors on the last 4 trials performed by each hand. Newman-Keuls corrections were used for post hoc t-tests

to correct for multiple comparisons. A conventional 0.05 significance threshold was used for all analyses.

Results

Representative trials

Figure 4 shows representative trials performed by two naïve participants at baseline performance during early exposure to the visuomotor rotation. As can be seen on the left side, baseline manual tracking was more accurate for the right hand than for the left one. Moreover, tracking performance was altered when the rotation was introduced, albeit possibly less extensively for the left hand. Finally, on the extreme right column, it can be observed that prior training with one hand benefited to initial tracking with the other hand, thereby arguing for interlimb transfer effect. In the next sections we analyze in more details these preliminary observations.

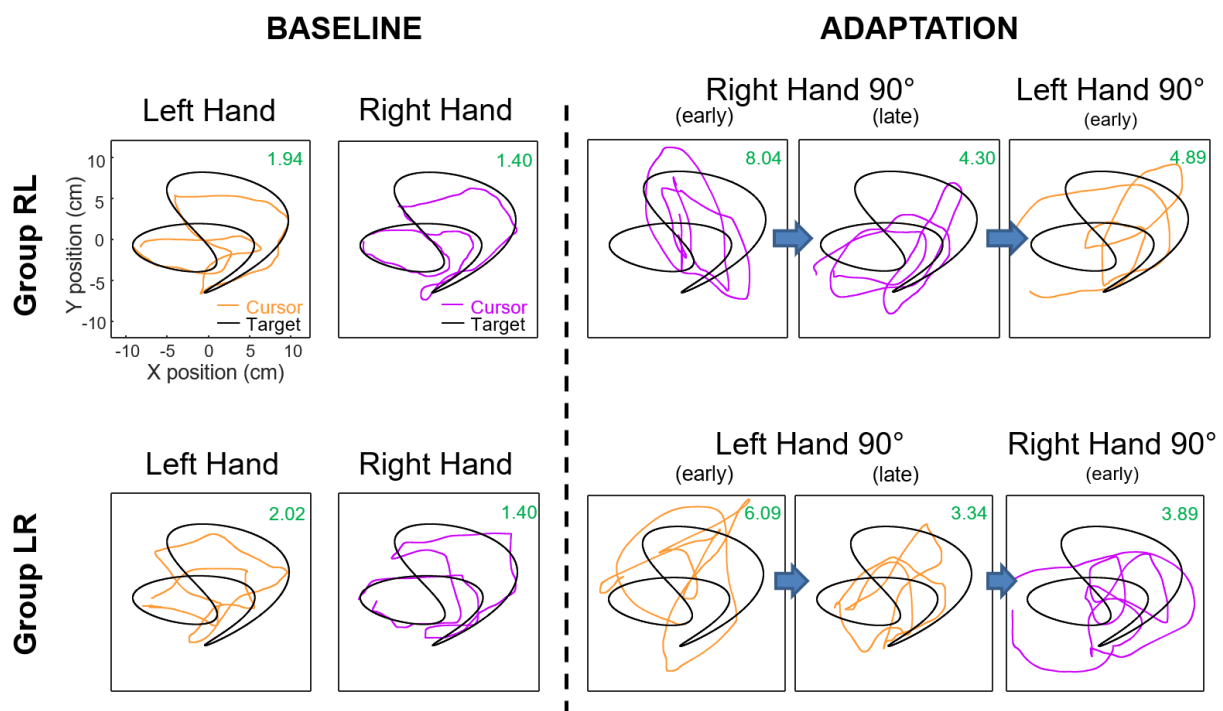


Fig. 4 Representative trials under each experimental condition. Cursor and target signals during baseline and early exposure to the visuomotor rotation. The top and bottom row show trials performed respectively by a participant of the RL and LR group. Although each trial was

10 s long, only 5 s of signals are displayed for clarity, with the corresponding tracking error (in cm) shown in green. To make the comparison easier, we display trials with the same target trajectory. Note the better performance of the right hand during baseline, and the better performance of the left hand during early adaptation.

Baseline trials

In Figure 5, we present the mean group tracking performance over each successive trial as a function of hand and group. As shown by the left side of Figure 5 (denoted as Base1 and Base2), tracking performance was less accurate when moving the joystick with the left hand than with the right one. Indeed, on average, the cursor-target distance was 15% larger when using the left hand (2.01 vs. 1.74 cm). The two-way ANOVA confirmed a main effect of HAND ($F(1,42)=79.32$; $p<0.001$), but there was no effect of GROUP ($F(1,42)=0.071$; $p=0.79$) nor an interaction between the two ($F(1,20)=2.59$; $p=0.11$). These results are consistent with a similar right (dominant) hand advantage in both groups of participants, thereby facilitating the interpretation of possible group differences later in our protocol.

Regarding trial-to-trial movement variability, as assessed by the difference in cursor position across trials that relied upon the same target pattern, we found that the left hand was 19% more variable in its trajectory than the right one (1.84 vs. 1.54 cm). This was confirmed by a two-way ANOVA showing a main effect of HAND ($F(1,42)=135.94$; $p<0.001$). However, there was no effect of GROUP ($F(1,42)=0.097$; $p=0.75$). Still, there was a GROUP by HAND interaction ($F(1,42)=8.40$; $p<0.001$) associated with a greater left-right asymmetry in Group LR (1.89 vs. 1.52 cm; $p<0.001$) compared to Group RL (1.78 vs. 1.56 cm; $p<0.001$), but with no significant group difference for either hand ($p>0.37$). Regarding task exploration, we found that on average, the surface covered by the cursor was 18% greater when driven by the left hand as compared to when it was driven by the right one (37.7 vs. 32.0 cm²). This was confirmed by a main effect of HAND ($F(1,42)=70.03$; $p<0.001$). As in the previous case, the two-way ANOVA

showed no effect of GROUP ($F(1,42)=0.096$; $p=0.75$), and a significant GROUP by HAND interaction ($F(1,42)=5.36$; $p<0.05$) associated with greater left-right asymmetry in Group LR (38.8 vs. 31.5 cm²; $p<0.001$) than in Group RL (36.6 vs. 32.5 cm²; $p<0.001$), but with no significant group difference for either hand ($p>0.28$). Overall, these analyses provide clear evidence that during baseline tracking, the left hand was both less accurate and more variable than the right hand.

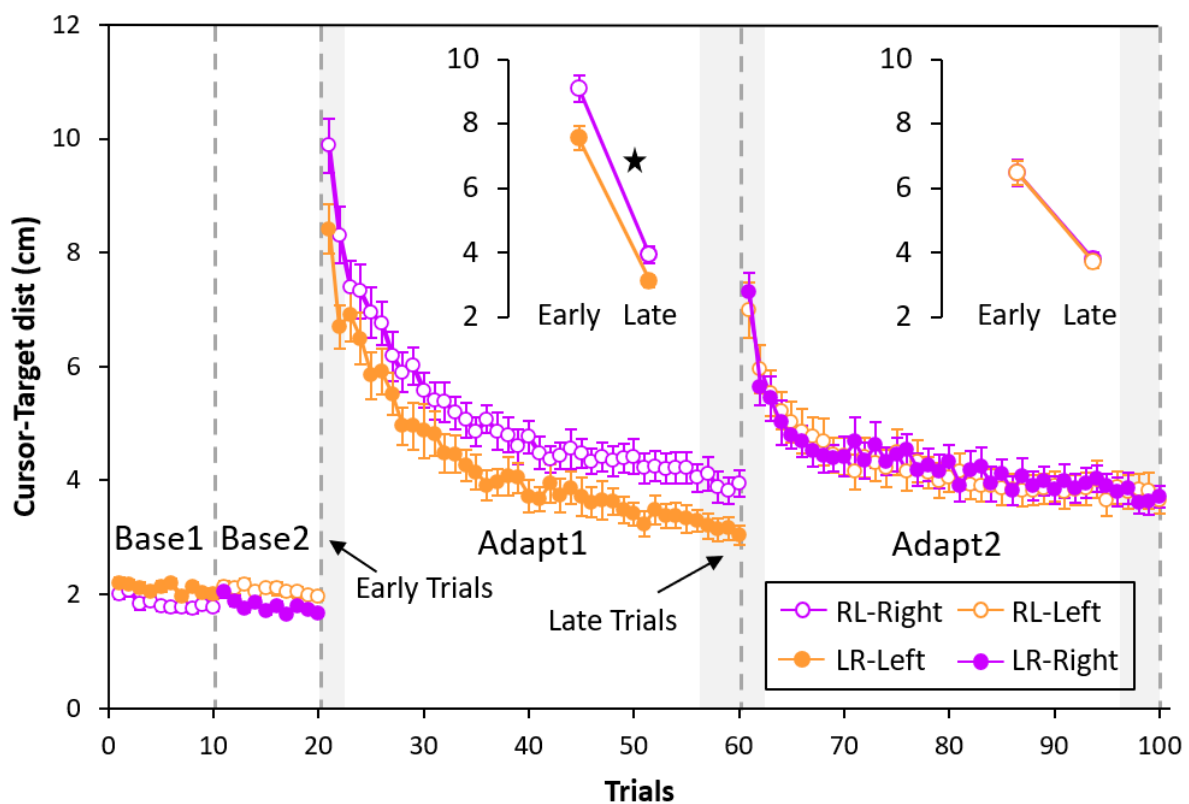


Fig. 5 Time course of tracking performance over the whole experiment as a function of hand and group. Right hands are shown in violet, left hands in orange. The mean cursor-target distance in Group RL is represented with hollow circles, and that of Group LR with filled circles. Error bars correspond to SEM across participants. Base1 and Base2 correspond to baseline trials with both hands, one after the other. The two early trials and the four late trials considered in the analyses are indicated with vertical grey shaded areas, and average tracking errors on those trials are plotted in the insets.

Adaptation of right vs. left hand with no prior experience with the rotation

In the central section of Figure 5 (Adapt1), we show the time course of adaptation when first encountering the rotation either with the right hand (Group RL) or with the left hand (Group

LR). As expected, during early exposure to the rotation, manual tracking was clearly impaired. However, in contrast to baseline trials, in which a right hand advantage was found, under rotated feedback, tracking error appeared smaller for the left hand. Indeed, averaged across the 40 trials of exposure, tracking error was 16% smaller when using the left hand (4.29 vs. 5.13 cm). To investigate this issue in more detail, we run a two-way ANOVA with TRIAL (2 early vs. 4 late) and GROUP (here this factor also accounts for HAND). Results revealed an effect of GROUP ($F(1,42)=10.30$, $p<0.01$) consistent with a left hand advantage under the rotation, and a main effect of TRIAL ($F(1,42)=504.6$, $p<0.001$) consistent with a reduction of error as exposure to the rotation increased. The fact that the interaction was not significant ($F(1,42)=2.06$, $p=0.16$) indicates that the left hand advantage held during both early and late adaptation trials (with tracking error being respectively -17 et -20% lower). Altogether, those results contrast with the right hand advantage found under baseline trials.

Interlimb transfer of adaptation

We focus first on whether prior experience with the rotation by the left hand benefits to learning the rotation with the right hand. In Figure 6A, we compare right hand adaptation in participants who have previously adapted their left hand (Group LR) with right hand adaptation in participants who did not (Group RL). As can be seen, prior adaptation with the left hand immediately transferred to the right hand as evidenced by its lower initial tracking error (-29%). The two-way ANOVA with TRIAL (2 early vs. 4 late) and GROUP showed a main effect of GROUP ($F(1,42)=15.72$, $p<0.001$), a main effect of TRIAL ($F(1,42)=312.8$, $p<0.001$), and a GROUP by TRIAL interaction ($F(1,42)=28.43$, $p<0.001$). Post-hoc analysis of the interaction revealed a significant group difference for early trials ($p<0.001$; RL=9.09 vs. LR=6.47 cm) but not for late trials ($p=0.58$; RL=3.94 vs. LR=3.71 cm). Altogether these results provide clear

evidence of interlimb transfer from the left to the right hand, even though this benefit seems restricted to early adaptation.

Let us now examine whether prior adaptation of the right hand benefits to the left hand. In Figure 6B, we compare left hand adaptation in participants who previously adapted their right hand (Group RL) with those who did not (Group LR). Again, prior adaptation with the right hand transferred immediately to the left hand, as evidenced by its lower initial tracking error (-14%). In this case, the two-way ANOVA with TRIAL (2 early vs. 4 late) and GROUP showed no main effect of GROUP ($F(1,42)=0.29$, $p=0.59$), but a main effect of TRIAL ($F(1,42)=222.9$, $p<0.001$), and a GROUP by TRIAL interaction ($F(1,42)=5.34$, $p<0.001$). Post-hoc analysis supported the observation of smaller tracking error in experienced participants during early trials, ($p<0.05$; RL=6.47 vs. LR=7.56 cm), but not during late ones (RL=3.78 vs. LR=3.13 cm; $p=0.17$).

Altogether, these results speak for interlimb transfer of adaptation, albeit more intensively from the left to the right hand than the other way around (-29 vs. -14%). Because our experimental design does not allow to assess interlimb transfer at the individual level, assessing the reliability of this asymmetry was not straightforward. As an attempt to circumvent this issue, individual transfer was estimated by pairing RL with LR participants who had comparable tracking performance during baseline trials. For each hand, two key criteria for pairing participants were employed, either the mean cursor-target distance or the cursor variability across trials. In each case, participants were matched according to their rank in their respective group. No matter which criteria was employed to match participants, we found that the decrease in tracking error provided by earlier experience with the other hand was significantly greater for the right hand than for the left one (-2.62 vs. -1.08 cm; $t(42)<2.082$, $p<0.05$). Overall, these analyses support the view of an asymmetrical transfer between the right and the left hand.

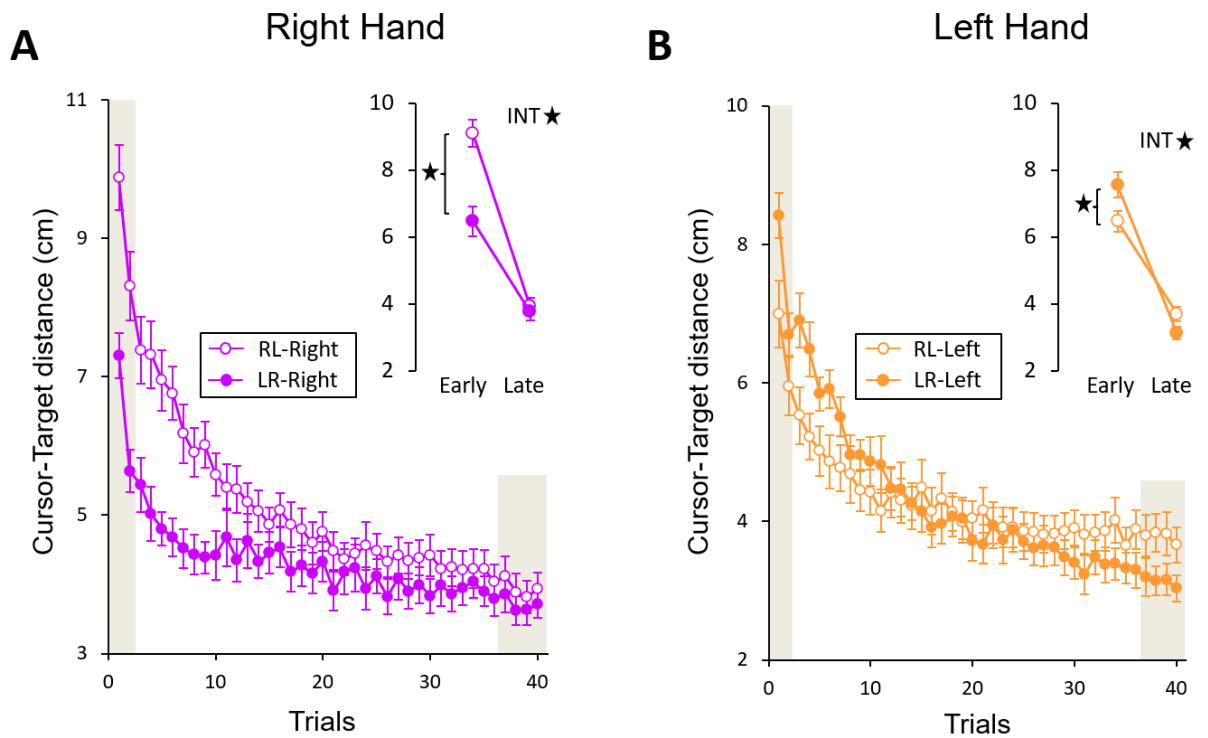


Fig. 6 Tracking performance as a function of hand and prior experience with the other hand. A. Tracking performance of the right hand for naïve (Group RL) and for experienced participants (Group LR). B. Tracking performance of the left hand for naïve (Group LR) and for experienced participants (Group RL). Right hand is shown in violet, left hand in orange. The mean cursor-target distance in Group RL is represented by hollow circles and that of Group LR by filled circles. Error bars correspond to SEM. The two early trials and the four late trials considered in the analyses are indicated with vertical grey shaded areas, and average tracking errors on those trials are plotted in the insets. Note the higher transfer observed from the left to the right hand. Stars indicate the significant GROUP by TRIAL interactions (INT*), as well as the significant difference between Early trials across groups (*).

Post-adaptation trials

After-effects are crucial to validate the presence of sensorimotor adaptation. Following the adaptation phase, participants performed four additional trials under the regular mapping (no rotation), two with the right hand and two with the left hand. To assess the presence of after-effects, we averaged tracking error for each hand separately in the two post-adaptation trials and compared these with tracking error obtained during baseline trials (see Fig. 7). This comparison showed that on average, in both groups, tracking error was almost two times greater during post-adaptation trials as compared to baseline ones (3.68 vs. 1.88 cm), thereby providing evidence for reliable after-effects. Further statistics conducted with a two-way ANOVA with

GROUP and HAND on post adaptation trials revealed a main effect of HAND ($F(1,42)=13.98$, $p<0.001$), a GROUP by HAND interaction ($F(1,42)=6.68$, $p<0.05$), and a marginal effect of GROUP ($F(1,42)=3.59$, $p=0.07$). The main effect of HAND revealed that on average, after-effects were 11% greater for the left hand (3.88 vs. 3.47 cm). Post-hoc of the interaction revealed that after-effects on the right hand of RL participants were smaller than any of the 3 other types of after-effects (3.13 vs. 3.86 cm, $p<0.05$), with no significant difference between the latter ($p>0.41$). Namely, although deadapting the left hand induces deadadaptation of the right hand (smaller post-effects in RL participants right hand), deadapting the right hand has much less effect on the left hand (same right/left after-effects in LR participants). This finding fits well with our earlier observation that adaptation of the left hand had a greater impact on the right hand than the other way around.

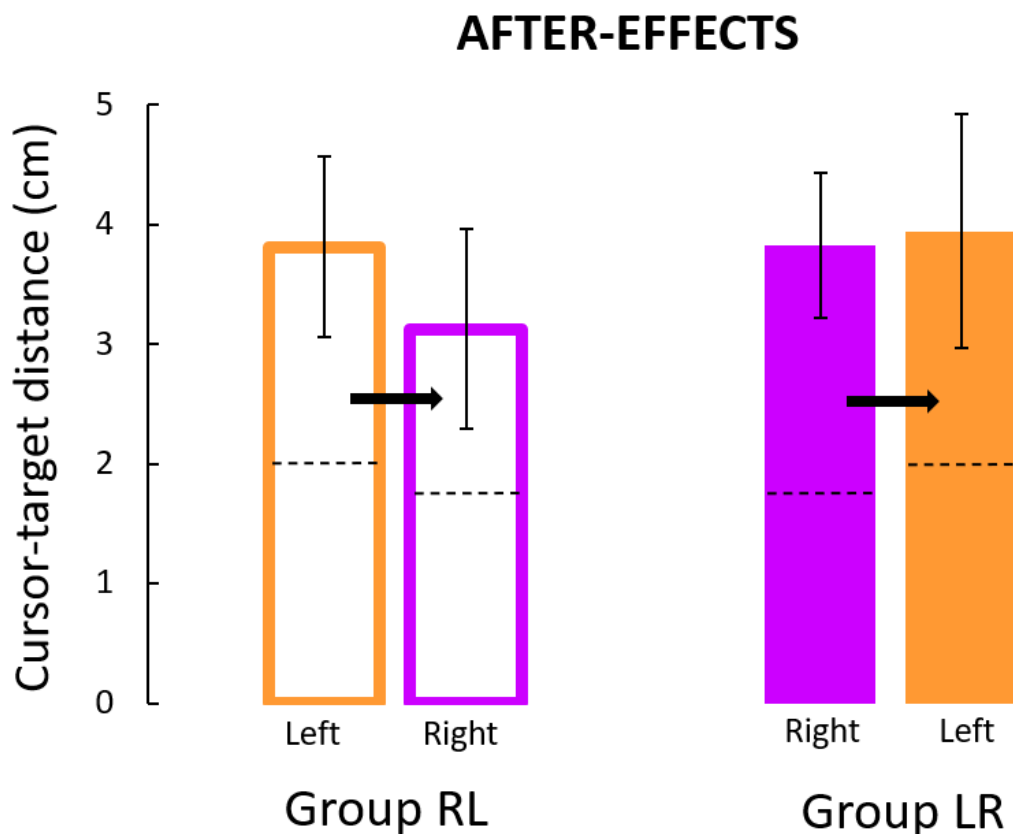


Fig. 7 After-effects in tracking performance as a function of experimental group and hand. Arrows indicate the order in which the after-effects were collected. Each histogram represents the average of the two trials and error bars correspond to SEM. Dotted lines indicate baseline

performance for each hand. Note the presence of after-effects in each case, albeit smaller for the right hand in group RL.

Extra analyses

One may argue that ten trials of practice may be insufficient to assess baseline performance, especially for the left hand which is assumed to need longer practice. To investigate this issue, we analyzed for each hand the progress obtained in tracking performance over the 10 baseline trials. The two-way ANOVA with TRIAL and HAND showed a main effect of HAND ($F(1,43)=99.77$, $p<0.001$), TRIAL ($F(9,387)=8.75$, $p<0.001$), and an interaction between the two ($F(9,387)=3.39$, $p<0.001$). The effect of HAND was consistent with the right hand advantage exposed previously, and the effect of TRIAL was consistent with an improvement of the tracking performance with practice. Post-hoc of the interaction confirmed the presence of a right hand advantage for any of the trials ($p<0.03$). However, if anything, this advantage tended to build up with practice, rather than decreasing. Indeed, during the first four baseline trials, the left hand exhibited a tracking error that was 11% greater (2.12 vs. 1.91 cm), a difference reaching 15% during the last four baseline trials (2.01 vs. 1.74 cm). This means that we found no evidence that extended practice would help reducing the asymmetry between the performance of the right and the left hand. Finally, for right hand, post-hoc indicated that tracking accuracy stopped improving after the 5th trial (no difference between any of the last five trials, $p>0.53$). Comparable findings were obtained for the left hand given that its tracking accuracy failed to improve after the sixth trial (no difference between any of the last four trials, $p>0.27$). We conclude that 10 baseline trials were sufficient to obtain steady state performance for each hand, and that the asymmetry between right and left hand tracking performance was robust.

Despite clear asymmetry in hand behavior during baseline tracking, we seek to identify whether the right and left hand behaviors could nevertheless remain correlated. To address this

issue, we examined right/left correlations across the 44 participants. Results showed significant correlations in terms of tracking accuracy ($R=0.74$, $p<0.001$), variability of cursor position across loops ($R=0.72$, $p<0.001$), and variability of cursor-target distance ($R=0.44$, $p<0.01$). Altogether, even though we found evidence of right/left differences, these analyses speak for shared processes across the two hands during baseline behavior.

Let us now consider the left hand advantage during adaptation trials. Because under rotated feedback the bias in position increases as the cursor moved away from the center of the screen, this left hand advantage could result from a strategy that relies on employing smaller cursor eccentricity, and consequently slower movements. To address this possibility, we have compared across hands the average cursor eccentricity and tangential velocity for each adaptation trial. Results showed that, averaged across all 40 adaptation trials, there was no significant difference in cursor eccentricity between the right and the left hand (6.10 vs. 6.12 cm, $p=0.75$). Regarding cursor velocity, somewhat slower movements were observed for the left hand, but that difference (5%) did not reach significance (21.36 vs. 22.09 cm/s, $p=0.07$). Altogether, these extra analyses suggest that greater resilience of the left hand under rotated trials does not merely result from a strategy that consists in freezing the hand nearby the center of the screen.

DISCUSSION

Our main objective was to evaluate interlimb differences and transfer when adapting to rotated visual feedback during manual tracking. Along this line, the current study provides the following key observations. First, as expected, baseline manual tracking was more accurate but also less variable with the (dominant) right hand than with the (non-dominant) left hand. However, when first confronted to the visuomotor rotation, manual tracking became more accurate with the left hand than with the right one. Third, interlimb transfer effects were

observed in both directions, but more strongly from the left to the right hand than the other way around. We discuss these findings and their implications in more details below.

Right hand advantage during baseline conditions

As anticipated, this study provides further evidence that, in right-handed participants, manual tracking is more accurate with the right hand. On average the cursor-target distance was found 15% larger in the left hand. Importantly, this asymmetry did not seem to level out with practice. This observation is consistent with previous studies that explored the effect of hand dominance during manual pursuit tracking (Aoki et al., 2016; Carey et al., 2003; Freeman & Chapman, 1935; Mathew et al., 2019, 2020; Peña-Pérez et al., 2023; Simon et al., 1952), but also echoes with some reports obtained in the context of reaching movements (Carey & Liddle, 2013; Carson, 1993; Elliott et al., 1993; Schaffer & Sainburg, 2017).

Still, our study demonstrates that the behavior of the left hand is both less consistent across trials, and more exploratory than that of the right hand. Indeed, in the first case we found that the mean cursor-cursor distance across trials was 19% larger in the left hand. In the second case, the amount of task space explored by the cursor was 18% greater when maneuvered by the left hand. These asymmetries found in our tracking task echo with other studies in which the authors focused on movement variability during pointing movements (Freitas & Scholz, 2009; Roy & Elliott, 1989; Schaffer & Sainburg, 2017), drawing movements (Zarandi et al., 2023), or during isometric force production (O'Sullivan et al., 2009; Salimpour & Shadmehr, 2014). Altogether, our analyses of pursuit accuracy and consistency show that the control strategy employed by the left hand is less effective, while producing more variable behavior and greater task space exploration, than the control strategy utilized by the right hand.

Left hand advantage under visuomotor rotation

In contrast to baseline conditions in which a right hand advantage was observed, we found a left hand advantage under first exposure to the rotated feedback, and this not only early in the adaptation, but throughout the adaptation phase (see Fig. 5). This observation echoes with studies on reaching movements showing right-left hand asymmetries in visuomotor adaptation (Chase & Seidler, 2008; Taylor et al., 2011), although this is far from being always the case (Balitsky Thompson & Henriques, 2010; Kirby et al., 2019; Kumar et al., 2020; Sainburg, 2002; Yamagami et al., 2021). Unfortunately, in most of these previous studies, the presence/absence of a possible asymmetry during baseline conditions was rarely considered (although see Chase & Seidler, 2008; Taylor et al., 2011). Interestingly, smaller errors by the left hand have been reported during early adaptation to force field (Schabowsky et al., 2007), but other studies insist on the lack of differences in adaptation rate (Reuter et al., 2016; Stockinger et al., 2015). Finally a left hand advantage has been evoked for the acquisition of new motor skills (Perelle et al., 1981; Wang et al., 2020; Yadav & Mutha, 2020), but as in the earlier cases, this is far from being the rule (Cho et al., 2006; Garry et al., 2004; McGrath & Katak, 2016; Noguchi et al., 2005; Schulze et al., 2002).

What could be the reason(s) leading to a switch from a right hand advantage during baseline trials to a left hand advantage during exposure to the rotation? When examining the possibility that the left hand employed a “stay still” strategy under the rotation (minimizing the effect of the rotation when staying nearby the center), our analyses failed to show reliable differences in cursor velocity or eccentricity across hands. In the introduction, we proposed two lines of reasoning. The former predicted that the right hand advantage would persist under rotated feedback, whereas the second one predicted the opposite, namely a left hand advantage. The current set of data does not support the view that the advantage for visual feedback processing exhibited by the right (dominant) hand/left hemisphere extends from baseline to the

rotated mappings. In contrast, the current data supports the view that, in right handers, the update of the control strategy is more effective in the non-dominant hand. This proposition was formulated based on the following points. First, although the relation between motor variability and sensorimotor adaptation is certainly more complex than initially envisaged (He et al., 2016), it has been argued that movement variability and task exploration during baseline condition promotes motor learning in humans (Dhawale et al., 2017; Wu et al., 2014). Second, it has been shown that greater uncertainty in state estimation is associated with faster adaptation (Wei & Koerding, 2010). Here we showed that the left hand was both more variable and less accurate during baseline, an effect that likely results from greater state uncertainty and/or greater slack in its control strategy. Although we certainly do not preclude the influence of other factors, the left hand features listed above appear useful to account for its better handling of the visuomotor rotation.

Asymmetrical interlimb transfer

The issue of interlimb transfer following visuomotor adaptation has been largely explored in the context of reaching movements (Balitsky Thompson & Henriques, 2010; Chase & Seidler, 2008; Kumar et al., 2020; Sainburg & Wang, 2002; Taylor et al., 2011; Werner et al., 2019). Although, this issue has been occasionally investigated in the context of continuous movements by means of visual inversion during writing words, printing letters or drawing figures (Latash, 1999; Parlow & Kinsbourne, 1989; Thut et al., 1996), we are not aware of a single study that explored interlimb transfer in the context of manual tracking and visuomotor rotation. Our results showed clear interlimb transfer effects, thereby demonstrating that some knowledge acquired by one hand is available to the other hand. However, interlimb transfer appeared twice greater from the left hand to the right one (-29%), than from the right hand to

the left one (-14%). Below we propose to address the possible reasons that led to this asymmetric transfer of visuomotor adaptation.

The fact that we observed greater transfer from the left to the right hand resonates with some earlier studies that employed either continuous (Parlow & Kinsbourne, 1989; Thut et al., 1996) or discrete actions (Chase & Seidler, 2008; Sainburg, 2002; Wang & Sainburg, 2004), but not all of them (Balitsky Thompson & Henriques, 2010; Imamizu & Shimojo, 1995; Yamagami et al., 2021). Importantly our results match with the hypothesis we formulated in the introduction. Namely we proposed that interlimb transfer should be facilitated from the hand that acquired more knowledge (Chase & Seidler, 2008), or reached the highest level of implicit adaptation (Kumar et al., 2020). Not only we showed that left hand tracking error was smaller during initial exposure, but it also returned closer to baseline performance at the end of practice. Indeed, by the end of the first adaptation session, tracking error of the left hand was 54% higher than during baseline, while it was 121% higher for the right hand (see Fig. 5), thereby arguing for more extensive adaptation in the left hand. In addition, the fact that we observed stronger and reliable (2 trials of 10 s) after-effects for the left hand, further supports the view that this hand reached higher level of implicit adaptation. Altogether, the fact that interlimb transfer was stronger when the left hand was first adapted is well accounted for by the fact that this hand managed more efficiently the visuomotor rotation.

About 20 years ago, Sainburg and colleagues proposed a dynamic dominance hypothesis to account for asymmetries in reaching movements during baseline performance and interlimb transfer (Bagesteiro & Sainburg, 2002; Sainburg, 2002, 2005; Sainburg & Kalakanis, 2000). This hypothesis is grounded upon the observation that the dominant arm has an advantage in controlling limb dynamics (i.e. initial direction of movement), whereas the non-dominant arm has an advantage in controlling final position. In the context of our tracking task, the accuracy of movement was measured through cursor-target distance, an index that reflects

efficiency in both positional and directional control of the cursor. Altogether, how much the current observations might follow the scheme of the dynamic-dominance hypothesis is unclear. Despite the fact that our task relies on multiple abilities, some of them being possibly better for the right hand (e.g. directional control), while others could be better for the left hand (e.g. positional control), our study speaks for clear asymmetries in manual tracking, not only during baseline conditions, but also during visuomotor adaptation and interlimb transfer. We believe that the merit of our study is not to provide a general frame that can reconcile all previous observations, but rather to suggest that, in some cases (here tracking under rotated feedback), a right-left asymmetry during baseline performance may be responsible for subsequent asymmetries in adaptation and transfer.

Conclusion

The main messages brought by this study are the followings. First, our results show that hand dominance exhibited during baseline tracking is reversed when participants are first exposed to a visual perturbation. To account for this phenomenon, we propose that lower confidence in input-output properties and/or higher variability of the non-dominant (left) hand promotes its adaptation to the rotation. Second, this study shows that interlimb transfer is asymmetrical, occurring more strongly from the non-dominant to the dominant hand. We suggest that this asymmetry follows from a greater adaptation of the left hand. Finally, at a more general level, our observations encourage careful examination of manual asymmetry during both baseline condition and initial adaptation when investigating interlimb transfer.

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