RESEARCH ARTICLE

Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand

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Abstract Reaching with visual feedback that is misaligned with respect to the actual hand's location leads to changes in reach trajectories (i.e., visuomotor adaptation). Previous studies have also demonstrated that when training to reach with misaligned visual feedback of the hand, the opposite hand also partially adapts, providing evidence of intermanual transfer. Moreover, our laboratory has shown that visuomotor adaptation to a misaligned hand cursor, either translated or rotated relative to the hand, also leads to changes in felt hand position (what we call proprioceptive recalibration), such that subjects' estimate of felt hand position relative to both visual and non-visual reference markers (e.g., body midline) shifts in the direction of the visuomotor distortion. In the present study, we first determined the extent that motor adaptation to a translated cursor leads to transfer to the opposite hand, and whether this transfer differs across the dominant and non-dominant hands. Second, we looked to establish whether changes in hand proprioception that occur with the trained hand following adaptation also transfer to the untrained hand. We found intermanual motor transfer to the left untrained (non-dominant) hand after subjects trained their right (dominant) hand to reach with translated visual feedback of their hand. Motor transfer from the left trained to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike visuomotor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

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Introduction

Moving the hand while its visual feedback is distorted leads to a mismatch of vision and action that results in sensorimotor remapping and adaptation. For example, when subjects first reach to a target with distorted visual feedback (e.g., a cursor that is rotated or translated relative to the hand's actual motion), the cursor reaches are initially deviated but are then gradually adjusted or adapted across trials so that later reaches bring the cursor more directly to the target (Krakauer et al. 1999; Sainburg and Wang 2002; Simani et al. 2007). This visuomotor adaptation has also been shown to transfer across arms, which is referred to as intermanual transfer. In such cases, learning with one

hand facilitates subsequent performance with the opposite, untrained hand. Intermanual transfer has been observed in such tasks as drawing (Thut et al. 1996), grasping (Chang et al. 2008), pointing and tracking (Abeele and Bock 2003). More importantly for the current study, intermanual transfer also occurs after adapting reaching movements to displacing prisms (Hamilton and Bossom 1964), force perturbations (Dizio and Lackner 1995), mirror-reversed visual feedback (Dionne and Henriques 2008) and rotated visual feedback of the hand or cursor (Wang and Sainburg 2003, 2004, 2006, 2007; Balitsky Thompson and Henriques 2010). Typically, intermanual transfer of adaptation to these various perturbations is assessed by testing the untrained hand to the same perturbation that the trained hand has adapted to. Transfer is said to occur when initial errors in response to the perturbation are smaller and/or the learning rate is faster for the untrained hand following training of the opposite hand compared to when there is no initial adaptation in the opposite hand.

The pattern of intermanual transfer is not necessary the same across the two hands. In a series of experiments by Sainburg and Wang (2002), they found that when subjects adapted one of their hands to a rotated cursor (visuomotor rotation), the transfer of this learning to the opposite arm was asymmetric, in that the size and types of intermanual transfer depended on the hand trained. Specifically, they found that final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. They proposed that this intermanual transfer pattern reflects basic differences in or specialization of the two arm controllers, such that the initial direction information transferred to the right arm controller from the non-dominant arm; however, the endpoint configuration of the limb, but not the initial direction, transferred to the left arm controller from the dominant arm. In contrast, Balitsky Thompson and Henriques (2010) found intermanual transfer occurred only from the dominant right hand to the left hand, but not from the non-dominant left hand to the right hand, and this was the case when subjects adapted to a rotated cursor or to a rotated video image of the hands (based on angular deviations at peak velocity when the untrained hand reached with the same altered visual feedback). Other motor adaptation studies where subjects adapted to velocity-dependent force fields (Criscimagna-Hemminger et al. (2003), also measuring deviations at peak velocity during training with the previously untrained hand) and displacing prisms (Redding and Wallace (2008), measuring reach endpoint deviations of the opposite arm without the prisms, e.g., aftereffects) have shown a similar asymmetry, training with the dominant hand leads to facilitation with the non-dominant hand.

In the current study, our first goal was to investigate the nature and extent of intermanual transfer after adaptation to a translated cursor. We used a translated cursor (i.e., the cursor appeared rightward of the actual position of the hand and it moved parallel with the hand) as our perturbation rather than the usual rotated cursor (i.e., while the subject moves his/her hand forward, the cursor heads off on a directional angle relative to the hand) since previous results from our laboratory suggest that proportional changes in reaches measured by the resulting aftereffects (relative to the magnitude of the distortion) are greater after adaptation to a translated cursor than to a rotated cursor (Cressman and Henriques 2009). In fact, previous studies by Ghahramani et al. (1996) and Vetter et al. (1999) suggest that adapting to a shifted or translated cursor may also lead to greater generalization across the workspace compared to adapting to a rotated cursor (Krakauer et al. 2000). This difference in both generalization and size of aftereffects following adaptation to a translated cursor compared to a rotated cursor makes sense in that the translated feedback of the hand resembles the kind of visual perturbation one may experience in everyday life, like refracted light from submerging our hand in water, or using a tool that extends or shifts our end-effector. Even a computer mouse resembles a translated shift of the hand more than a rotated shift. In contrast, a rotation perturbation is something we would not experience in everyday life and hence may be more difficult to adapt to. Thus, we used a translated cursor for adapting the hand to provide the greatest possibility of observing intermanual transfer, which is a type of generalization, and one that has not been studied before following translated cursor adaptation. We assessed the extent and pattern of this intermanual transfer of reach adaptation by using a no-cursor (open-loop) reaching task to measure aftereffects of both the trained and untrained hand. We also examined whether this transfer differed across the dominant and non-dominant hands. Given the previous studies mentioned above and those in our laboratory (Balitsky Thompson and Henriques 2010; Salomonczyk et al. 2010) demonstrating that intermanual transfer occurs asymmetrically depending upon the trained hand, in the current study, we hypothesized a similar asymmetry after training with a translated cursor.

In addition to examining intermanual transfer of reach adaptation, we investigated whether changes in felt hand position (i.e., proprioceptive recalibration) also transferred between limbs (what we will call intermanual sensory transfer). Recent studies have shown that visuomotor adaptation leads not only to changes in trajectory of the trained hand, but that the felt position of the hand is also modified (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Ostry et al. 2010; Cressman and Henriques 2011; Salomonczyk et al. 2011, 2012). In our own laboratory, we

have found that adapting to either a rotated or translated cursor leads to changes in hand proprioception, such that people perceived their unseen hand as being shifted in the direction of the visual distortion (Cressman and Henriques 2009, 2010). To determine changes in felt hand position, we have subjects estimate the location of their unseen hand relative to a visual or proprioceptive (body midline) reference marker both before and following visuomotor adaptation (Cressman and Henriques 2009, 2010). To date, it has been shown that this proprioceptive recalibration is robust in that it occurs under various task constraints (i.e., adapting to a visuomotor distortion- or velocity-dependent force field) (Cressman and Henriques 2009, 2010; Ostry et al. 2010), regardless of how the hand is displaced during this proprioceptive estimation task (passive arm displacement vs. active reaching movements) (Cressman and Henriques 2009, 2010), the modality of the reference markers (visual vs. proprioceptive) and the age of the patients (young vs. older adults) (Cressman and Henriques 2009, 2010).

Previous studies examining proprioceptive recalibration have focused on assessing shifts in felt right-hand position following motor learning of the right arm in right-handed individuals. It is currently unclear whether, like motor adaptation, such sensory changes transfer to the opposite untrained hand as well. Thus, after establishing the nature and extent of intermanual motor transfer, the second goal of this study was to test whether proprioceptive recalibration transfers from the trained (right or left) hand to the untrained (left or right) hand following adaptation to a visuomotor distortion, and whether this transfer occurs asymmetrically depending upon the hand trained.

Methods

Subjects

In total, 35 right-handed subjects (mean age = 22.9, SD = 5.62, 11 males) were randomly assigned to either the left-hand ($n = 17$) or right-hand ($n = 18$) training groups. All subjects had normal or corrected-to-normal vision. Subjects were prescreened verbally for self-reported handedness and any history of visual, neurological, and/or motor dysfunction. All subjects provided informed consent in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee and received credit toward an undergraduate psychology course.

General experimental setup

The experimental setup is illustrated in Fig. 1a. Subjects were seated in a chair and the height of the chair was adjusted to ensure that they could easily see all of the targets presented on a reflected screen and comfortably reach to target locations. Subjects were asked to hold on (either with their right or left hand) to the vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA) so that their thumb rested on top of the handle. The reflective screen was mounted horizontally 8.5 cm above the robot manipulandum. A monitor (Samsung 510 N, refresh rate 72 Hz) located 17 cm above the robotic handle projected visual stimuli, such that images displayed on the monitor appeared to lie in the same horizontal plane as the robotic handle. The room lights were dimmed, and the subjects' view of their own hand was blocked by the reflective surface, as well as a black cloth draped over their shoulders.

Procedure

The experiment consisted of 2 test sessions run on 2 separate days. Each test session consisted of 8 tasks (See Fig. 2). The first session had subjects reach to visual targets, after training to reach with a cursor that was *aligned* with either their right or left hand's position. The second session, however, had subjects complete the same reach trials after the right or left hand reached with a cursor that was *misaligned* from their hand's position. The misaligned cursor was translated 4 cm to the right of their actual hand position, with this translation being introduced gradually (as described below).

Aligned reach Training task

The first testing session included aligned reach training (Boxes 1 and 5 in Fig. 2), where subjects were asked to reach to one of five targets with their right or left hand, hidden from view, but represented by a cursor (green circle, 1.4 cm in diameter, Fig. 1b) located above their thumb. In front of the home position, which was approximately 20 cm in front of subjects' chests, there were 5 reach targets represented by 1-cm-diameter yellow circles, located along two lines, 8.66 or 10 cm above the home position. One reach target was located 10 cm directly in front of the home position. Four additional visual reach targets were located 5 and 7.5 cm to the left and right of the center reach target, 8.66 cm in front of the home position. The reach trial was considered complete when the center of the cursor had moved to within 0.5 cm of the target's center. At that point, both the target and cursor were removed and the robot was locked to a grooved path. This grooved path guided subjects back to the home position by a direct linear route in the absence of visual feedback. If subjects attempted to move outside of the established path, a resistance force [proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s)]
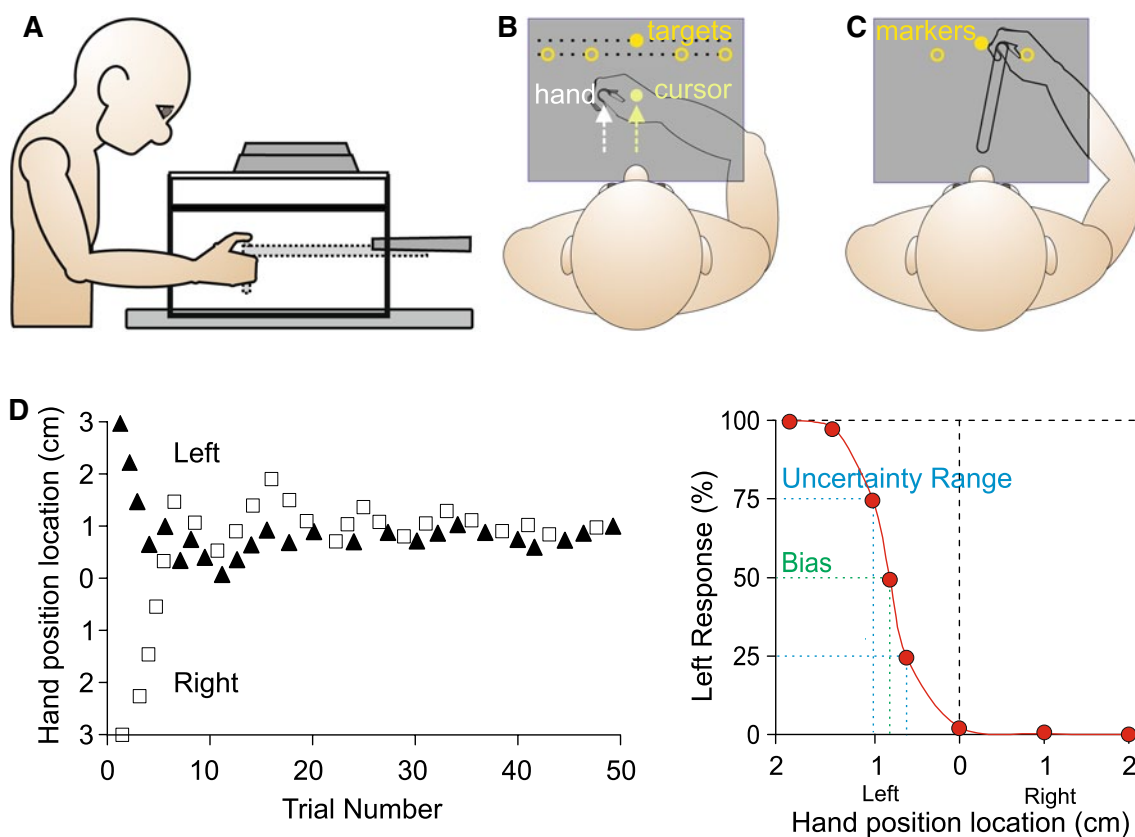
Fig. 1 Experimental setup and design. **a** Side view of the experimental setup. **b** Top view of experimental setup visible to subjects in the reaching tasks. The center home position was represented by a 1-cm *green circle* and was located about 20 cm in front of subjects' chests, aligned with the body midline, this position was not illuminated, and visual feedback was provided only when the hand had travelled 4 cm outwards from the home position. Five targets were located along 2 lines; one target was located 10 cm directly in front of the home position and was represented by a *yellow circle* 1 cm in diameter. Four additional targets were located 5 and 7.5 cm to the left and right of the center target, 8.66 cm in front of the home position. The visuomotor distortion was introduced gradually until the cursor was translated 4 cm rightward with respect to the hand. This shift ensured that the *green cursor* (representing the hand) appeared to come from a central position. **c** Top view of experimental surface visible to subjects in the proprioceptive estimates tasks. One reference marker was

located 10 cm directly in front of the home position and was represented visually by a *yellow disk*, 1 cm in diameter or proprioceptively (body midline). Two additional reference markers were located 5 cm to the left and right of the center reference marker, 8.66 cm in front of the home position. **d** Staircase and uncertainty range for the data of one subject for one reference marker. For the left panel, the staircase depicted with triangles illustrated the adjusted hand position across trials for the staircase starting at 3 cm leftward of the reference marker, while the squares illustrate the staircase starting 3 cm rightward. In the right panel, *circles* represent the mean percentage of responses by which the subject reported the hand was left of the visual reference marker across various hand locations. The *green line* intersecting the *x*-axis shows the bias (the point at which the probability of responding left was 50 %), while the *blue lines* depict the uncertainty range (the difference between the values at which the probability of responding left was 25 and 75 %)
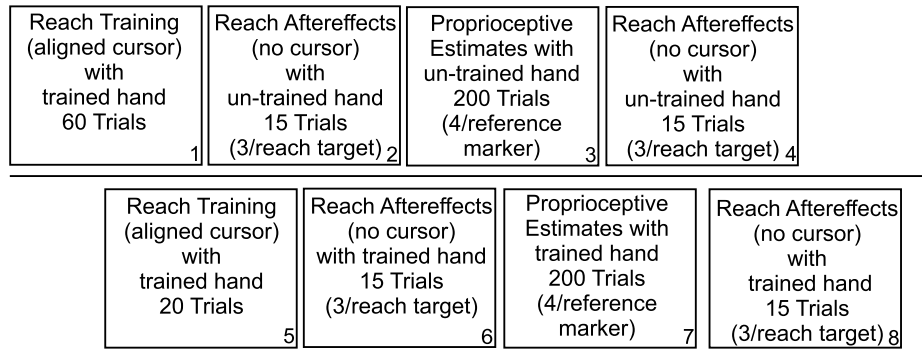
was generated perpendicular to the grooved wall (Henriques and Soechting 2003). In this task, there were 60 trials, 12 trials for each target.

No-cursor reaching task: reach errors assessment

Immediately after the aligned reach training task, subjects reached to the same five targets 3 times each without a cursor (Box 2 in Fig. 2). In this task, a trial started with the robot handle at the home position, and, after 500 ms, the home position disappeared and one of the five reach targets

would appear. Subjects were asked to reach to the visible target (as in the previous task) with the robot handle without the cursor or any visual feedback of their hand. Once the reach movement was complete (final position was held for 250 ms), the target and the home position disappeared. This cued subjects to actively move their unseen hand back to the home position along a constrained path to begin the next trial. This task was completed twice by each hand, first by the untrained hand from the previous training task (Boxes 2 and 4 in Fig. 2) and then by the trained hand (Boxes 6 and 8 in Fig. 2).

A Testing Sessions with Aligned-Visually Guided Reaches: BASELINE

| Reach Training (aligned cursor) with trained hand 60 Trials [1] | Reach Aftereffects (no cursor) with un-trained hand 15 Trials (3/reach target) [2] | Proprioceptive Estimates with un-trained hand 200 Trials (4/reference marker) [3] | Reach Aftereffects (no cursor) with un-trained hand 15 Trials (3/reach target) [4] |

| Reach Training (aligned cursor) with trained hand 20 Trials [5] | Reach Aftereffects (no cursor) with trained hand 15 Trials (3/reach target) [6] | Proprioceptive Estimates with trained hand 200 Trials (4/reference marker) [7] | Reach Aftereffects (no cursor) with trained hand 15 Trials (3/reach target) [8] |

B Testing Sessions with Misaligned-Visually Guided Reaches

| Reach Training (misaligned cursor) with trained hand 150 Trials [1] | Reach Aftereffects (no cursor) with un-trained hand 15 Trials (3/reach target) [2] | Proprioceptive Estimates with un-trained hand 200 Trials (4/reference marker) [3] | Reach Aftereffects (no cursor) with un-trained hand 15 Trials (3/reach target) [4] |

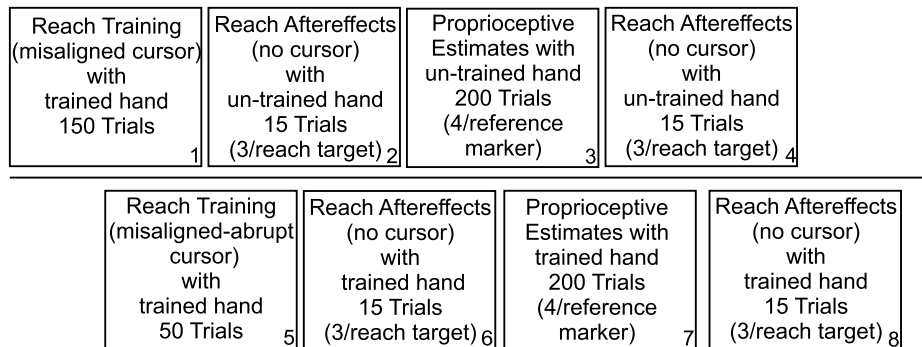| Reach Training (misaligned-abrupt cursor) with trained hand 50 Trials [5] | Reach Aftereffects (no cursor) with trained hand 15 Trials (3/reach target) [6] | Proprioceptive Estimates with trained hand 200 Trials (4/reference marker) [7] | Reach Aftereffects (no cursor) with trained hand 15 Trials (3/reach target) [8] |

Fig. 2 Breakdown of the testing sessions within each experiment. **a** Testing session(s) which provided baseline measures of performance. Subjects began their first testing session by reaching to visual targets with their right or left hand (trained hand) while a cursor accurately represented the location of their unseen hand (*box* 1). After completing 60 visually guided reach trials, subjects then reached with their opposite hand (untrained hand) to each of the 5 reach targets, three trials each, without a cursor to assess visuomotor adaptation (reach aftereffect trials, *box* 2). Subjects then completed 200 proprioceptive estimates trials with their untrained hand (*box* 3). After completing the proprioceptive estimate task, subjects completed 15 reaches without the cursor, 3 reaches to all 5 target positions with their untrained hand (*box* 4). Then, they completed a short aligned training task with the trained hand (*box* 5). After completing 20 visually guided reach trials, subjects (trained hand) completed 15 reach trials without the cursor using the trained hand (*box* 6). Subjects then completed 200 proprioceptive estimates trials with their trained hand (*box* 7). The end of this session consisted of 15 reach trials, without a cursor, using their trained hand (*box* 8). **b** In the testing session(s) completed on the second day of the experiment, subjects performed 150 visually guided reaching trials using their right or left trained hand in which the 4-cm rightwards distortion was introduced gradually (*box* 1). Subjects then performed the same tasks as on the first day with their untrained hand (*boxes* 2, 3 and 4). After completing these tasks, subjects completed 50 visually guided reaching trials with the trained hand with a misaligned cursor, which was presented abruptly (*box* 5). Then, subjects did the same tasks as done on the first day with their trained hand (*boxes* 6, 7 and 8)

Proprioceptive estimates task: sense of felt hand position assessment

In the proprioceptive estimate trials (Boxes 3 and 7 in Fig. 2), we determined the position at which subjects perceived their unseen hand was aligned with the four reference markers. A proprioceptive estimate trial began with subjects grasping the robot manipulandum that was positioned at the home position. Subjects were then to actively push the robot handle outwards along a constrained path to a location somewhere along the dotted line shown in Fig. 1b (dotted line is for illustration purposes only and was not visible to the subjects). Once the hand arrived at its final position, one of the three visual reference markers appeared or subjects would hear a beep (which indicated that they were to use their body midline as a reference marker). At this point, subjects were to indicate whether their hand was to the right or left of the reference marker (using the right or left arrow keys on a keyboard). The four reference markers for the proprioceptive estimates were located along two lines, 8.66 or 10 cm, in front of the home position (yellow circles, Fig. 1c). One reference marker was located 10 cm directly in front of the home position and was represented visually (yellow disk, 1 cm in diameter) or proprioceptively. This proprioceptive reference marker position was based on an internal representation of body midline. Two

additional visual reference markers were located 5 cm to the left and right of the center target, 8.66 cm in front of the home position. There were 200 trials in this task, 50 trials for each target.

The position of the hand with respect to each reference marker was adjusted over trials using an adaptive staircase algorithm (Treutwein 1995). For each reference marker, there were two corresponding staircases, a left and a right (illustrated as triangles and squares in the left panel of Fig. 1d), that were adjusted independently and randomly interleaved. Each staircase began such that the hand was 3 cm to the left or right of the reference marker. The position of the hand was then adjusted over trials depending on subjects' pattern of responses, such that the differences between hand locations in subsequent trials (step size) decreased each time subjects reversed their response pattern from left to right or from right to left within a particular staircase. This ensured that subjects were tested more frequently at positions closer to their sensitivity threshold. If subjects responded consistently, the two staircases converged toward a certain position at which subjects had an equal probability of reporting left or right. This position represented the location at which subjects perceived their hand was aligned with the reference marker (Fig. 1d).

Misaligned reach training task

The tasks for the second testing session were similar to the first except for the reaching training tasks, which involved a misaligned cursor (Boxes 1 and 5 in Fig. 2b). In this misaligned reach training task, the cursor was translated 4 cm rightwards with respect to the actual hand location in the reach training task. To ensure that subjects were unaware of the visuomotor distortion, this shift in cursor position was introduced gradually over the first 41 reach training trials, and thus continue at this maximum cursor translation for the remaining 109 trials for this task (Box 1 in Fig. 2b) and for the subsequent task (Box 5 in Fig. 2b). This was done by shifting the start position of the hand 1.0 mm leftward every trial until it reached 4 cm. The same targets and cursor were used as those in the aligned reach training tasks. For the gradual translation task, there were 150 trials, 30 trials for each target. And for the abrupt translation task, there were 50 trials, 10 trials for each target. These tasks were completed by the trained hand in either the left- or right-hand training group.

Data analysis

Visuomotor adaptation

Directional deviations of the hand made during reaching trials without visual feedback were analyzed to assess motor adaptation. Since the cursor was shifted horizontally (to the

right of actual hand position), we were only interested in errors in this horizontal direction. Reaching endpoint errors were defined as the horizontal difference between a movement vector (from the home position to reach endpoint) and reference vector (from the home position to the target). Reach errors at peak velocity were defined as the horizontal difference between a movement vector joining the home position and the position of the hand at peak velocity and the reference vector. Both of these errors, which we will refer as aftereffects (i.e., baseline values subtracted from adaptation results), were analyzed to determine whether subjects adapted their reaches to the targets after aiming with a translated cursor, and whether there were any changes in reach adaptation following the proprioceptive estimate trials. To compare the transfer of aftereffects following training with translated-cursor feedback from the trained to the untrained hand 2 Group (right hand trained vs. left hand trained) × 2 Training condition (aligned vs. translated cursor) × 2 Hand used (trained vs. untrained) × 2 Time (following reach training trials vs. following proprioceptive estimate trials), mixed ANOVAs were performed on reaching endpoints and reach errors at peak velocity. To assess intermanual transfer, we specifically looked at the difference between these no-cursor reaches following training with the aligned versus translated cursor in the untrained hand and also compared this to the differences for the trained hand. Hand used, Training condition and Time were treated as within-group variables, while Group was treated as a between-group variable. Additionally, due to our study goals, pairwise comparisons were made across three main factors (Group, Training, Hand used).

Finally, we assessed the extent of intermanual transfer using an independent t test to compare the aftereffects (to reduce factors in the analysis, we subtracted no-cursor reach errors on day 1 (baseline) from those on day 2, so that our new dependent variable was a difference in errors) of the trained and untrained hand for each hand; i.e., trained left hand (from the Left hand group) versus untrained left hand (from the Right hand group), and trained right hand (from the Right hand group) versus untrained right hand (from the Left hand group).

Proprioceptive estimates of hand position

A logistic function was fitted to each subject's responses for each reference marker in each testing session in order to determine the location at which subjects perceived their hand to be aligned with a reference marker, as illustrated in the right panel in Fig. 1d. From this logistic function, we calculated the bias (the point at which the probability of responding left was 50 %, shown in green) and uncertainty (the difference between the values at which the probability of responding left was 25 and 75 %, shown as blue lines). The bias value is a measure of subjects' accuracy of
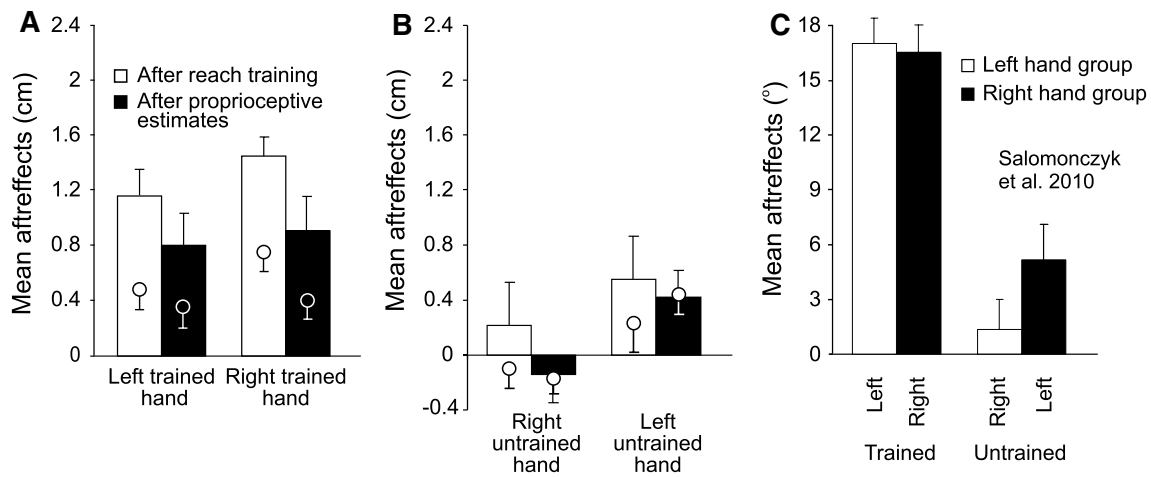
Fig. 3 Mean endpoint aftereffects (*bars*) and errors at peak velocity (*circles*) following reach training with misaligned visual feedback of the hand. **a** Values reflect baseline-subtracted aftereffect errors in the trained left and right hands (*left* and *right bars,* respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **b** Values reflect baseline-subtracted aftereffect errors in the untrained right and left hands (*left* and *right bars,* respectively) following reach training trials (*white bars*) and proprioceptive estimate trials (*black bars*). **c** Mean endpoint aftereffects from (Salomonczyk et al. 2010) for (*left* and *right*) trained hands and (*right* and *left*) untrained hands (*left* and *right bars,* respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). *Error bars* reflect standard error of the mean

proprioceptive sense of hand position, while the magnitude of the uncertainty range defines its precision (Cressman and Henriques 2009; Cressman et al. 2010).

Proprioceptive recalibration was assessed by comparing the proprioceptive biases or estimates of hand position after training with a translated cursor with those following an aligned cursor (baseline), not only for the trained hand, but also for the untrained hand, so that we could test for intermanual sensory transfer. To do this, we ran a 2 Group (right hand training vs. left hand training) × 2 Hand used (trained vs. untrained) × 2 Training condition (aligned vs. translated cursor) × 4 Marker location (5 cm to the right vs. 5 cm to the left vs. middle visual vs. middle proprioceptive) mixed ANOVA on the proprioceptive estimates or biases. A similar mixed ANOVA was also run to compare the uncertainty values. Again, due to our interest in examining whether the intermanual transfer differs across hands, we followed these ANOVAs with preplanned comparisons.

All ANOVA results are reported with Greenhouse–Geisser corrected *P* values. Differences with a probability of 0.05 were considered to be significant. A Bonferroni correction was applied to all preplanned pairwise comparisons.

Results

Visuomotor adaptation

Figure 3 depicts mean reaching endpoint errors (aftereffects) for (A) the left and right trained hands, and (B) the

right and left untrained hands immediately following reach training trials (white bars) and following the proprioceptive estimate trials (black bars) relative to baseline performance (i.e., errors achieved on the first day of testing after training with an aligned cursor were subtracted from errors achieved after reaching with a translated cursor). No-cursor reaches were significantly shifted in the direction of the distortion following translated-cursor training compared to aligned-cursor training ($F(1, 33) = 45.60$, $p < .001$). But as expected, the changes in open-loop reaches varied depending on whether they were completed by the trained or untrained hand ($F(1, 33) = 21.82$, $p < .001$). However, given the low power of higher-order interactions, we were not able to find a significant three-way interaction when including the factor of Group ($F(1, 33) < 1$, $p = .532$), nor a four-way interaction when including Group and Time ($F(1, 33) < 1$, $p = .276$). Thus, we proceeded to our planned, pairwise comparisons for the trained hand and the untrained hand, in order to explore the difference in performance between aligned and translated training conditions, as a function of Group. In the next two paragraphs, we first report pairwise comparisons for the trained hand and then untrained hand for each group.

For the trained hands, the significant shift in no-cursor reaches for both the left and right hands was on average 1 cm ($F(1, 33) = 33.681$, $p < .001$) and 1.2 cm ($F(1, 33) = 53.090$, $p < .001$), respectively. The fact that there was no further interaction across Groups ($F(1, 33) < 1$) suggests that this adaptation was achieved, and by a similar amount, for both the left and right trained hands. Analysis

also revealed smaller reach aftereffects following the proprioceptive estimate trials compared to those immediately after the reach training trials ($F(1, 33) = 4.512$, $p = .041$). Specifically, reach aftereffects of 1.18 and 1.45 cm were observed in the first set of no-cursor reach trials (white bars in Fig. 3a) for the left and right hands, respectively, while the following set of no-cursor reaches (black bars in Fig. 3a) revealed that reach aftereffects had diminished to 0.8 and 0.9 cm for the left and right hands, respectively. Despite the decay in reach aftereffects following the proprioceptive estimate trials compared to those immediately after reach training, the aftereffects for the trained hands were still significantly different from baseline conditions.

On the other hand, reaching errors in the untrained hand showed evidence of intermanual transfer only in the untrained left hand following opposite right-hand adaptation ($F(1, 33) = 5.412$, $p = .026$), both when measured right before the proprioceptive estimate task and again right after, despite a small but non-significant decay in aftereffects over time ($F(1, 33) = 1.298$, $p = .263$). Changes in reach endpoint for the untrained right hand did not differ following opposite left-hand training ($F(1, 33) < 1$, $p = .856$). In other words, the untrained right hand (dominant hand) did not benefit from the left-hand (non-dominant) training, while the left hand benefited from the dominant hand (opposite hand) training. Analysis of reach errors at peak velocity (as indicated by the circles in Fig. 3a, b) revealed a similar pattern of results. Specifically, reach deviations at peak velocity in the untrained hand showed evidence of intermanual transfer only in the untrained left-hand following opposite right-hand adaptation ($F(1, 33) = 4.896$, $p = .034$), while reach errors at peak velocity for the untrained right hand did not differ following opposite left-hand training ($F(1, 33) < 1$, $p = .543$). This suggests that endpoint accuracy and initial directional errors transferred between hands, but from right to left not from left to right.

In order to assess the extent of the intermanual transfer to the left untrained hand, we compared the aftereffects (for trials following both reach training and proprioceptive estimates) of this untrained hand with those of the trained left hand from the other group. We found endpoint reach errors in the untrained left hand were less than aftereffects of the trained left hand, but not significantly ($t(33) = 1.85$, $p = .073$), while difference between the trained and untrained right hand was significant ($t(33) = 4.38$, $p < .001$). These findings confirm that the untrained left hand (non-dominant) benefited from previous training with the right hand (dominant) using a gradually introduced translated cursor; however, the untrained right hand did not benefit from the prior training with the left hand.

Interestingly, Salomonczyk et al. (2010) found similar results in their study of intermanual motor transfer when they introduced a 30° rotation to two subjects groups, one group which trained with the right hand and the other which trained with the left hand (Fig. 3c). Specifically, after reaching with a rotated cursor subjects adapted their reaches in both the right and left trained hands ($F(1, 44) = 265.4$, $p < .001$), however, only following right-hand adaptation did the opposite untrained left hand show a significant difference in endpoint errors (5°; $F(1, 44) = 7.646$, $p = .008$). In other words, the right untrained hand did not differ following opposite left-hand training (<1°; $F(1, 44) < 1$, $p = .935$). Also, analysis of reach errors at peak velocity revealed the same pattern of effects. These results suggest that prior training with the right hand led to a transfer of learning to the unexposed left hand.

Proprioceptive recalibration

Bias

Figure 4 depicts a two-dimensional view of the positions at which subjects in the left (A)- and right (B)-hand training groups perceived their hands to be aligned with the reference markers after training with an aligned (empty symbols) and translated cursor (filled symbols) for the trained hand (squares) and untrained hand (triangles). While we found a significant change in proprioceptive biases after adapting to a translated cursor ($F(1, 33) = 8.449$, $p = .006$), we found no significant three-way interaction including Hand used and Group ($F(1, 33) < 1$, $p = .529$) or four-way interaction and including Hand used, Group and Reference marker ($F(3, 99) = 1.062$, $p > .05$). We then continued to our planned comparisons for the trained hand and the untrained hand in order to investigate the performance difference between aligned and translated training conditions, as a function of Group.

Following training with aligned-cursor feedback, subjects estimated their trained hand was aligned with the reference marker when it was on average 1.17 cm to the right of it (left-hand training group) or .46 cm to the left of it (right-hand training group). After subjects trained with the translated cursor, the bias of their trained hand (squares) estimates of hand position shifted to the left, on average 0.65 cm, and thus in the direction of the visuomotor distortion ($F(1, 33) = 12.350$, $p < .001$). The magnitude of this change is shown in the left bars in Fig. 4c. This shift in proprioceptive estimates was comparable across the left- and right-hand training groups ($F(1, 33) < 1$, $p = .721$) and again comparable across the four reference markers ($F(3, 99) = 2.019$, $p = .150$), regardless of whether the center reference marker was proprioceptive or visual for the left ($p = 1$)- and right-hand ($p = .350$) training groups.
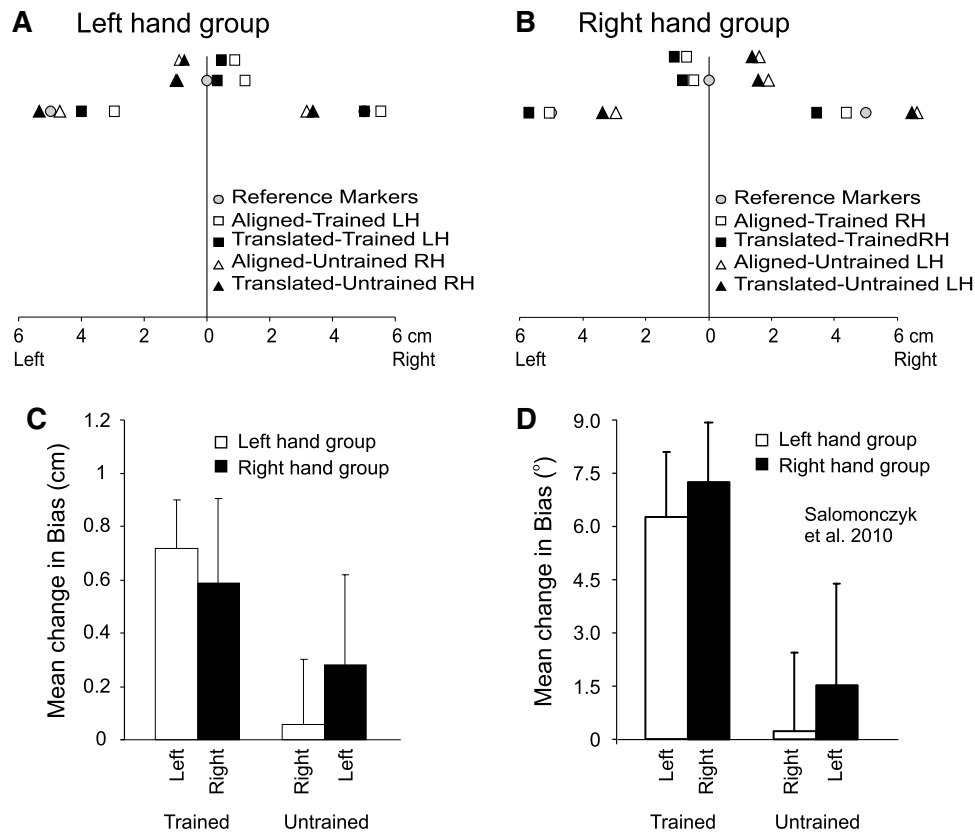
Fig. 4 Proprioceptive estimates for the trained and untrained hands. **a** Left-hand training group mean 2D biases in the proprioceptive estimate tasks for the left trained (*squares*) and right untrained (*triangles*) hands following left-hand training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. The actual reference marker positions are represented as *filled gray circles*. **b** Right-hand training group mean 2D biases in the proprioceptive estimate tasks for the right trained (*squares*) and left untrained (*triangles*) hands following training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. Proprioceptive estimates relative to the body midline have been shifted above those made at visual markers for both **a** and **b** (*above*) to avoid overlap. **c** Mean change in bias for the (*left and right*) trained hands and (*right and left*) untrained hands (*left and right bars,* respectively) for the left-hand training group (*white bars*) and the right-hand training group (*black bars*). **d** Mean change in bias from (Salomonczyk et al. 2010). *Error bars* reflect standard error of the mean

While the positions at which subjects felt their left and right trained hands (squares in Fig. 4a, b) to be at a reference marker were significantly shifted following training with translated feedback, when we measured the untrained right and left hands, the mean biases were shifted only .05 and .27 cm leftwards (triangles in Fig. 4a, b and bars on the right in Fig. 4c), respectively. These shifts were not statistically significant from biases following training with the aligned-cursor feedback (right hand: $F_{(1, 33)} < 1$, $p = .848$; left hand: $F_{(1, 33)} < 1$, $p = .349$).

Again, our findings are consistent with previous results observed by Salomonczyk et al. (2010) (Fig. 4d). Specifically, they found that the position at which subjects' felt their trained hand coincided with the reference marker was shifted leftwards by 6.6° (approximately 20 % of the distortion introduced) after training with a 30° rotated cursor compared to after reaching with an aligned cursor ($F_{(1, 44)} = 28.8$, $p < .001$). While the mean biases in the untrained left and right hands were shifted by 1.50° and .14° leftwards, respectively, however, these shifts were not statistically significant ($F_{(1, 44)} < 1$, $p = .953$; $F_{(1, 44)} < 1$, $p = .564$, respectively).

Uncertainty

Figure 5 depicts the magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (white bars) and translated (white dashed bars) cursor feedback, and the right and left untrained hands following reach training with aligned (black bars) and translated (black dashed bars) cursor feedback. The uncertainty ranges did not differ across any of the factors; nor were there any interactions ($p > 0.05$).
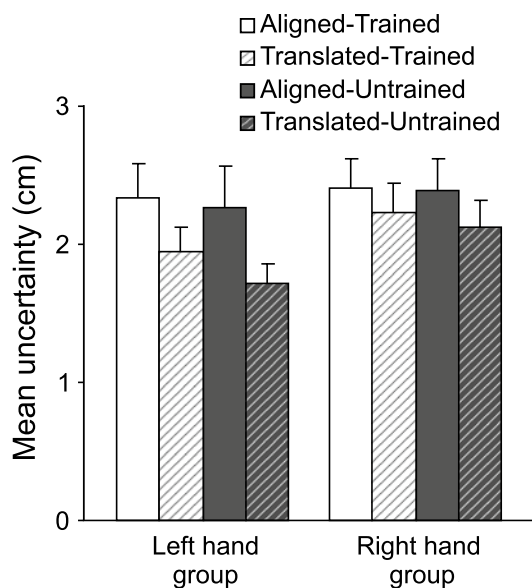
Fig. 5 Magnitude of the uncertainty ranges for the left and right trained hands following reach training with aligned (*white bars*) and translated (*white dashed bars*) hand-cursor feedback. Magnitude of uncertainty ranges for the right and left untrained hands is also displayed following reach training with aligned (*black bars*) and translated (*black dashed bars*) cursor feedback. *Error bars* reflect standard error of the mean

Discussion

We sought to assess the extent that adapting to a translated cursor leads to transfer of motor adaptation to the opposite hand, and whether this transfer differs between the dominant and non-dominant hands. Additionally, we wanted to determine whether changes in hand proprioception that occur with the trained hand following motor adaptation transfer to the untrained hand. We found intermanual motor transfer to the left untrained hand after subjects trained their right hand to reach with translated visual feedback of their hand, while transfer from the left trained hand to the right untrained hand was not observed. Despite finding changes in felt hand position in both trained hands, we did not find similar evidence of proprioceptive recalibration in the right or left untrained hands. Taken together, our results suggest that unlike motor adaptation, proprioceptive recalibration does not transfer between hands and is specific only to the arm exposed to the distortion.

Motor transfer and arm asymmetry

While visuomotor adaptation was observed to the same extent in both the left and right trained hands of right-handed individuals following adaptation to a visuomotor distortion, these findings were not symmetrically transferred to the untrained hands. Small but significant reach

aftereffects were observed in the untrained left hand following training with the right hand, suggesting some of the motor adaptation of the right hand had been transferred to the untrained left hand. Unsurprisingly, these transferred aftereffects were smaller than those observed in the trained left hand, suggesting that transfer between the two hands is incomplete. No transfer of reach aftereffects was observed in the untrained right hand following training with the left hand.

Our results are consistent with previous findings from our laboratory (Salomonczyk et al. 2010), in which a different distortion was employed. Salomonczyk et al. found that subjects adapted their reaches in both the right and left trained hands (and with comparable magnitude) after training with a 30° CW rotated cursor; however, intermanual transfer only occurred after right-hand adaptation and only the untrained left hand produced significant aftereffects. Together, these results suggest the asymmetry in transfer is not due to the type of distortion (i.e., translated or rotated cursor), as it occurred in both cases. While adaptation to a translated cursor may result in greater generalization overall (Ghahramani et al. 1996; Vetter et al. 1999; Cressman and Henriques 2009), it did not result in greater or different patterns of intermanual transfer compared to that produced following adaptation to a comparably sized visuomotor rotation (Salomonczyk et al. 2010). Specifically, from the aftereffects observed in the present study and those by Salomonczyk et al.'s (2010) (Fig. 3c), it appears that there were no real differences in the size and pattern of the intermanual motor regardless of the extent of motor adaptation achieved.

Our pattern of intermanual motor transfer, based on measuring changes in endpoint errors in the open-loop reaches (i.e., aftereffects), is different from that found by Sainburg and Wang (2002) and Wang et al. (2011) when assessing how well the untrained hand could adapt to the same perturbation experience by the trained hand. The authors found that adaptation of both the untrained left and untrained right hand was facilitated with prior training with the opposite hand to the same visuomotor rotation. However, the measures by which these two untrained arms showed this advantage, or transfer, differed depending on the arm. Specifically, final position accuracy transferred from the dominant (right) to the non-dominant (left) hand, while initial directional accuracy measured as the error at peak velocity transferred from the non-dominant to the dominant hand. The asymmetries in their studies differ from our own in that we found evidence of transfer of initial directional accuracy and final position accuracy to the non-dominant hand, while we also failed to observe either effect from the non-dominant to the dominant hand. The difference between our studies (including that by Salomonczyk et al. (2010)) and theirs may have to do with how we

assessed adaptation and transfer. In Sainburg and Wang's (2002) paradigm, as well as other studies on intermanual transfer, the untrained hand was exposed to the distortion and the learning rate (across trials) was assessed. Intermanual transfer is indicated by a steeper learning rate (also known as savings) as well as a smaller deviation in the first trials with the untrained hand following opposite-hand training. However, we assessed intermanual transfer by examining directional errors at peak velocity and endpoint errors during open-loop reaches to determine the magnitude of transfer. One explanation for this inconsistency, as outlined above, could be that direction and pattern of asymmetry of intermanual transfer differs depending on the measures of assessment. However, research from our laboratory using a different paradigm (Balitsky Thompson and Henriques 2010) where intermanual transfer was assessed by measuring facilitation following opposite-hand training revealed facilitation only from the right (dominant) arm to the left (non-dominant) arm. This pattern of transfer occurred across different magnitudes of distortion (45°, 60°, 75°) and different feedback representations (cursor vs. video image of the hand). Thus, this motor transfer to only the non-dominant arm found in three of ours studies (separate subjects and even different equipment for the Balitsky Thompson and Henriques study) may be beyond merely how transfer was measured, or the extent of motor adaptation. Another possible explanation of these different results in our study and studies of Sainburg and Wang is that the magnitude of aftereffects in our study was around 30 % of the visuomotor distortion, so that learning may not have been complete, and thus may have influenced the direction and the extent of the intermanual transfer.

Our observed asymmetric transfer is similar to transfer found by Redding and Wallace (2008) following adaptation to displacing prisms. The authors found that aftereffects (as assessed by reaches made following removal of the prisms) transferred from the right trained hand to the left untrained hand but not vice versa. The magnitude of transfer, as in our study, was approximately one-third of the aftereffects observed in the trained hand. These authors suggest that this asymmetric transfer between the right and left trained hands is due to symmetrically lateralized limb control but asymmetrical spatial mapping, where the right limb is represented in both hemispheres, while the left limb is represented only in the right hemisphere (Corbetta et al. 1993; Farne et al. 2003; Butler et al. 2004). The asymmetrical motor transfer of reach aftereffects we observe in the current study is consistent with this proposal.

Proprioceptive transfer and arm symmetry

We used a sensory estimation task that did not require any goal-directed movements, to assess proprioceptive recalibration independent of motor changes. Our findings replicate those from previous studies (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Salomonczyk et al. 2012) in that subjects experienced a shift in the position at which they felt their hand was aligned with a reference marker by roughly 20 % of the visuomotor distortion. However, proprioceptive recalibration did not transfer from the dominant or non-dominant trained to the opposite untrained hand. In particular, the mean biases of the untrained right and left hands were shifted only .05 and .27 cm leftwards, respectively, following reach training with a translated cursor compared to reach training with an aligned cursor, and these shifts were not statistically significant. Training with rotated visual hand feedback revealed a similar lack of transfer between the hands. Specifically, when Salomonczyk et al. (2010) introduced a 30° rotation to left- and right-hand trained groups, the authors found that subjects recalibrated proprioception equivalently in both groups, while the mean biases remained unchanged following opposite-hand training. Of course, given that proprioceptive change is much smaller than the change in reach movements (aftereffects) following visuomotor adaptation, it is possible that the felt position of untrained hand is shifted but by an amount that it is too small to detect. The magnitude of proprioceptive recalibration is typically a third of the aftereffects (Cressman and Henriques 2009, 2010), and in this study, the relative change in felt position for the trained hand (compared to the aftereffects) was closer to 70 %. Thus, given that aftereffects produced with the untrained left hand were about 0.6 cm in size, then the 33 % change in the proprioceptive perception of this hand would be about 0.2 cm, while a 70 % change would be closer to 0.4 cm. Indeed, we do find that the change in bias of the left hand was closer to 0.4 cm (see right black bar in Fig. 4c). However, given that this shift was not large enough to be detected statistically, we must conclude that hand proprioception was not changed for the untrained hands.

We assume that changes in biases of the trained hand following reach training are due to changes in proprioceptive estimates of the trained hand and not to some changes in the representation of visual space. This is based on the fact that in the current study, as well as in previous results, we have shown change in perceived hand position is equivalent between visual and proprioceptive (the body midline) markers (Cressman and Henriques 2009; Salomonczyk et al. 2011). The present results further argue against a possible shift in the visual representation of space following adaptation, as changes in bias for the trained and untrained hands would be similar if the visual representation of the marker was shifted. Indeed, this was not observed.

Several studies have suggested that the two arms may be specialized at using different types of sensory information

for localizing a target. For instance, Goble and Brown (2008) have suggested that the left limb is better at matching proprioceptive targets and the right limb for matching visual targets. However, we did not find similar asymmetries between the two hands in our sensory task. Moreover, Carson et al. (1990) and Jones et al. (2010, 2012) found that right-handed participants estimated their hand location with error magnitudes between the two hands, although errors were opposite in direction. Additionally, Jones et al. (2010, 2012) reported that the magnitude of proprioceptive biases and uncertainty ranges across the two hands, measured without a preceding reach training task, did not differ at all. In the present study, we found the same magnitude of proprioceptive biases when subjects judged the right hand with respect to a body midline (i.e., proprioceptive) and visual reference markers.

In summary, we found no arm-dependent differences in either proprioceptive estimates or unseen hand movements made to visual targets. Moreover, given that we did not find evidence of proprioceptive recalibration transferring between hands, it appears that unlike visuomotor adaptation, proprioceptive recalibration is specific to the hand exposed to the distortion. Further studies are required to characterize motor adaptation and sensory recalibration and determine the extent that these two processes are responsible for intermanual transfer of motor adaptation.

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