

Proprioceptive recalibration in the right and left hands following abrupt visuomotor adaptation

Danielle Salomonczyk · Denise Y. P. Henriques ·
Erin K. Cressman

Received: 19 May 2011 / Accepted: 9 December 2011 / Published online: 24 December 2011
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Abstract Previous studies have demonstrated that after reaching with misaligned visual feedback of the hand, one adapts his or her reaches and partially recalibrates proprioception, such that sense of felt hand position is shifted to match the seen hand position. However, to date, this has only been demonstrated in the right (dominant) hand following reach training with a visuomotor distortion in which the rotated cursor distortion was introduced gradually. As reach adaptation has been shown to differ depending on how the distortion is introduced (gradual vs. abrupt), we sought to examine proprioceptive recalibration following reach training with a cursor that was abruptly rotated 30° clockwise relative to hand motion. Furthermore, because the left and right arms have demonstrated selective advantages when matching visual and proprioceptive targets, respectively, we assessed proprioceptive recalibration in right-handed subjects following training with either the right or the left hand. On average, we observed shifts in felt hand position of approximately 7.6° following training with misaligned visual feedback of the hand, which is consistent

with our previous findings in which the distortion was introduced gradually. Moreover, no difference was observed in proprioceptive recalibration across the left and right hands. These findings suggest that proprioceptive recalibration is a robust process that arises symmetrically in the two hands following visuomotor adaptation regardless of the initial magnitude of the error signal.

Keywords Proprioception · Visuomotor adaptation · Sensory recalibration · Vision · Learning · Plasticity

Introduction

The central nervous system (CNS) integrates visual and proprioceptive information when planning a movement. If these sensory cues conflict and one is reaching to a visual target, one tends to rely more on the visual estimate of the hand than on the actual or felt position to guide motor output. For example, subjects reaching to a visual target with misaligned visual feedback of the hand (e.g. reaching in a virtual-reality environment or while wearing prism goggles) adjust their movements in order for the visual representation of the hand to achieve the desired endpoint. Furthermore, subjects reach with these adapted movement patterns following removal of the distortion (i.e. exhibit aftereffects; Martin et al. 1996; Krakauer et al. 1999; Krakauer et al. 2000; Baraduc and Wolpert 2002; Buch et al. 2003). This form of motor learning is referred to as visuomotor adaptation.

In addition to visuomotor adaptation, reaching with misaligned visual feedback of the hand has been shown to result in changes in sense of felt hand position (i.e. proprioceptive recalibration). Specifically, proprioceptive recalibration has been suggested to arise following reaches made

D. Salomonczyk · D. Y. P. Henriques
Centre for Vision Research, York University, Toronto,
ON, Canada

D. Salomonczyk
Department of Psychology, York University, Toronto,
ON, Canada

D. Y. P. Henriques
School of Kinesiology and Health Science, York University,
Toronto, ON, Canada

E. K. Cressman (✉)
School of Human Kinetics, University of Ottawa,
125 University St., Ottawa, ON K1N 6N5, Canada
e-mail: Erin.Cressman@uOttawa.ca

while wearing prism goggles, where the visual distortion is introduced immediately and in full (Harris 1963; Hay and Pick 1966), and following reaches made in a virtual-reality environment (Cressman and Henriques 2009; Cameron et al. 2010; Ostry et al. 2010; Simani et al. 2007). Until recently, this sensory recalibration was demonstrated following visuomotor adaptation by asking subjects to reach with the adapted hand to proprioceptive targets (Redding and Wallace 1996; van Beers et al. 2002; Simani et al. 2007). While results from these tasks indicated that reaches to proprioceptive targets were adapted, it is unclear whether these changes in reaches reflected proprioceptive recalibration *per se*. Given that subjects used their adapted arm, these resulting reaching movements to localize proprioceptive targets could have been influenced by motor adaptation. Thus, in attempt to assess proprioceptive recalibration independent of motor changes, Henriques and colleagues (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Salomonczyk et al. 2011) and Ostry et al. (2010) designed sensory estimation tasks that do not require any goal-directed movement. Specifically, in Cressman and Henriques' (2009) estimation task, subjects indicated the position of their hand relative to a visual or proprioceptive reference marker. In general, results revealed that subjects shifted the position at which they felt their hand was aligned with a reference marker $\sim 6^\circ$ (or about 20% of the visuomotor distortion), in the direction that they adapted their movement following reaches with a gradually introduced visuomotor distortion (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Salomonczyk et al. 2011). This shift in felt hand position has been shown to be remarkably consistent across several parameters, including the type of distortion (rotation vs. lateral displacement), the magnitude of the distortion (up to 70°), the extent of reach training (up to 300 trials), the type of reference marker (visual vs. proprioceptive), method of hand positioning (active vs. passive placement of the hand), and even across different age groups (young adults vs. adults 60 years and older).

Previous work from our laboratory examining sensory changes following motor adaptation has introduced the visuomotor perturbation (e.g. a visuomotor rotation around the hand) gradually during adaptation trials. In the current study, we sought to determine whether the size of the initial error signal influences sensory recalibration. To address this question, we introduced the visuomotor distortion abruptly, such that subjects initially experienced large reaching errors. To date, research comparing adaptation to large and small error signals has focused on examining resulting changes in movements, without a similar investigation into sensory changes. With respect to visuomotor adaptation, results indicate that motor learning (aftereffects) is greater in subjects who train to reach with misaligned

sensory feedback of the hand when the distortion is introduced gradually and subjects experience small reaching errors compared to when the distortion is introduced abruptly and subjects initially experience large reaching errors after subjects reach while wearing prism goggles (Michel et al. 2007), with a visuomotor rotation (Kagerer et al. 1997; Abeele and Bock 2001) or with a force perturbation (Criscimagna-Hemminger et al. 2010). Furthermore, retention of motor learning is reportedly greater in subjects that adapt to an incrementally introduced distortion compared with an abruptly introduced one (Klassen et al. 2005). By establishing whether proprioceptive recalibration arises following adaptation to an abrupt visuomotor distortion, we will be able to determine whether the size of initial error signals experienced also affects sensory plasticity.

Additionally, we sought to determine whether proprioceptive recalibration is comparable between the left and right hands of right-handed individuals. 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. Given that Goble and colleagues (Goble and Brown 2008; Goble and Anguera 2010) have recently shown that the left arm performs better for matching proprioceptive targets and the right arm for visual targets, reaching with misaligned visual feedback may have different effects on proprioceptive recalibration in the two arms. For example, the left arm, which has demonstrated an advantage for position-related proprioceptive sense in comparison with the right arm, may be more susceptible to sensory recalibration. If we do find an arm effect of proprioceptive recalibration, it would suggest hemispheric asymmetry for encoding visual and proprioceptive information.

Methods

Subjects

Forty-six right-handed young adults (mean age = 21.0 years, $SD = 3.58$, 29 women) were recruited from York University and volunteered to participate in the tasks described below. Data from three subjects were eliminated from analyses and hence not included in the results provided, as they were unable to consistently report the position of their hand in space (i.e. their uncertainty ranges (defined below) were greater than 3 times the average uncertainty range). Subjects were pre-screened verbally for self-reported handedness and any history of visual, neurological, and/or motor dysfunction. Following pre-screening, subjects were randomly assigned to either the right-hand training ($n = 20$) or left-hand training ($n = 26$; analysis with $n = 23$) groups. All subjects provided informed consent in

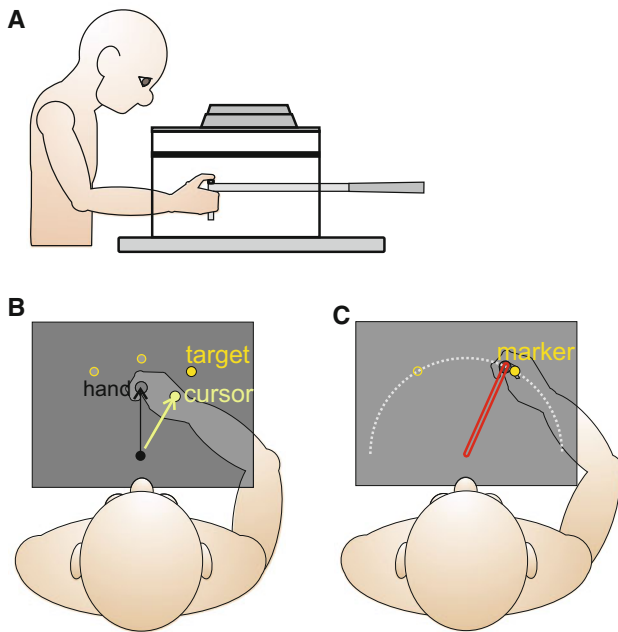


Fig. 1 Experimental set-up and design. **a** Side view of the experimental set-up. **b–c** Top view of the experimental surface visible to subjects. **b** Visuomotor distortion introduced in the rotated Reach Training Task. The *cursor* representing the hand was rotated 30° clockwise with respect to the actual hand location (*circle*). Reach targets (*circles*) were located at 0° in line with body midline and 30° *left* and *right* of body midline. **c** Reference markers (*circles*) were located at 30° *left* and *right* of midline. The grooved path along which the subjects' unseen hand travelled is represented by the *rectangle*

accordance with the ethical guidelines set by the York Human Participants Review Subcommittee.

General experimental set-up

A side view of the set-up is provided in Fig. 1a and is similar to the set-up used in Cressman and Henriques (2010) and Cressman et al. (2010). Subjects were seated in a

height-adjustable chair so that they could comfortably see and reach to all target and marker locations presented on an opaque, reflective surface. Subjects grasped the vertical handle of a two-joint robot manipulandum mounted in the horizontal plane (Interactive Motion Technologies). Visual stimuli were projected from a monitor (Samsung 510N, refresh rate 72 Hz) installed 17 cm above the robot onto a reflective surface aligned in the same horizontal plane as the robot. The room lights were dimmed, and subjects' view of their hand was blocked by the reflective surface and a black cloth draped between the experimental set-up and subjects' shoulders.

General procedure

Similar to our previous study (Cressman and Henriques 2009), the experiment consisted of two separate testing sessions completed on two separate days. Each testing session involved two tasks. On the first testing day, subjects completed the reaching trials outlined below while seeing a green cursor disc 1 cm in size that was aligned with their unseen hand. On the second testing day, subjects completed the reaching trials while viewing a cursor that was misaligned from the actual location of their unseen hand (Fig. 1b). The misaligned cursor was rotated 30° clockwise (CW) relative to actual hand position, with the origin of the rotation at the starting hand position. The cursor was represented by a green disc 1 cm in diameter (Fig. 1b). The descriptions and order of tasks are outlined below and in Fig. 2.

Training and adaptation

While grasping the robot manipulandum with either the right or left hand, subjects were instructed to reach to a yellow visual target disc, 1 cm in size, as quickly and accurately as possible while viewing either an aligned (first

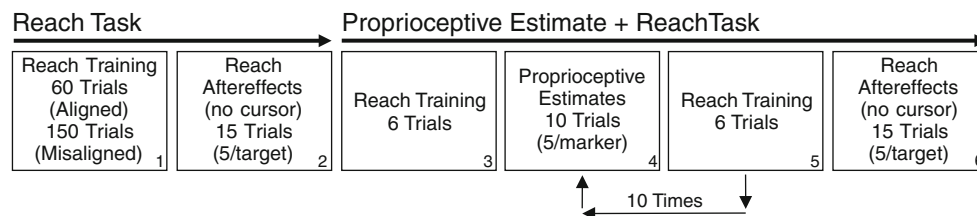


Fig. 2 Breakdown of the testing sessions within the experiment. In the first testing session, subjects reached with an aligned cursor that accurately represented the position of their hand in the reach training trials. In the second testing session, subjects reached with a misaligned cursor that was rotated 30° clockwise with respect to the actual hand location during the reach training trials. Using their *right* or *left* hand, subjects began a testing session by reaching to visual targets with a *green* cursor that provided visual feedback of hand position (*Box 1*). After completing either 60 (*aligned* cursor) or 150 (*misaligned* cursor) reach training

trials, subjects next reached to each of the three targets 5 times without a cursor in order to assess visuomotor adaptation (reach aftereffects trials, *Box 2*). Subjects then completed 6 reaches to the reach targets with the cursor present (*Box 3*). This was followed by 10 sets of 10 proprioceptive estimate trials (*Box 4*) and 6 visually guided reaches (*Box 5*) for a total of 100 proprioceptive estimate and 60 reach training trials. Following this, subjects again reached to each of the three targets 5 times without a cursor in order to assess maintenance of visuomotor adaptation (*Box 6*)

testing session) or misaligned (second testing session) cursor that moved with their hand. The reach targets were located radially 10 cm from the home position at 0° (centre), 30° left (CCW) and 30° right (CW) of centre (circles in Fig. 1b). The home position was located approximately 40 cm in front of the subjects along their body midline (indicated by the black circle in Fig. 1b). This position was not illuminated, and visual feedback was provided only when the hand had travelled 4 cm outwards from the home position. The reach was considered complete once the centre of the cursor had moved to within 0.5 cm of the target's centre. At this point, both the cursor and target discs disappeared and subjects moved their hands back to the home position in the absence of visual feedback along a linear route. 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)] was generated perpendicular to the path wall (Henriques and Soechting 2003; Cressman and Henriques 2009; Jones et al. 2010).

Each session began with subjects completing either 60 reaches with an aligned cursor (1st session) or 150 reaches with the misaligned cursor (2nd session) (box 1 in Fig. 2). Afterwards, subjects reached to the same targets 5 times each without cursor feedback for a total of 15 trials (box 2 in Fig. 2) to assess visuomotor adaptation (i.e. aftereffects in the second testing session). Subjects then reached again with the aligned or misaligned cursor for an additional 6 trials (box 3 in Fig. 2). Following these reaching trials, we began to assess subjects' estimates of hand position (box 4 in Fig. 2) as described below.

Proprioceptive estimate trials + reach trials

A proprioceptive estimate trial began with the subject grasping the robot manipulandum at the home position, which was indicated by a 1-cm green disc. After 500 ms, this disc disappeared and the subject was instructed to push his or her hand outward along a constrained robot-generated linear path (as described previously and shown by the rectangle in Fig. 1c). On all trials, once the hand reached the end of the path, a reference marker located 30° left (CCW) or 30° right (CW) of centre represented by a circle 1 cm in diameter appeared (circles, Fig. 1c) and subjects made a two-alternative forced-choice judgment about the position of their hand (left or right) relative to the reference marker. There was no time constraint for giving a response. After responding, the reference marker disappeared and the subject moved the robot directly back to the home position along a linear route to begin the next trial.

The position of the hand with respect to each reference marker was adjusted over trials using an adaptive staircase algorithm (Kesten 1958; Treutwein 1995) as described by

Cressman and Henriques (2009). Subjects alternated between 10 proprioceptive estimate trials and 6 reach trials with cursor feedback for a total of 100 proprioceptive estimate trials and 60 reaching trials (boxes 3–5 in Fig. 2). Subjects then reached 15 more times without the cursor (box 6 in Fig. 2) as a final measure of reach adaptation.

Data analysis

Visuomotor adaptation

Directional deviations of the hand made during reaching trials without visual feedback were analysed to assess motor adaptation. Reach endpoint errors were defined as the angular difference between a movement vector (from the home position to reach endpoint) and a reference vector (from the home position to the target). Reach errors at peak velocity were defined as the angular difference between a movement vector joining the home position and the position of the hand at peak velocity and the reference vector. Both errors at reach endpoint and at peak velocity were analysed to determine whether subjects adapted their reaches to the targets after aiming with a rotated cursor, and whether there was any change in reach adaptation following the proprioceptive estimate trials. Analyses were conducted using separate 2 Group (right-hand group vs. left-hand group) \times 2 Feedback condition (aligned vs. misaligned cursor) \times 2 Epoch (preceding proprioceptive estimate trials vs. following proprioceptive estimate trials) \times 3 Target (30° CW vs. 0° vs. 30° CCW) mixed repeated measures analysis of variance (RM-ANOVA). Group was treated as a between-subjects factor, while all others were treated as within-group factors. A Bonferroni correction was applied to post hoc pairwise comparisons.

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. From this logistic function, we calculated the bias (the point at which the probability of responding left was 50%) and uncertainty (the difference between the values at which the probability of responding left was 25 and 75%). The bias value is a measure of subjects' accuracy of proprioceptive sense of hand position, while the magnitude of the uncertainty range defines its precision (Cressman and Henriques 2009, 2010). A 2 Group (right-hand group vs. left-hand group) \times 2 Feedback condition (aligned vs. misaligned cursor) \times 2 Marker location (30° CW vs. 30° CCW) mixed RM-ANOVA was used to compare bias and uncertainty values following reach training with the right and left hands. Group was

treated as a between-subjects factor, while all others were treated as within-group factors. Proprioceptive recalibration was examined by comparing the bias values after training with a misaligned cursor with those following an aligned cursor (baseline). A Bonferroni correction was applied to all post hoc pairwise comparisons.

Results

Visuomotor adaptation

Directional endpoint reach errors made following reach training (i.e. before the proprioceptive estimation trials) are presented in Fig. 3a. After training with an aligned cursor, subjects in the left-hand group (open squares) had reach errors that were on average 2° leftwards of the targets and subjects in the right-hand group (open triangles) made reach errors that were on average 1° to the right of the targets. This is consistent with estimates of hand position (see Fig. 4a for bias results) and previous work suggesting that an inherent systematic bias exists in the two hands when reaching to targets (Jones et al. 2010; Wilson et al. 2010). After training with a rotated cursor (filled symbols), subjects in both groups had reach errors that deviated more leftwards than after training with an aligned cursor (filled symbols). Figure 3b depicts the mean changes in endpoint errors for the left- and right-hand groups preceding proprioceptive estimate trials (empty bars) and following the proprioceptive estimate trials (filled 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 rotated cursor), along with endpoint errors from Cressman and Henriques (2009). A significant change in average reach aftereffects from aligned to misaligned training was observed ($F(1, 41) = 244.5, P < .001$). Aftereffects observed in the left-hand group did not differ from those observed in the right-hand group ($F(1, 41) = 1.63, P = .21$). In addition, these aftereffects are consistent with previous results following a gradually introduced misaligned reach cursor (Cressman and Henriques 2009). Analysis of the epoch factor revealed greater reach aftereffects following the proprioceptive estimate trials (14° and 17° for the left- and right-hand groups, respectively) compared to those preceding the proprioceptive estimate trials (12° and 13° for the left- and right-hand groups, respectively; $F(1, 41) = 12.76, P = .001$). This pattern was consistent for both groups ($F(1, 41) < 1, P = .35$). While larger aftereffects were also observed in Cressman and Henriques (2009) following proprioceptive estimate trials compared to those preceding proprioceptive estimate trials, this difference did not achieve statistical significance. Lastly, there was a significant effect of target ($F(2, 82) = 19.32, P < .001$) such that reaching errors around the lateral targets were slightly compressed towards the central workspace (i.e. reaching errors tended to be to the left of the CW target and right of the CCW target), although this effect did not differ between aligned and rotated conditions ($F(2, 82) = 2.63, P = .07$).

Reach aftereffects at peak velocity were analysed and revealed a similar pattern of results (Fig. 3b, circles). After training with a rotated cursor, subjects reached significantly more leftwards of the target than after training with an aligned cursor ($F(1, 41) = 154.71, P < .001$).

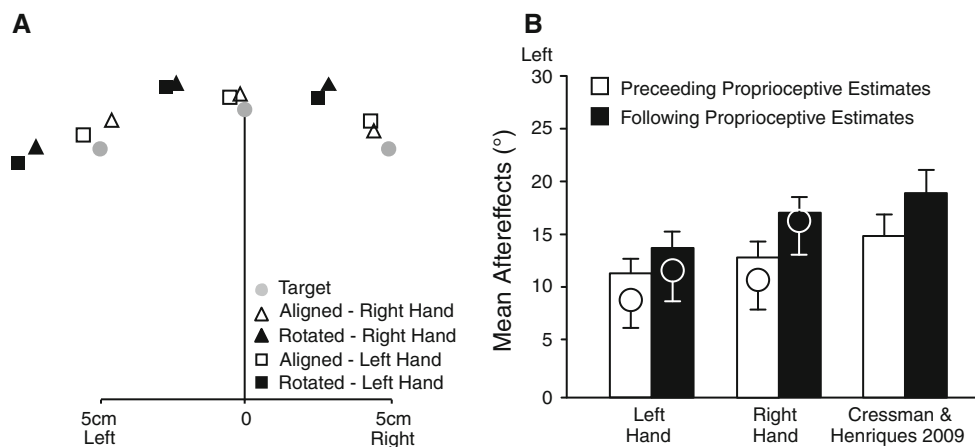


Fig. 3 Reaching errors for the *left-* and *right-*hand groups. **a** Mean 2-D representation of movement endpoint errors for the *left-*(squares) and *right-*(triangles) hand groups after training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. The target locations are represented as *filled grey circles*. **b** Mean change in directional reach endpoint errors (*bars*) and errors at peak velocity (*circles*) after reaching with misaligned visual feedback of the

hand for the *left-* and *right-*hand groups and data from Cressman and Henriques (2009). Values reflect baseline-subtracted aftereffect errors preceding proprioceptive estimate trials (*empty bars* and *black outlined circles*) and following proprioceptive estimate trials (*filled bars* and *white outlined circles*). Aftereffects of 30° would reflect 100% adaptation. *Error bars* reflect standard error of the mean

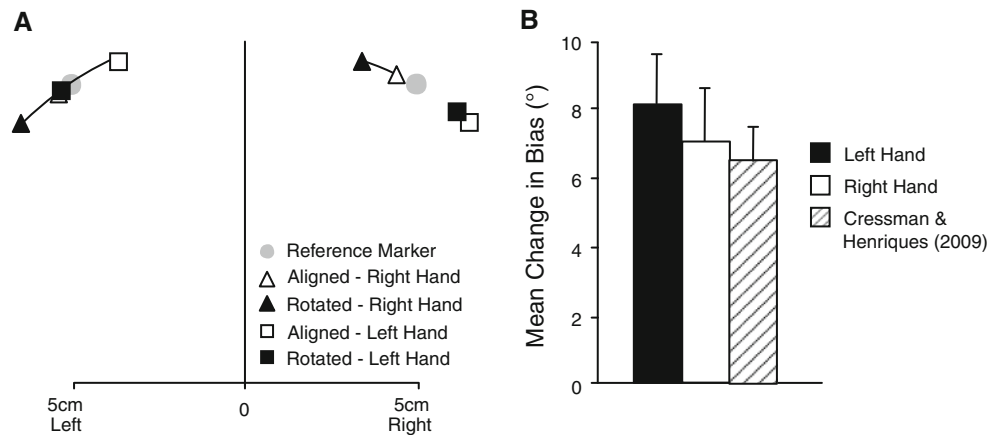


Fig. 4 Proprioceptive estimates for the *left-* and *right-*hand groups. **a** Mean angular biases in the proprioceptive estimate trials for the *left* (*squares*) and *right* (*triangles*) hand groups following training with aligned (*empty symbols*) and misaligned (*filled symbols*) visual feedback of the hand. The actual reference marker positions are represented as *filled grey circles* and a line connects each proprioceptive estimate

These aftereffects were comparable across groups ($F(1, 41) = 3.07, P = .08$). As with endpoint aftereffects, aftereffects at peak velocity following proprioceptive estimates (11.8° and 16.8° for the left- and right-hand groups, respectively) were greater than those preceding proprioceptive estimate trials (9.1° and 11.0° for the left- and right-hand groups, respectively; $F(1, 41) = 6.89, P = .01$). This pattern was again consistent for both groups ($F(1, 41) < 1, P = .35$), although the compression of reaching errors around the targets towards the centre was only observed for reaches made following aligned training ($F(2, 28) = 18.94, P < .001$). The similarity between directional reach errors at peak velocity and reach endpoint suggests that subjects did not make online corrections to their reach trajectories in the absence of visual feedback of hand position.

Proprioceptive estimates of hand position

Bias

Figure 4a depicts the positions at which subjects in the left- and right-hand groups perceived their hands to be aligned with the reference markers after training with an aligned (*empty symbols*) and misaligned cursor (*filled symbols*). Estimates of hand position following training with aligned cursor feedback significantly differed between left- and right-hand groups ($F(1, 41) = 70.12, P < .001$). Specifically, subjects in the left-hand group judged their hand to be in line with the reference marker when it was 9° to the right of it, while subjects in the right-hand group estimated their hand to be in line with the reference marker when it was 3° to the left of it. These results

of hand position after training with an aligned and rotated cursor for either the *left* or *right* hand with its corresponding reference marker. **b** Mean changes in bias for the *left-* and *right-*hand groups, as well as from subjects from Cressman and Henriques (2009), averaged across reference marker positions and subjects. *Error bars* reflect standard error of the mean

are in agreement with previous hand biases observed when subjects were asked to judge the position of their hand prior to any reach training: subjects estimated their right hand was more rightwards than it actually was and their left hand was more leftwards than it actually was (Jones et al. 2010). Figure 4b depicts the mean change in bias for the left (*filled bar*) and right (*empty bar*) hand groups. On average, the position at which subjects' felt their hand coincided with the reference marker was shifted leftwards by 7.6° after training with a misaligned cursor compared to after reaching with an aligned cursor ($F(1, 37) = 69.56, P < .001$). This shift is consistent with changes observed by Cressman and Henriques (2009; Fig. 4b, patterned bar), in which subjects estimated the position of their right hand following reach training trials in which the visuomotor distortion was gradually introduced. In the present study, post hoc tests revealed that subjects in both groups recalibrated their proprioceptive estimates of hand position around the 30° CW and 30° CCW reference markers ($P < .005$ for all contrasts). No differences in estimates between the left and right reference marker locations were observed between conditions for the right-hand group, suggesting that recalibration was comparable across the locations; however, estimates following rotated training were different between the two reference marker locations for the left-hand group, suggesting that subjects experienced greater recalibration around the CCW marker (11°) than the CW marker (4° ; $P = .01$). This effect does not appear to be dependent on initial proprioceptive estimates as there was no difference in biases following reaches with the aligned cursor between the two reference markers for the left-hand group (CCW marker = 8.9° , CW marker = 9.0° ; $P = .95$).

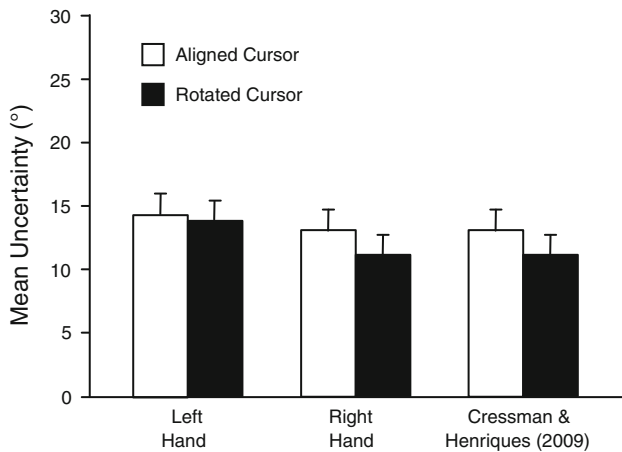


Fig. 5 Magnitude of the uncertainty ranges in the proprioceptive estimate trials for the *left-* and *right-*hand groups and data from Cressman and Henriques (2009) averaged across reference marker positions and subjects after reaching with an aligned cursor (*empty bars*) or misaligned cursor (*filled bars*). *Error bars* reflect standard error of the mean

Uncertainty

Figure 5 depicts the magnitude of the uncertainty ranges for the left- and right-hand groups following reaches made with aligned (empty bars) and misaligned (filled bars) cursor feedback. Subjects’ levels of precision in estimating the location of their unseen hands were comparable after reach training with an aligned and misaligned cursor ($F(1, 41) < 1, P = .40$), at all reference markers ($F(1, 41) < 1, P = .93$). Precision of estimates did not differ between the two groups ($F(1, 41) < 1, P = .24$). These results are in accordance with previous results following adaptation to a gradually introduced distortion (Cressman and Henriques 2009).

Visuomotor adaptation vs. proprioceptive recalibration

Figure 6 shows a summary of the changes in proprioceptive recalibration (bias) and reach adaptation (aftereffects) following training with a misaligned cursor as a percentage of the visuomotor distortion introduced and with respect to the overall magnitude of the distortion introduced (i.e. 30°). Specifically, Fig. 6 depicts the mean changes in proprioceptive biases (bars) and reach endpoint aftereffects (diamonds) following training with a misaligned cursor compared to training with an aligned cursor for each group. From this figure, we see that on average, subjects recalibrated proprioception by approximately 25% of the distortion introduced. In addition, after training with the misaligned cursor, subjects showed aftereffects equal to approximately 50% of the distortion introduced. We subsequently examined the relationship between the motor

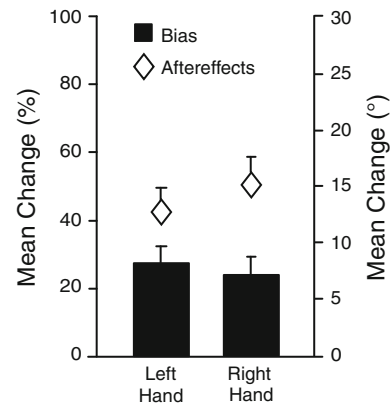


Fig. 6 Mean changes in proprioceptive biases and aftereffects after reach training with a misaligned cursor compared to an aligned cursor. The mean change in bias (*bars*) is plotted along with the mean change in aftereffects (*diamonds*) for the *left-* and *right-*hand groups. Results are shown in degrees and as a percentage of the distortion introduced during reach training trials. *Error bars* reflect standard error of the mean

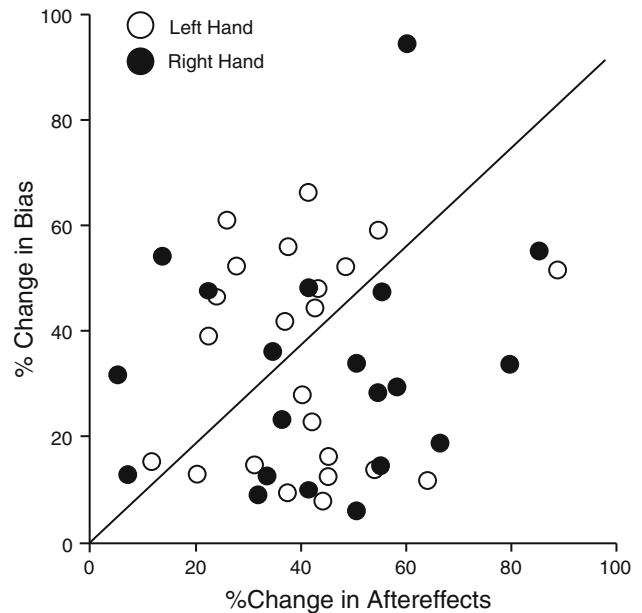


Fig. 7 Changes in proprioceptive biases and aftereffects are expressed as a percentage of the visuomotor distortion introduced for the *left-* (*empty circles*) and *right-* (*filled circles*) groups. The *solid line* is a unit slope and so indicates equivalent levels of proprioceptive recalibration and visuomotor adaptation

changes (aftereffects) and sensory changes (proprioceptive recalibration) expressed as a percentage of the visuomotor distortion introduced using a bivariate correlation (Fig. 7). Consistent with previous works (Cressman and Henriques 2009; Salomonczyk et al. 2011), results revealed that all subjects adapted their movements and recalibrated proprioception, though a significant relationship between these changes was not observed ($r = .052, P = .74$).

Discussion

The present study examined whether proprioceptive recalibration occurs following visuomotor adaptation to an abrupt distortion and whether this recalibration is comparable across the left and right hands of right-handed individuals. On average, subjects adapted their reaches by 14° and recalibrated the position at which they felt their hand was aligned with a reference marker by 7.6° after training with a rotated cursor compared to reach training with an aligned cursor. This change in felt hand position was in the same direction that subjects' adapted their reaches during reach training and was approximately 25% of the magnitude of the visuomotor distortion introduced. These results address our first question of interest and suggest that proprioceptive recalibration does occur following visuomotor adaptation to an abrupt distortion. Given that subjects in both groups adapted their reaches and recalibrated, proprioception around all targets and reference markers indicates that proprioceptive recalibration occurs comparably in the left and right hands, which addresses our second question of interest. Furthermore, our findings for our right-hand group replicate those of Cressman and colleagues (Cressman and Henriques 2009, 2010) wherein proprioceptive recalibration was observed following adaptation to a visuomotor distortion that was introduced gradually. In fact, recalibration was comparable in magnitude across these studies (approximately 7° leftwards), regardless of both the hand used and whether the perturbation was introduced gradually or abruptly.

Effect of initial error on recalibration

We found similar changes in hand proprioceptive estimates and no-cursor (open-loop) reaches as we did in our previous studies where the cursor was gradually rotated during training. These findings are consistent with previous results that suggest adaptation is comparable between abrupt and gradual perturbations (Klassen et al. 2005). For example, Klassen and colleagues introduced a 30° visuomotor rotation either abruptly or gradually (in 0.125° increments) and found no difference in motor learning retention when subjects were tested 24 h later. However, Kagerer et al. (1997) introduced a 90° visuomotor rotation either at once or in 10° increments and observed increased retention (aftereffects) in subjects who reached with a gradually introduced 90° visuomotor perturbation compared to those in which the perturbation was abruptly introduced (43.1° and 28.22° , respectively). In contrast to these findings, Buch et al. (2003) reported *decreased* aftereffects following gradual exposure to a 90° visuomotor rotation compared with abrupt exposure; however, this trend was only described for older adults. The differences in motor adaptation following

reaches with an abruptly versus gradually introduced distortion appear to depend on the initial error signals experienced, such that differences in aftereffects following gradual or abrupt learning seem to occur only for visuomotor rotations greater than the 30° rotation used in our current study. According to Abeele and Bock (2001), different mechanisms are engaged when learning large (over 90°) versus small rotations, and these separate mechanisms, which may further be differentially engaged when learning abrupt versus gradual rotations, lead to the inconsistency between findings of increased or decreased adaptation depending on the magnitude of the initial error signal. It could also be that adapting to a very large and thus difficult or less relevant perturbation may be easier to do when the error signals and overall difficulty increase gradually; for instance, correct credit assignment for reaching error in the case when the cursor is suddenly deviated from the hand movement by a rotation of 90° or more may be quite different than that for smaller or gradual deviations (Wei and Kording 2009).

In instances when the distortion is introduced abruptly and large reach errors are initially experienced, it has been suggested that explicit, strategic control processes are engaged early in the learning process in order to produce rapid corrections in motor performance (Redding and Wallace 1996). In contrast, when the distortion is introduced gradually and small reach errors are experienced, reach adaptation is proposed to arise through implicit processes that reduce the discrepancies between vision and proprioception. The fact that we found similar changes in movements and sensory recalibration following abrupt-cursor adaptation compared to gradual-cursor adaptation suggests that these changes are not cognitively or strategically driven as proposed by previous research using prism adaptation paradigms (Redding and Wallace 1996). In fact, given the results of Mazzoni and Krakauer (2006), the sensory and motor changes observed in the present study most likely arise implicitly rather than explicitly.

Arm symmetry

It has been suggested that the two arms may be better 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. In the current study, biases measured following reach training with an aligned cursor did produce a small asymmetry across the two hands, where larger rightward biases were present in the left-hand group and smaller leftward biases were present in the right-hand group. These results are consistent with Goble and Brown's (2008) proposal, in that subjects were able to more accurately localize their right

hand relative to a visual reference marker compared to the left hand. Yet in our previous study, we found the same magnitude of proprioceptive biases when subjects judged the position of the right hand with respect to body midline (i.e. proprioceptive reference) and a visual reference. Likewise, we found no differences in the magnitude of reaching errors to a visual target made without any cursor feedback following either right or left-hand training with an aligned or rotated cursor; absolute reach endpoint errors were 1.5° on average following aligned-cursor training and were not different between the two groups. Differences in findings between our work and Goble's may arise due to the nature of the task. Goble and Brown's findings were observed during a task that involved moving the arm around the elbow joint in order to match the angle of the opposite arm in a bimanual task or to match a visual reference. In contrast, our task was a unimanual task and we did not find similar asymmetries between the two arms in either our sensory or motor tasks. In the current study, and in our previous work (Jones et al. 2010), the extent of the misestimates of proprioceptive biases of the unseen hand position of the two arms was similar. Moreover, we have shown that proprioceptive biases and uncertainty ranges, measured without a preceding reach-training task, do not differ at all in magnitude (just in direction) across the two hands (Jones et al. 2010; Rincon-Gonzalez et al. 2011; Wilson et al. 2010). Thus, perhaps arm asymmetry is only observable when the two arms are working together to complete the same task.

While sense of felt hand position was shifted at all reference markers and movements adapted at all targets examined, proprioceptive recalibration was significantly less at the rightwards (CCW) marker than at the leftwards (CW) marker for the left-hand group; this asymmetry was not observed in the right-hand group. Previous results suggest that motor adaptation asymmetries may arise following reaches with prism goggles due to asymmetries in underlying attentional biases (Goedert et al. 2010). However, given that we found that movement aftereffects were comparable in magnitude across all targets suggests that the asymmetric proprioceptive recalibration we observed may not have arisen due to attentional biases. Moreover, no differences in bias between the two reference markers following aligned reach training were observed in the left-hand group, further weakening the argument for an attentional bias underlying asymmetrical recalibration. An alternative explanation may involve asymmetries in encoding limb position and interactions with workspace locations. As discussed previously, Goble and Brown (2010) suggest that the left hand is more accurate at matching proprioceptive targets than the right hand. Moreover, Goble (2010) recently demonstrated that joint matching is better when the tested joint is in the far-left workspace. That proprioceptive estimates of hand position were shifted following rotated training more so for a

reference marker in the left workspace than the right may be a result of an inherent workspace bias for the left limb, which only becomes evident when information from proprioceptive and visual modalities are incongruent. More research is required in order to address this question specifically.

Proprioceptive recalibration

While the precise relationship between sensory and motor changes arising from reaching with altered visual feedback of the hand remains to be determined, results from the current study (i.e. Fig. 7) and previous studies from the Henriques' laboratory (Cressman and Henriques 2009; Salomonczyk et al. 2011) and recent work by de Grave et al. (2011) suggest that these processes may occur simultaneously, yet independently of each other. Specifically, we find that proprioceptive recalibration is uncorrelated with motor changes (aftereffects) following visuomotor adaptation paradigms (Cressman and Henriques 2009; Salomonczyk et al. 2011). Moreover, de Grave et al. (2011) recently demonstrated that visuomotor adaptation in response to a cursor perturbation that was shifted in depth relative to the body was not related to changes in the perceived "reachability" of a target (i.e. changes in subjects reaches were not correlated with their perceptions regarding their ability to successfully reach a target). In accordance with these findings, recent work from Block and Bastian (2011) suggests that sensory realignment (i.e. proprioceptive recalibration) also arises independently of sensory weighting.

Recalibration of proprioception may arise because the central nervous system performs motor tasks optimally when a unified estimate of hand position is available. When sensory estimates of hand position are incongruent, the brain may seek to resolve this sensory discrepancy by recalibrating a less salient sense (proprioception) to match the more reliable visual input. In the current study, we only asked subjects to estimate the position of their hand with respect to visual reference markers. Thus, it could be argued that our results demonstrate sensory (visual-proprioceptive) realignment without providing evidence that proprioception was recalibrated, such that subjects experienced an overall shift of sense of felt hand position that was independent of having to align one's hand with a visual cue. Based on our previous results, in which we demonstrate similar shifts in proprioceptive biases regardless of whether subjects are required to judge the position of their hand relative to a visual or proprioceptive reference marker at the same location (Cressman and Henriques 2009), we are confident that the changes in felt hand position we observe at visual reference markers reflect a more global shift in felt hand position, as opposed to intersensory realignment. In

addition, we have recently not only repeated these results using proprioceptive and visual reference markers, but also have shown similar shifts in proprioceptive biases when subjects were required to indicate the position of their right (adapted) hand with their left hand [i.e. a proprioceptive–proprioceptive alignment task (Clayton et al. 2011)]. Similar to the results we have reported previously, we again find a shift in proprioceptive biases that are reflective of proprioceptive recalibration.

Acknowledgments We wish to thank Orysia Kachmarchuk for help with data collection. This work was supported by Canadian Institute of Health Research, Institute of Neurosciences, Mental Health and Addiction and the Banting Foundation (DYPH) and the Natural Sciences and Engineering Research Council (NSERC). DS is supported by an NSERC doctoral scholarship. DYPH is an Alfred P. Sloan Fellow.

References

- Abeele S, Bock O (2001) Sensorimotor adaptation to rotated visual input: different mechanisms for small versus large rotations. *Exp Brain Res* 140:407–410
- Baraduc P, Wolpert DM (2002) Adaptation to a visuomotor shift depends on the starting posture. *J Neurophysiol* 88:973–981
- Block HJ, Bastian AJ (2011) Sensory weighting and realignment: independent compensatory processes. *J Neurophysiol* 106:59–70
- Buch ER, Young S, Contreras-Vidal JL (2003) Visuomotor adaptation in normal aging. *Learn Mem* 10:55–63
- Cameron BD, Franks IM, Inglis JT, Chua R (2010) The adaptability of self-action perception and movement control when the limb is passively versus actively moved. *Conscious Cogn* [Epub ahead of print]
- Clayton H, Cressman E, Henriques D (2011) Visuomotor adaptation and proprioceptive recalibration in Ehlers-Danlos Syndrome patients and healthy controls. Society for Neuroscience, Washington, DC
- Cressman EK, Henriques DY (2009) Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102:3505–3518
- Cressman EK, Henriques DY (2010) Reach adaptation and proprioceptive recalibration following exposure to misaligned sensory input. *J Neurophysiol* 103:1888–1895
- Cressman EK, Salomonczyk D, Henriques DY (2010) Visuomotor adaptation and proprioceptive recalibration in older adults. *Exp Brain Res* 205:533–544
- Crisicimagna-Hemminger SE, Bastian AJ, Shadmehr R (2010) Size of error affects cerebellar contributions to motor learning. *J Neurophysiol* 103:2275–2284
- de Grave DD, Brenner E, Smeets JB (2011) Judgments of reachability are independent of visuomotor adaptation. *Perception* 40:962–974
- Goble DJ (2010) Proprioceptive acuity assessment via joint position matching: from basic science to general practice. *Phys Ther* 90:1176–1184
- Goble DJ, Anguera JA (2010) Plastic changes in hand proprioception following force-field motor learning. *J Neurophysiol* 104:1213–1215
- Goble DJ, Brown SH (2008) Upper limb asymmetries in the matching of proprioceptive versus visual targets. *J Neurophysiol* 99:3063–3074
- Goble DJ, Brown SH (2010) Upper limb asymmetries in the perception of proprioceptively determined dynamic position sense. *J Exp Psychol Hum Percept Perform* 36(3):768–775
- Goedert KM, Leblanc A, Tsai SW, Barrett AM (2010) Asymmetrical effects of adaptation to left- and right-shifting prisms depends on pre-existing attentional biases. *J Int Neuropsychol Soc* 16:795–804
- Harris CS (1963) Adaptation to displaced vision: visual, motor, or proprioceptive change? *Science* 140:812–813
- Hay JC, Pick HL Jr (1966) Visual and proprioceptive adaptation to optical displacement of the visual stimulus. *J Exp Psychol* 71:150–158
- Henriques DY, Soechting JF (2003) Bias and sensitivity in the haptic perception of geometry. *Exp Brain Res* 150:95–108
- Jones SA, Cressman EK, Henriques DY (2010) Proprioceptive localization of the left and right hands. *Exp Brain Res* 204:373–383
- Kagerer FA, Contreras-Vidal JL, Stelmach GE (1997) Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp Brain Res* 115:557–561
- Kesten H (1958) Accelerated stochastic approximation. *Ann Math Stat* 29:41–59
- Klassen J, Tong C, Flanagan JR (2005) Learning and recall of incremental kinematic and dynamic sensorimotor transformations. *Exp Brain Res* 164:250–259
- Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. *Nat Neurosci* 2:1026–1031
- Krakauer JW, Pine ZM, Ghilardi MF, Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20:8916–8924
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT (1996) Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119(Pt 4):1199–1211
- Mazzoni P, Krakauer JW (2006) An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci* 26:3642–3645
- Michel C, Pisella L, Prablanc C, Rode G, Rossetti Y (2007) Enhancing visuomotor adaptation by reducing error signals: single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. *J Cogn Neurosci* 19:341–350
- Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL (2010) Somatosensory plasticity and motor learning. *J Neurosci* 30:5384–5393
- Redding GM, Wallace B (1996) Adaptive spatial alignment and strategic perceptual-motor control. *J Exp Psychol Hum Percept Perform* 22:379–394
- Rincon-Gonzalez L, Buneo CA, Helms Tillery SI (2011) The proprioceptive map of the arm is systematic and stable, but idiosyncratic. *PLoS One* 6:e25214
- Salomonczyk D, Cressman EK, Henriques DY (2011) Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. *Neuropsychologia* 49:3053–3062
- Simani MC, McGuire LM, Sabes PN (2007) Visual-shift adaptation is composed of separable sensory and task-dependent effects. *J Neurophysiol* 98:2827–2841
- Treutwein B (1995) Adaptive psychophysical procedures. *Vis Res* 35:2503–2522
- van Beers RJ, Wolpert DM, Haggard P (2002) When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol* 12:834–837
- Wei K, Kording K (2009) Relevance of error: what drives motor adaptation? *J Neurophysiol* 101:655–664
- Wilson ET, Wong J, Gribble PL (2010) Mapping proprioception across a 2D horizontal workspace. *PLoS One* 5:e11851