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RESEARCH ARTICLE

The role of the cross-sensory error signal in visuomotor adaptation

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

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Abstract Reaching to targets with misaligned visual feedback of the hand leads to changes in proprioceptive estimates of hand position and reach aftereffects. In such tasks, subjects are able to make use of two error signals: the discrepancy between the desired and actual movement, known as the sensorimotor error signal, and the discrepancy between visual and proprioceptive estimates of hand position, which we refer to as the cross-sensory error signal. We have recently shown that mere exposure to a sensory discrepancy in the absence of goal-directed movement (i.e. no sensorimotor error signal) is sufficient to produce similar changes in felt hand position and reach aftereffects. Here, we sought to determine the extent that this cross-sensory error signal can contribute to proprioceptive recalibration and movement aftereffects by manipulating the magnitude of this signal in the absence of volitional aiming movements. Subjects pushed their hand out along a robot-generated linear path that was gradually rotated clockwise relative to the path of a cursor. On all trials, subjects viewed a cursor that headed directly towards a remembered target while their hand moved out synchronously. After exposure to a 30° rotated hand-cursor distortion, subjects recalibrated their sense of felt hand position and adapted their reaches. However, no additional increases in recalibration or aftereffects were observed following further increases in the cross-sensory error signal (e.g. up to 70°). This is in contrast to our previous study where subjects freely reached to targets with misaligned visual hand position feedback, hence experiencing both sensorimotor and cross-sensory errors, and the distortion magnitude systematically predicted increases in proprioceptive recalibration and reach aftereffects. Given these findings, we suggest that the cross-sensory error signal results in changes to felt hand position which drive partial reach aftereffects, while larger aftereffects that are produced after visuomotor adaptation (and that vary with the size of distortion) are related to the sensorimotor error signal.

Keywords Visuomotor adaptation · Vision · Proprioception · Proprioceptive recalibration · Error-driven learning

Introduction

When reaching with a visuomotor distortion (i.e. when wearing prism goggles or in a virtual-reality environment), one adjusts his or her movements in order to bring the visual representation of the hand to the desired target (Martin et al. 1996b; Krakauer et al. 1999, 2000; Redding and Wallace 2000; Simani et al. 2007). In general, it is proposed that motor adaptation arises primarily due to error-based learning (Tseng et al. 2007; Berniker and Kording 2008; Wei and Kording 2009; Hinder et al. 2010; Shadmehr et al. 2010), where the difference between one's desired performance and actual performance, or between the predicted and actual sensory consequences of one's movements, is reduced. Specifically, if the "seen" hand movement does

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D. Salomonczyk
Centre for Vision Research, York University, Toronto, Canada

D. Salomonczyk · D. Y. P. Henriques
Department of Psychology, York University, Toronto, Canada

E. K. Cressman
School of Human Kinetics, University of Ottawa, Ottawa, Canada

D. Y. P. Henriques (✉)
School of Kinesiology and Health Science, York University,
4700 Keele Street, Toronto, ON M3J 1P3, Canada
e-mail: deniseh@yorku.ca

not reach the desired goal or differs from the predicted outcome, then the brain uses this *sensorimotor error signal* (Wong and Shelhamer 2011) to change one's motor performance on subsequent movements. Moreover, these movements continue to deviate even when (misaligned) visual feedback of hand position is removed (Martin et al. 1996a; Krakauer et al. 1999, 2000; Redding and Wallace 2000; Simani et al. 2007). These persistent movement deviations, known as aftereffects, are robust evidence that the central nervous system (CNS) has learned a new visuomotor mapping in response to the sensorimotor error signal.

Evidence suggests that in addition to motor changes observed following visuomotor adaptation, sensory changes occur as well. More specifically, one's sense of felt hand position shifts in the direction of the visual feedback provided. This has been demonstrated following adaptation to prism goggles, in which the entire visual field is displaced (Harris 1963; Hay and Pick 1966; Redding and Wallace 1996, 2004) and more recently following adaptation in a virtual setup, where only the visual feedback of hand position is displaced (van Beers et al. 2002; Simani et al. 2007). Using this second paradigm, we have shown that this shift is approximately 20 % of the visuomotor distortion introduced, or roughly one-half to one-third of the extent of reach adaptation achieved (Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012). While this shift in felt hand position, which we term proprioceptive recalibration, is small, it is robust and occurs coincidentally with motor changes under a variety of contexts. For example, we have observed this shift in felt hand position following motor adaptation to rotated and translated cursor distortions (Cressman and Henriques 2009), during active and passive hand placement (Cressman and Henriques 2009), in both the left and right hands (Salomonczyk et al. 2012) and in healthy young and older adults (Cressman et al. 2010).

Recently, we have suggested that a second error signal arising from the discrepancy between seen and felt positions of the reaching hand (what we term the *cross-sensory error signal*) may contribute to sensory and motor adaptation (Cressman and Henriques 2010; Henriques and Cressman 2012). In particular, we have proposed that this cross-sensory error signal leads to the observed changes in perceived hand position, such that sensory signals are recalibrated to provide a unified state estimate of the hand/effector. To investigate the role of this cross-sensory error signal in motor learning, we devised a novel learning paradigm that isolated the visual-proprioceptive discrepancy (and thus this cross-sensory error signal) from the usual visuomotor discrepancy (Cressman and Henriques 2010). In particular, we employed a paradigm where subject did not make free, goal-directed reaches to the target during training, but instead moved their hand (active movement condition), or had their hand passively moved by the manipulandum (passive movement condition), along a robot-constrained pathway while they viewed a cursor that moved directly towards a remembered target. The pathway that the unseen hand travelled was gradually rotated with respect to the cursor-target pathway over trials, creating a discrepancy between the seen and felt motion of the hand. Since the actual direction of the hand motion was not under the control of the subject, and the hand-cursor always headed towards the target, subjects did not experience any reaching errors or sensory consequences of a goal-directed action and hence any sensorimotor error. Furthermore, those in the passive exposure training condition experienced no volitional movement as their hand was passively moved for them. However, like previous adaptation paradigms, subjects in both active and passive movement conditions experienced a cross-sensory error signal as their felt sense of hand position was gradually misaligned from the cursor representation of their hand. Following active or passive exposure to this cross-sensory error signal, we found that all subjects still recalibrated proprioception, and the magnitude of this proprioceptive shift was comparable to that achieved following typical learning paradigms in which subjects were able to reach freely to targets with the visuomotor distortion (and utilize both the cross-sensory and sensorimotor error signals). Additionally, we found that following active and passive exposure training, subjects adapted their movements such that reaches made without visual feedback of their hand position were deviated in the direction opposite the cursor distortion. However, these movement aftereffects were two-thirds smaller than those observed following typical training with a visuomotor discrepancy. As well, unlike any of our previous studies, the observed proprioceptive recalibration and motor aftereffects were correlated with each other, suggesting that they may have been driven by the same mechanism (Cressman and Henriques 2010). Taken together, the findings of this study suggest that exposure to a sensory discrepancy alone is sufficient to form a new visuomotor mapping in the absence of a sensorimotor error signal. More importantly, results imply that the cross-sensory error signal alone may drive partial motor learning.

In the present study, we looked to investigate the extent that this cross-sensory error signal can contribute to motor learning by determining if induced changes in perceived hand position can be used in computing subsequent motor commands. To do so, we examined motor and sensory changes following exposure to a cross-sensory error signal that was systematically increased and compared these results to those from a previous study that examined motor and sensory changes following typical visuomotor adaptation (Salomonczyk et al. 2011). The influence of the size of the sensorimotor error (and hence combination of increases in the sensorimotor error signal and cross-sensory error signal) on motor learning and sensory plasticity has been previously characterized (Marko et al. 2012; Abeele and Bock 2001; Wei and Kording 2009; Salomonczyk et al. 2012), yet the influence of the cross-sensory error signal on its own remains to be determined. Thus, we sought to determine the extent that proprioception can be recalibrated with an increasing cross-sensory error signal and further characterize its role in motor control.

Methods

Subjects

Twenty-three healthy, right-handed young adults (mean age = 20.58, SD = 3.08 years, 11 females) volunteered to participate in the experiment described below. All subjects were pre-screened verbally for self-reported handedness and a history of visual, neurological and/or motor dysfunction. Subjects were then randomly assigned to either the 50° or 70° training groups (50° group: $n = 12$; 70°: $n = 11$). All subjects provided informed consent, and the study was conducted in accordance with the ethical guidelines approved by the York University Human Participants Review Subcommittee.

General experimental setup

A side view of the setup is illustrated in Fig. 1a and is similar to that used by Cressman and Henriques (2009, 2010). Subjects were seated at a table such that the distance of the chair from the table and the height of the chair were adjusted in order to ensure that each subject could comfortably see and reach to all target positions. Once the chair was adjusted, it remained in the same position for the entire experiment. Subjects were instructed to grasp the vertical handle of a two-joint robot manipulandum (Interactive Motion Technologies) with their right hand such that their thumb was positioned on a top marker (1.4 cm in diameter). The position of the robot manipulandum was recorded throughout trials at a sampling rate of 50 Hz and a spatial accuracy of 0.1 mm. Visual stimuli were projected from a monitor (model: Samsung 510 N, refresh rate: 72 Hz) installed 17 cm above the robot and viewed by subjects as a reflected image. The reflective surface was opaque and positioned so that the imaged displayed on the monitor appeared to lie in the same horizontal plane as the robot handle. The room lights were dimmed, and subjects' view of their right hands were blocked by the reflective surface and a black cloth draped between the experimental setup and subjects' right shoulders.

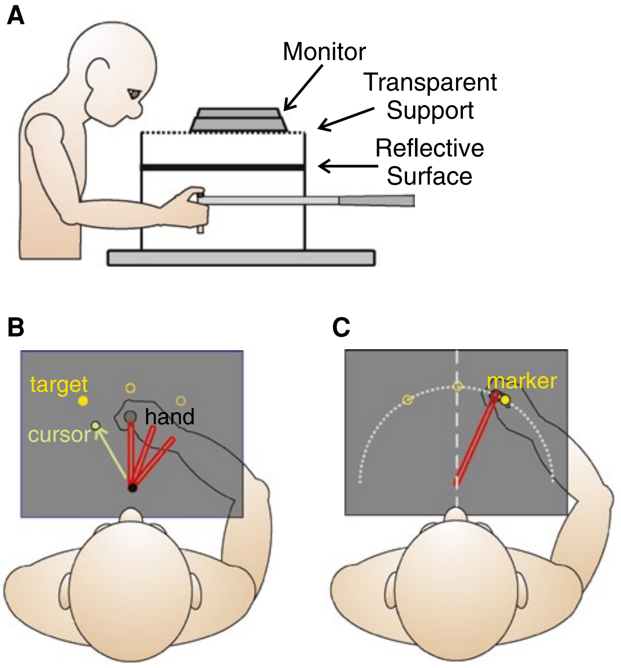

Fig. 1 Experimental set up and design. (**a**) Side view of the experimental set up. **b** and **c** top view of the experimental surface visible to subjects. **b** Cross-sensory discrepancy introduced in the rotation exposure training task and target locations. The unseen hand's constrained pathway was rotated 30° clockwise (CW) with respect to the cursor-target pathway during the first rotation exposure training block and increased to 50° or 70° CW for the second rotation exposure training block for the 50° training group and 70° training group, respectively. Targets (*yellow rings*) 1 cm in size were located 10 cm from the home position (*black circle*) at 0° and 30° left and right of midline. **c** In the proprioceptive estimate task, subjects actively pushed their hand out 10 cm along a constrained linear path (depicted by the *red rectangle*) from the home position and judged the position of their hand with respect to a reference marker. Reference markers (*yellow rings*) were located at 0° and 30° left and right of midline

General procedure

The experiment consisted of two separate testing sessions completed on two testing days. Each testing session involved four tasks (comprising one block), and on the second day of testing, these tasks were repeated two times (i.e. subjects completed two blocks, Fig. 2). On the first testing day, subjects completed the exposure training trials outlined below while viewing a cursor that was veridical, or aligned, with their unseen hand. On the second testing day, subjects completed the exposure training trials while viewing a cursor that was misaligned from the actual location of their unseen hand (grey circle, Fig. 1b). Specifically, a subject's unseen hand moved out along a path that was gradually rotated to 30°, 50° or 70° clockwise (CW) relative to the cursor position, which was represented by a green disc 1 cm in diameter (green circle, Fig. 1b). The 50° training

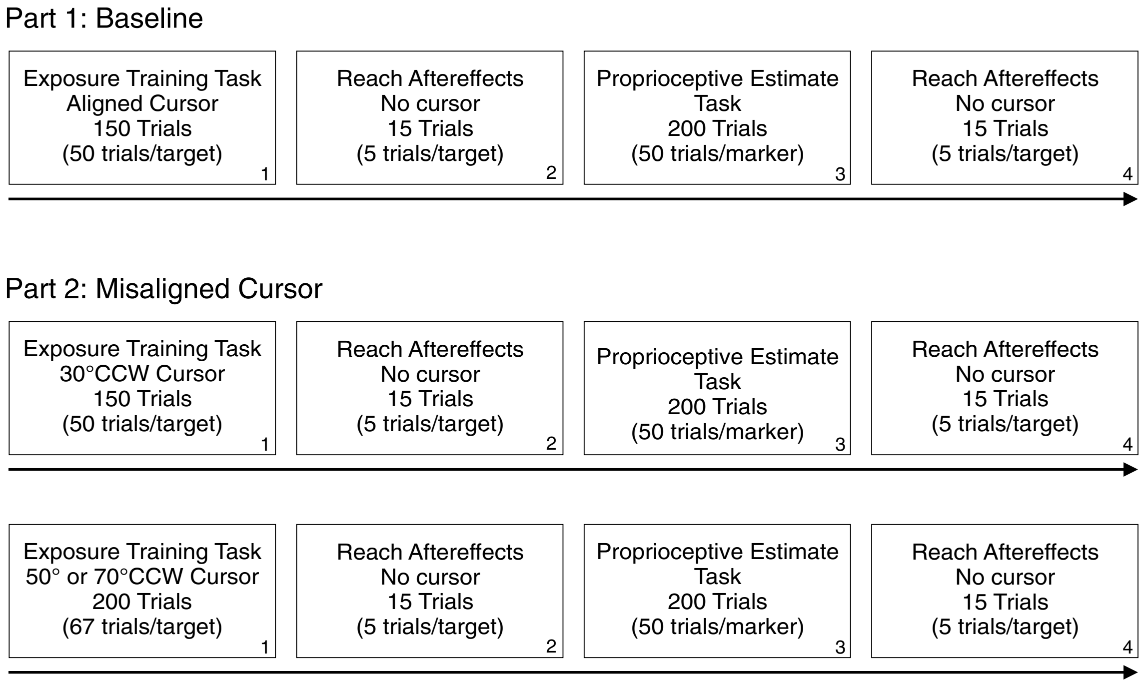

Fig. 2 Breakdown of the testing sessions within the experiment. In the first testing session (*top row*), subjects moved the robot arm with an aligned cursor that accurately represented the position of their hand during the exposure training trials. In the second testing sessions (*second* and *third rows*), subjects' unseen hand path was increasingly misaligned from the cursor-target pathway by 30° (*first rotated block*) up to 50° or 70° clockwise (*second rotated block*). After completing 150 exposure trials with an aligned or misaligned cursor, subjects next reached freely to each of three reach targets 5 times each without a cursor in order to assess motor adaptation (reach aftereffect trials, *Box 2* in each row). Subjects then completed 200 proprioceptive estimate trials (*Box 3* in each row) followed by another set of free, no cursor reaches (*Box 4* in each row) to examine the maintenance of reach aftereffects. In the first testing session, subjects only completed one block of exposure training trials with aligned visual feedback of the hand. In the second testing session, subjects completed two training blocks with misaligned visual feedback of the hand

group completed the first block of trials of the second testing session such that their hand moved out along a path that was rotated 30° CW relative to the cursor, and in the second block of trials, their hand was rotated 50° CW relative to the cursor motion. The 70° training group completed the first block of trials of the second testing session with the same 30° CW hand-cursor distortion as the 50° training group; however, they were exposed to a 70° CW hand-cursor discrepancy during the second block of training trials. For both groups, the 30° hand-cursor rotation was introduced gradually such that on the first trial, the path that the unseen hand moved out along was rotated 0.75° CW with respect to the cursor. The rotation then increased by 0.75° each trial, until the full 30° distortion was achieved. The distortions in the 50° and 70° blocks (i.e. second blocks of trials of the second testing session) were also introduced gradually by 0.75° per trial, starting from the rotation of the previous block (i.e. in the first trial of block two, the distortion was introduced at 30.75° and increased by 0.75° per trial up to 50° or 70°).

Task 1: exposure training

At the start of each trial, the robot manipulandum was positioned below the home position, which was indicated by a green circle 1 cm in diameter and located approximately 25 cm directly in front of subjects' midline. This circle then disappeared and a yellow target circle 1 cm in diameter (yellow circle in Fig. 1b) was presented for 500 ms. The targets were located radially 10 cm from the home position at 0° (in line with subjects' midline), 30° right (CW) and 30° left (CCW) from centre. Once the target disappeared, subjects were instructed to actively push the robot manipulandum out along a robot-generated constrained linear path (red rectangle, Fig. 1b) while viewing a cursor that represented their unseen hand position. On all trials, the cursor headed directly to the remembered target position. 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 channel wall (Henriques and Soechting 2003). In each session, the trials were pseudo-randomized such that each target was displayed at least once before any target was repeated.

To ensure that subjects paid attention to the cursor, we had them both (1) stop their movement when they felt their hand had reached the remembered target location, and (2) after stopping their movement, indicate via a key press if the cursor had "blinked" during the movement (for 50 % of trials, the cursor was extinguished (i.e. blinked) for 30 ms in the middle portion of its trajectory). Thus, subjects controlled the distance that their hand moved outwards away from their body, but not the lateral direction that the hand travelled.

Subjects completed 150 training trials with a cursor that was aligned with their hand (first testing session; Fig. 2, Part 1, Box 1), 150 training trials with a gradually introduced 30° hand-cursor path discrepancy (second testing session, block 1; Fig. 2, Part 2, Box 1), and 200 trials with a gradually introduced 50° or 70° hand-cursor path discrepancy (second testing session, block 2). Thus, subjects were exposed to the full 50° or 70° hand-cursor path discrepancy on 173 or 146 trials, respectively. This is a greater number of training trials at the full hand-cursor discrepancy than our previous paradigms (e.g. Cressman and Henriques 2010; Salomonczyk et al. 2011). Given this large number of trials we had subjects complete in the current experiment, and the fact that we have previously shown that there are no further changes in performance after training with misaligned visual hand feedback for 160 trials versus 60 trials (i.e. motor adaptation and proprioceptive recalibration do not increase after training for more than 60 trials), we are confident that the results discussed below are not due to the slightly different number of exposure trials at the full exposure completed by our 50° and 70° training groups.

Task 2: reach aftereffects to assess visuomotor adaptation

This task was performed twice in each block, immediately after the exposure training task and immediately after the proprioceptive estimate task (boxes labelled 2 and 4 in Fig. 2). During these trials, the robot-generated constrained pathway was removed and subjects could freely move the robot. A trial would start with the robot handle illuminated at the home position. One of three reach targets located at 0°, 30° right (CW) and 30° left (CCW) of centre (Fig. 1b) would then appear, and after 500 ms, the home position would disappear. This was the cue for subjects to reach to the visible target using the robot handle without any visual cursor feedback of their hand position. Once subjects believed they were at the target, they were to hold their final position. Once the final position was held for 250 ms, the reach movement was deemed complete. The target would then disappear, and subjects were to return their hand to the home position guided by a robot-generated constrained linear path. Subjects completed 5 trials to each of the three targets for a total of 15 trials.

Task 3: proprioceptive estimates to assess perceived hand position

To evaluate sensory changes resulting from motor adaptation, previous studies have typically employed tasks which required subjects to make goal-directed reaches using the adapted hand (Simani et al. 2007; van Beers et al. 2002). Reach errors arising in these paradigms could be due to changes in felt hand position resulting from proprioceptive recalibration, changes in motor commands resulting from an updated internal model, or a combination of sensory and motor changes. The present task was designed to isolate subjects' sense of felt hand position from goal-directed movement by removing any visual feedback during hand movement and having subjects make an estimate of their hand's static position with respect to a visual or proprioceptive (body midline) reference marker. We have previously shown that subjects' estimates are similar regardless of whether they actively guide their hand into position along a robot-generated constrained linear path, or their hand is moved along the same path into position by the robot (Cressman and Henriques 2009). Moreover, estimates appear to be similar regardless of the path taken by the hand to its final position (Jones et al. 2012), suggesting that subjects use final hand position information to estimate the location of their hands, independent of how the hand was moved into position and the path taken. Due to time constraints associated with passive movement and the number of trials completed by subjects in the current experiment, we employed the active version of the proprioceptive estimate paradigm described below.

A trial began with the subject grasping the robot manipulandum at the home position indicated by a green circle. After 500 ms, this circle disappeared, and subjects were instructed to push their hand outward along a robot-generated constrained linear path 10 cm in length (as described in task 1, red rectangle in Fig. 1c). Once the hand arrived at the end of the path (along the dotted arc shown in Fig. 1c), a visual reference marker located at 0°, 30° left (CCW) or 30° right (CW) of centre (yellow circles, Fig. 1c) appeared and subjects made a two-alternative forced-choice judgment about the position of their hand (left or right) relative to the visual reference marker. A visual reference marker appeared on 75 % of the proprioceptive estimate trials, while for the remaining 25 % of trials subjects were instructed to judge the location of their hand with respect to their body midline (indicated by the dashed vertical line in Fig. 1c); the midline trials were indicated with a sound cue (beep). There was no time constraint for giving a response.

After responding, the visual reference marker (for all non-body midline trials) disappeared, and subjects moved the robot directly back to the home position along the same 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, 2010) and Jones et al. (2010). In particular, for each reference marker, there were 2 staircases, one starting 20° to the left (CCW) of the reference marker and one starting 20° to the right (CW). The 2 staircases were adjusted independently and randomly interleaved as outlined by Cressman and Henriques (2009). Thus, if subjects responded consistently (i.e. associated a given felt hand position with a given reference marker), the two staircases converged.

Data analysis

Before examining motor adaptation and proprioceptive recalibration, we first wanted to ensure that subjects were (1) moving out smoothly with minimal lateral deviation from the force channel and (2) paying attention to the cursor during the aligned and misaligned exposure training trials. To ensure that subjects were moving smoothly with minimal lateral deviation from the force channel, we calculated the perpendicular deviations of the hand for all trials when the target was located at 0°. We observed a mean perpendicular deviation of 0.33 mm (with a mean SD across trials = .44 mm) which is within the 3 mm of the robot-generated channel. Averaged across all subjects, the maximum deviations were 1.3 mm left and 1.4 mm right of the home-target vector, which is again within the confines of the channel, suggesting that subjects stayed well within the confines of the force channel.

We found that, on average, the robot was stopped 10.08 cm (SD .70 cm) after movements were initiated, which is very close to the 10 cm movement target goal. In addition, subjects correctly reported whether the cursor had blinked or not on 90 % of all trials. A one-way ANOVA comparing the percentage of correctly reported blinks across training blocks revealed a non-significant block effect ($F(2,75) = 1.54$, $p = .22$), suggesting that subjects attended to the cursor in a similar manner across aligned and rotated training blocks.

Motor adaptation

We analysed reaching errors (i.e. aftereffects) made in the reach aftereffects trials in which no visual cursor was presented (Task 2) to (1) determine whether subjects adapted their reaches after exposure to misaligned visual-proprioceptive feedback of their hand position and (2) examine whether subjects maintained this adaptation across the proprioceptive estimate trials. Reach endpoint errors were defined as the angular difference between a movement vector (from the home position to reach endpoint) and a reference vector (joining the home position and the target). To determine whether subjects had indeed adapted their reaches, we analysed mean endpoints in aftereffect trials using a 2 training group (50° group vs. 70° group) × 3 visual feedback block (aligned feedback vs. first block of rotated feedback (30°) vs. second block of rotated feedback (50° or 70°)) × 3 target (0° vs. 30° CW vs. 30° CCW) repeated-measures analysis of variance (RM-ANOVA). Training group was a between-group factor, while visual feedback block and target were within-group factors. Post-hoc pair-wise comparisons were used to explore the loci of these differences, and a Bonferonni correction was applied (alpha = .05). In addition to revealing if subjects adapted their reaches following exposure training, this analysis allowed us to determine whether reach adaptation increased with the increasing hand-cursor distortion.

To determine whether subjects maintained their reach adaptation following proprioceptive estimate trials, we compared aftereffects between reaches following exposure training and those following proprioceptive estimate trials. To do so, we subtracted the reach errors following aligned exposure training from the two rotated exposure training blocks. These baseline-subtracted aftereffects were compared using a 2 training group (50° group vs. 70° group) × 2 visual feedback block (30° rotated feedback vs. 50° or 70° rotated feedback) × 2 time (reach aftereffects following exposure trials vs. reach aftereffects following proprioceptive estimate trials) RM-ANOVA. Post-hoc pair-wise comparisons were used to explore the loci of these differences and a Bonferonni correction was applied (alpha = .05).

Proprioceptive estimates of hand position

To examine the influence of the magnitude of the cross-sensory error signal on changes in proprioceptive recalibration, we determined the location at which subjects felt their hands were aligned with each reference marker after each block of exposure training trials (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Jones et al. 2010; Salomonczyk et al. 2011, 2012). This location was determined by fitting a logistic function to each subject's responses for each reference marker during each testing session. The position at which subjects responded "left" 50 % of the time (i.e. responded "left" and "right" equally often) represents their bias. In addition to calculating bias, we also determined subjects' uncertainty (or precision) by finding the difference between the values at which the point of responding "left" was 25 % and 75 %. Bias and uncertainty related to a particular reference marker were excluded if the associated uncertainty was greater than the mean uncertainty across all reference markers +2 standard deviations. Based on this analysis, only 1 proprioceptive estimate (less than 0.01 % of total estimates) was excluded. Biases and uncertainty ranges were analysed in a 2 training group (50° group vs. 70° group) × 3 visual feedback during the exposure trials (aligned feedback vs. first block of rotated feedback (30°) vs. second block of rotated feedback (50° or 70°)) × 4 marker location (0° vs. 30° CW vs. 30° CCW vs. body midline) RM-ANOVA. Post-hoc pair-wise comparisons were used to explore the loci of these differences, and a Bonferonni correction was applied (alpha = .05). In addition to revealing if subjects recalibrated proprioception following exposure training, this analysis allowed us to determine whether recalibration increased with an increasing hand-cursor distortion (i.e. cross-sensory error signal).

Results

Motor adaptation

Following exposure training with an aligned cursor, mean reach endpoint errors were on average 1.0° to the left of the target. These small reaching errors suggest that subjects were able to accurately reach to a target without visual feedback of their hand position after having been forced to repeatedly move their hands to the targets along a constrained path. Mean baseline-subtracted aftereffects following exposure training with a rotated cursor are displayed in Fig. 3 alongside results from Salomonczyk et al. (2011; filled bars). Mean reach endpoint errors differed significantly between the exposure training conditions ($F(2,42) = 17.82$, $p < .001$). Post-hoc analysis revealed that after exposure training with a hand-cursor discrepancy of 30° (empty bars, Fig. 3), all subjects on average made reaching errors significantly more rightwards of the targets compared to after training with a cursor that was aligned with their hand position (mean difference = 8.9°, $p < .001$). The magnitude of these errors is considerably less than those from 2011 results, in which subjects trained by making unconstrained reaching movements towards targets while visual feedback of the hand was rotated 30° CW with respect to the unseen hand. Following exposure training with either a 50° or 70° misaligned cursor, reaches were still more rightwards of the target compared to after training with an aligned cursor (mean difference = 9.9°, $p < .001$); however, they were not any greater than those following 30° misaligned exposure training (mean difference between first and second rotated blocks = 1.0°, $p > .99$). Furthermore, no difference in training group ($F(1,21) < 1$, $p = .42$) or interaction between exposure condition and training group was observed ($F(2,42) < 1$, $p = .42$). This is in contrast to our previous findings in which subjects showed increasing aftereffects after they reached voluntarily with a visuomotor distortion that increased in magnitude. These results suggest that reach adaptation following exposure to misaligned visual-proprioceptive feedback saturates, such that no further increase in aftereffects occurs with distortion magnitudes greater than 30°.

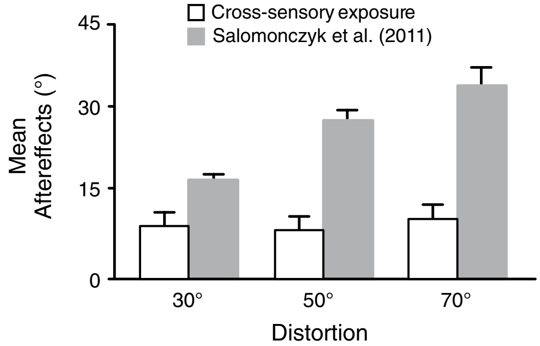

Fig. 3 Aftereffects following exposure training with misaligned visual feedback of the hand. *Endpoint errors* were calculated by subtracting angular reach endpoint errors in the no cursor reach aftereffect trials after training with an aligned cursor from errors completed in the no cursor reach aftereffect trials after training with a misaligned cursor. Errors at reach endpoints were averaged across targets and subjects, and are shown for the no cursor reaches completed after the two consecutive rotated training blocks. *Empty bars* reflect aftereffects following the exposure training paradigm while *filled bars* reflect aftereffects following visuomotor reaching from Salomonczyk et al. (2011). *Error bars* reflect SEM

There was an overall main effect of target location, such that reaches tended to fall to the right of the 30° CW and 0° targets and slightly to the left of the 30° CCW target ($F(2,42) = 36.34$, $p < .001$), indicating that subjects slightly expanded the workspace (consistent with previous work). Importantly, no interaction effects were observed between targets and training groups ($F(2,42) = 2.40$, $p = .12$) or targets and visual feedback conditions ($F(4,84) < 1$, $p = .62$), suggesting that reach adaptation occurred comparably between training groups and was not dependent on the location of the target in the workspace.

Analysis of baseline-subtracted endpoint errors using a RM-ANOVA revealed that the magnitude of these aftereffects decreased with time, such that those aftereffects measured following proprioceptive estimates were on average 5° smaller compared to those measured immediately following exposure training ($F(1,21) = 12.14$, $p < .01$). However, previously described results revealed a significant difference between the aligned and both the first and second rotated blocks ($F(2,42) = 17.82$, $p < .001$, see above), suggesting that while aftereffects may have diminished following proprioceptive estimates compared to those following exposure training, they were still present. No interaction effects were observed between time and rotated exposure training blocks ($F(1,24) < 1$, $p = .62$) or time and group ($F(1,21) = 1.32$, $p = .50$). Thus, aftereffects measured following proprioceptive estimates, while smaller, still showed a comparable pattern of effects as those aftereffects measured following exposure training.

Proprioceptive recalibration

Bias

Mean proprioceptive biases at each reference marker location (grey circles) for both training groups are displayed in Fig. 4a. The diamonds indicate bias values following exposure training with aligned visual feedback of hand position, while the triangles indicate biases following exposure training with a 30° misaligned cursor (empty triangles) or a 50° or 70° misaligned cursor (grey filled triangles). Bias estimates for the proprioceptive midline marker (dashed line) are displayed above visual marker estimates as dashed symbols. For both training groups, we see that estimates of unseen hand position were biased following aligned cursor-hand exposure training slightly towards the left (6°). Previous studies in our lab have suggested that this directional bias arises due to a systematic hand bias (Jones et al. 2010; Salomonczyk et al. 2012) where subjects overestimate how far right their right hand is, resulting in a leftward bias. Mean bias estimates differed significantly between the exposure training conditions ($F(2,42) = 17.73$, $p < .001$). Post-hoc analysis revealed that after exposure training with a 30° misaligned cursor, biases were shifted significantly rightwards (mean difference across all subjects = 5.3°, $p < .001$), consistent with the direction of motor adaptation

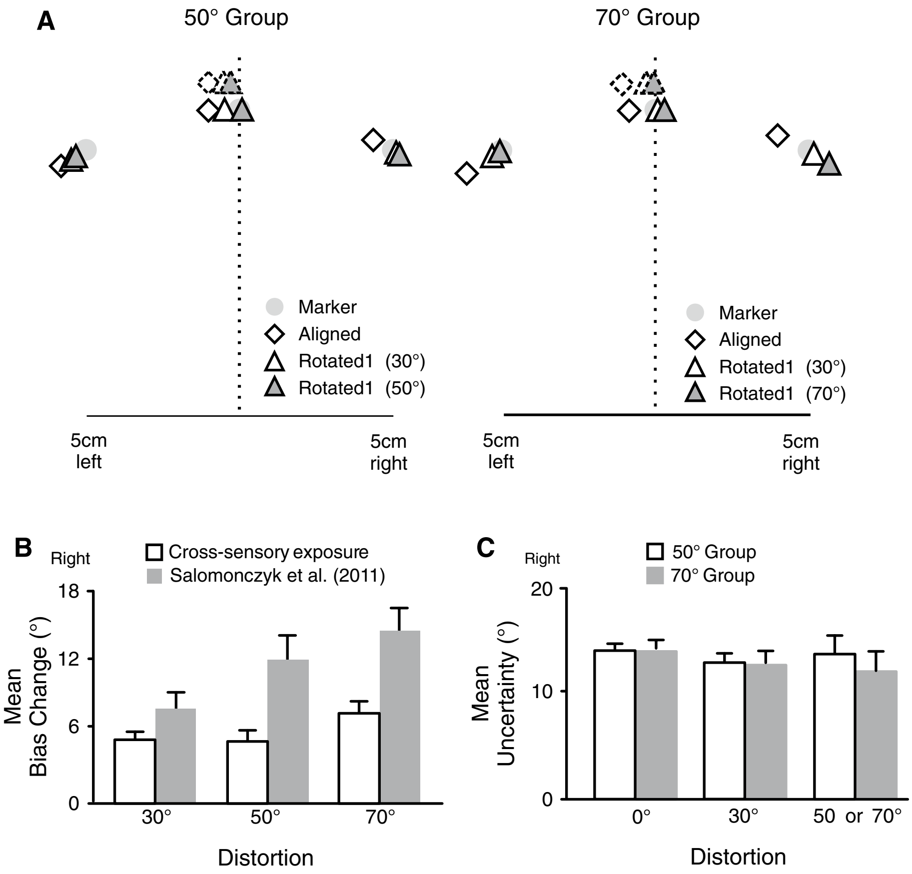

Fig. 4 Proprioceptive biases following training with aligned and misaligned visual feedback of the hand. **a** Mean 2-D proprioceptive biases following training with an aligned (*empty diamonds*) or misaligned (after the first 30° rotated block: *empty triangles*; after the second rotated block: *filled triangles*) cursor for subjects in the 50° training group (*left panel*) and 70° training group (*right panel*). The actual reference marker positions are represented as *grey circles*. Estimates around the midline (*dashed line*) are depicted on top of the estimates around the central visual marker and are outlined with a *dashed line*. **b** Mean changes in biases after training with a misaligned cursor compared to an aligned cursor were averaged across reference markers and subjects. *Empty bars* reflect proprioceptive recalibration following the exposure training paradigm while *filled bars* reflect proprioceptive recalibration following visuomotor reaching from Salomonczyk et al. (2011). **c** Mean uncertainty of proprioceptive estimates following training with an aligned (0°) or misaligned (30°, 50° and 70°) cursor for the 50° training group (*open bars*) and 70° training group (*filled bars*). *Error bars* reflect SEM

(aftereffects, Fig. 3). These results are also consistent with the magnitude of proprioceptive recalibration observed in results from Salomonczyk et al. (2011), shown as filled bars in Fig. 4b. Following exposure training with either a 50° or 70° misaligned cursor, bias estimates were still more rightwards of the target compared to after training with an aligned cursor (mean difference = 6.4, $p < .001$); however, they were not any greater than those following 30° misaligned exposure training (mean difference between first and second rotated blocks = 1.1°, $p = .45$). Furthermore, no difference in group ($F(1,21) < 1$, $p = .76$) or interaction between exposure condition and training group was observed ($F(2,42) < 1$, $p = .47$). These results suggest that proprioceptive recalibration following exposure to misaligned visual-proprioceptive feedback saturates, such that no further increase in aftereffects occurs with distortion magnitudes greater than 30°.

Proprioceptive estimates of hand position were comparable across all visual reference and body midline (Fig. 4a, b, dashed insets) marker locations ($F(3,63) = 1.96$, $p = .13$), and no interaction between marker location and exposure block was observed ($F(3,63) = 1.21$, $p = .31$).

Altogether, these results suggest that proprioception is recalibrated around both visual and midline reference markers following exposure to misaligned visual-proprioceptive hand feedback, although this sensory change saturates within a 30° distortion. This then indicates that a cross-sensory error signal available during exposure training on its own is not enough to drive additional sensory recalibration when the error signal increases above 30° cursor-hand misalignment.

Uncertainty

Mean uncertainty is displayed in Fig. 4c. On average, the overall magnitude of the uncertainty range was 13.2° and is consistent with measures of precision reported in previous exposure training paradigms (Cressman and Henriques 2010) and results from Salomonczyk et al. (2011). Uncertainty was comparable across all training blocks ($F(2,42) < 1$, $p = .48$) and reference marker locations ($F(3,63) = 1.61$, $p = .20$). There were no differences in uncertainty between training groups ($F(1,21) < 1$, $p = .53$). No interaction effects were observed ($p > .34$). Thus, subjects' precision in estimating the location of their unseen hand relative to the markers was not affected by the magnitude of the cross-sensory error signal experienced or the marker location.

Relationship between aftereffects and recalibration

Taken together, results indicate that subjects adapted their reaches and mis-estimated the position of their hand after viewing a rotated cursor that moved synchronously with their unseen hand. Both reach aftereffects and proprioceptive estimates were shifted clockwise by approximately 9° and 5°, respectively, regardless of the magnitude of the visuo-proprioceptive distortion experienced. A paired-samples t test did not reveal a significant difference between the magnitude of aftereffects and proprioceptive recalibration ($t(45) = .80$, $p = .43$). To examine the possibility that both aftereffects and bias rely on the cross-sensory error signal, we applied a step-wise regression procedure with the per cent change in bias and the size of the distortion as predictors of per cent change in aftereffects. Change in bias was selected as the predictor as we hypothesized that changes in felt hand position contributed to updates in the motor plan, resulting in adaptive reach movements (aftereffects). This relationship is displayed in Fig. 5. Results revealed that the change in bias significantly predicted the change in aftereffects ($\beta = .48$, $p = .\ 001$, one-tailed), though the magnitude of the distortion did not ($\beta = -.193$, $p = .08$, one-tailed). We observed that change in bias was a significant predictor of change in aftereffects for both training groups (50° group: $\beta = .39$, $p = .02$, one-tailed; 70° group: $\beta = .71$, $p = .004$, one-tailed). This correlation was also present at each training block (first rotated block: $\beta = .42$, $p = .03$, one-tailed; second rotated block: $\beta = .50$, $p = .02$,

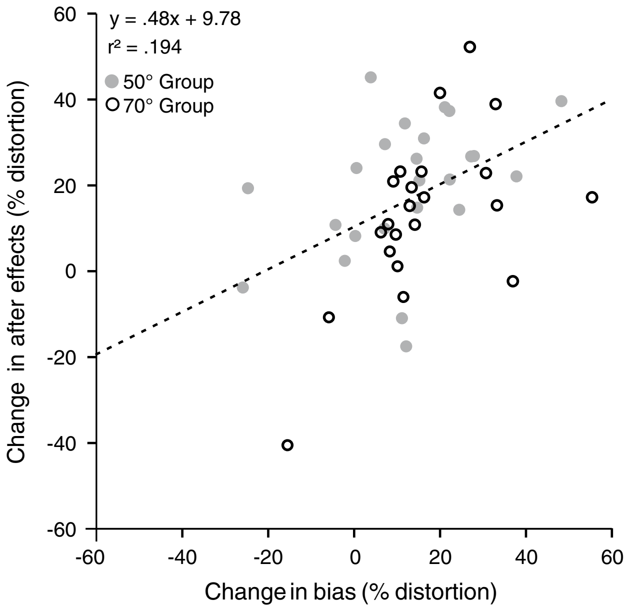

Fig. 5 Changes in sensory recalibration (bias) and motor adaptation (aftereffects) as a percentage of the visuomotor distortion introduced during each exposure training block for subjects in the 50° training group (*filled symbols*) and 70° training group (*empty symbols*) following rotated exposure training trials. Each symbol represents the percentage change in bias and percentage change in aftereffects averaged across marker and target locations (respectively) for each subject. The *solid line* indicates the line of best fit for all data points

one-tailed). These results, along with the observation that changes in bias and aftereffects were very similar, suggest that a similar error signal is underlying these processes. These findings are consistent with a previous study examining the relationship between changes in bias and aftereffects following exposure training (Cressman and Henriques 2010). However, these findings are in contrast to previous studies employing free reaching during visuomotor training (Cressman and Henriques 2009; Cressman et al. 2010; Salomonczyk et al. 2011; Salomonczyk et al. 2012), including our study investigating the role of the magnitude of the sensorimotor error signal (Salomonczyk et al. 2011). In these studies, bias and aftereffects were uncorrelated, and in our 2011 study, the magnitude of the error signal did predict changes in bias and aftereffects. These results suggest that the cross-sensory error signal, on its own, exerts an initial effect on sensory and motor changes (potentially up to when the distortion is 30°). Further changes in response to distortions greater than 30° appear to be driven by the sensorimotor error signal or a combination of the two.

Discussion

The goal of the present study was to examine the extent that a cross-sensory error signal can contribute to proprioceptive recalibration and motor adaptation. To do so, we exposed subjects to a cross-sensory error signal, such that subjects viewed a cursor that travelled towards a remembered target location while their hand travelled along a constrained, robot-generated channel that was increasingly misaligned from the cursor-target pathway. The robot-generated channel only allowed subjects to move volitionally in the forward direction and not in the lateral direction, where the discrepancy between the senses (and the error signal) was introduced. This ensured that subjects did not experience an error in their reaching direction as the visual representation of their hand was always in line with the target. We found that subjects adapted their reaches and recalibrated their sense of felt hand position after exposure to this visuo-proprioceptive discrepancy, which occurred in the absence of the typical sensorimotor error signal associated with error-dependent learning. Specifically, after viewing a cursor that misrepresented the location of their hand by 30° during a constrained movement, subjects misreached in the same direction that their hand had moved during exposure training trials (9° change) and began to feel that their hand had shifted in the direction opposite the cursor distortion (6° change). Furthermore, subjects in the present study demonstrated a proprioceptive shift at both the visual reference markers and around their body midline, suggesting that hand proprioception rather than vision (or a visuomotor mapping) was recalibrated. Interestingly, reach aftereffects and proprioceptive recalibration achieved early saturation, such that no further motor or sensory changes were observed after subjects were exposed to distortions greater than 30°.

Subjects completed a greater number of training trials in the current experiment than in previous paradigms (i.e. Salomonczyk et al. 2011). Thus, in order to ensure that we minimized subjects' fatigue and in attempt to keep subjects engaged in the task, we chose to have subjects actively push their hand out along a constrained pathway during the exposure training trials [as opposed to the passive exposure training in our previous study (Cressman and Henriques, 2010)]. Our previous exposure study, which compared active (subject-generated) and passive (robot-generated) movement during training, showed no differences in subsequent motor adaptation or proprioceptive recalibration between the two types of training (Cressman and Henriques 2010). This suggests that subjects were exposed to the same cross-sensory error signal in both paradigms. We believe that present results obtained with an active paradigm continue to reflect a purely cross-sensory error based on the following findings: firstly, present results are consistent with those of our 2010 study in which small yet persistent aftereffects were observed following exposure training with either an actively or passively placed hand. Thus, while the motor commands generated to push the hand along the constrained path may be used by forward models to predict sensory consequences of these movements, this contribution appears to be minimal since the absence of such motor commands (when the hand is passively led by the robot) leads to similar results for both exposure training and proprioceptive estimation. Second, present findings reflect saturation of reach aftereffects and proprioceptive recalibration following exposure training with distortions greater than 30°, which is inconsistent with results from Salomonczyk et al. (2011) as discussed below. Lastly, subjects' movements during exposure training were constricted in the lateral direction by a robot-generated force channel, yet we observed persistent changes in movements in this direction following misaligned exposure training. Altogether, these findings suggest that the present results reflect subjects' change in performance after exposure to a cross-sensory error signal, rather than a change in the forward model resulting from a sensorimotor error signal.

Role of error signals in adaptation and recalibration

In the present study, we systematically increased the discrepancy between the hand path and the cursor path over trials. While subjects initially showed motor aftereffects and proprioceptive recalibration following exposure to a 30° visuo-proprioceptive discrepancy, subjects did not show any further motor aftereffects or proprioceptive recalibration following exposure training with an increased cross-sensory error signal (up to 70°). Regression analysis further revealed that while changes in reaches and bias were highly correlated, the magnitude of this cross-sensory error signal did not predict changes in reaches or proprioceptive bias. In contrast, in a previous study in which subjects made unconstrained reaching movements towards targets with increasingly misaligned visual feedback of hand position (Salomonczyk et al. 2011), subjects' motor aftereffects and proprioceptive changes increased accordingly; furthermore, the magnitude of visuomotor distortion (including both sensorimotor and cross-sensory error signals) linearly predicted the magnitude of these motor and sensory changes. Thus, while the cross-sensory error signal appears to drive partial proprioceptive recalibration and movement adaptation even when there is no opportunity for goal-directed movement [or any volitional movement as demonstrated presently and previously (Cressman and Henriques 2010)], the influence of this signal saturates at a relatively small (30° or less) distortion due to limits in how the CNS can update felt hand position and/or modify body image. Additional work examining how the size of the sensorimotor error signal can influence motor changes has shown that adaptation to increasing visuomotor distortions results in greater motor aftereffects (Abeele and Bock 2001). However, Abeele and Bock also found that motor learning began to saturate with greater distortions such that facilitation from previously learned rotations was no longer observed with visuo-proprioceptive distortions greater than 80°. Moreover, Wei and Kording (2009) demonstrated that visuomotor adaptation (defined as subsequent trial error) was linearly related to the error signal only at small distortion magnitudes (i.e. ±2 cm), but sublinearly related at larger ones. Finally, using subsequent trial errors, Marko et al. (2012) also found that adaptation to increasingly larger force-field distortions saturated, such that training with additional increases in the force-field distortion did not lead to additional increases in reach error magnitude. The authors also observed that sensitivity to the distortion magnitude was reduced for larger distortions. Taken together, these findings suggest that motor adaptation may saturate with larger distortions (e.g. greater than 70°), such that there is an upper limit to how much the sensorimotor and/or cross-sensory error signals can influence sensory and motor adaptation, both separately and in combination.

In accordance with the observation of nonlinear motor changes as a function of error size, results from the present study also suggest (early) saturation for proprioceptive recalibration and motor changes when just the cross-sensory error signal is available (at or less than 30°). Following the present exposure training paradigm, reach aftereffects and proprioceptive recalibration did not increase with increases in the cross-sensory error signal and were considerably smaller than (roughly half) those produced after performing voluntary movements on trials in which misaligned visual feedback of the hand was introduced, and the sensorimotor error signal was also present (Krakauer et al. 1999, 2000; Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012). While it has been demonstrated that on-line corrective movements are not necessary for motor adaptation since straight and fast "shooting" hand movements (where the hand doesn't decelerate at the target) lead to similar adaptation as regular reaching movements (Tseng et al. 2007), the discrepancy between the actual movement and the desired movement (sensorimotor error signal) is still visible for all subject to use to adjust subsequent reaches in these studies. Moreover, in the present study where this signal was not present, movement aftereffects were more closely related in magnitude to changes in proprioceptive estimates than when following visuomotor adaptation with both the sensorimotor and cross-sensory error signals. Thus, changes in felt hand position derived from the cross-sensory error signal may initially drive motor adaptation, while the sensorimotor error signal contributes to greater motor adaptation and is responsible for motor adaptation with increasing distortions. Although the cross-sensory error signal only contributes to small adaptive changes, the functional implications could be quite significant as a few degrees can have large consequences.

Current models of adaptation

Error-based learning

The most commonly accepted mechanism underlying visuomotor adaptation relies on error-based (or goal-directed) learning using internal models. Typically, visual and proprioceptive signals are aligned, and the inverse model derives appropriate motor commands which compensate for arm dynamics and kinematics. Under altered conditions (e.g. when visual and proprioceptive feedback of the hand are misaligned), the inverse model initially derives motor commands that are insufficient to compensate for the altered visual feedback of the hand position. With practice, however, performance errors arising because of the distortion introduced are used to correct the position of the hand during the movement and/or for the subsequent trial; that is, the motor plan is adjusted to compensate for the distortion and align the actual movement with the desired motor command (Wolpert et al. 1995; Miall and Wolpert 1996; Wolpert and Kawato 1998). When the distortion is removed, the inverse model continues to generate the newly modified motor commands to compensate for the distortion, resulting in reach aftereffects (Kawato 1999).

When the brain generates a motor command, a prediction of the sensory consequences of that motor command is also produced. The forward model compares the desired and actual limb position using sensory information which is then fed back to the CNS to generate motor commands that will meet the given conditions (i.e. update the inverse model). Updating of the forward model has recently been implicated in the sensory (perceptual) changes associated with motor learning (Synofzik et al. 2008; Izawa et al. 2012). For example, by examining the role of sensory prediction errors on motor learning in cerebellar patients, Synofzik et al. (2008) showed that damage to the cerebellum resulted in impairments in linking sensory prediction errors to movements. In their task, subjects made pointing movements in the absence of visual feedback with the right hand, and perceptual judgements of those movements were made with the left hand using a cursor manipulated by a joystick. Results indicated that while motor adaptation for patients and controls was comparable, the perceived pointing direction was recalibrated to a lesser extent in patients than controls. Based on these results, the authors suggested that updates to the internal predictions of motor commands (i.e. the forward model) were responsible for perceptual changes and that this process was impaired in cerebellar patients. Furthermore, Izawa et al. (2012) recently showed that cerebellar patients are unable to learn to predict the visual sensory consequences of their motor commands. Realignment of perceived hand position was estimated following adaptation in a task in which subjects moved their right hand to a position within a circle (no explicit target was given) and then had their hand guided back to a start position. With their left hand, subjects then pointed to the location at which they perceived their right hand had crossed the circle. While motor adaptation was comparable, patients showed less perceptual realignment than controls, further suggesting the role for a forward model in sensory changes.

Sensory plasticity in motor learning

While an update in the forward model has been implicated in the sensory changes observed during visuomotor adaptation (Synofzik et al. 2008; Izawa et al. 2012), our results suggest that this sensory recalibration involves a shift in proprioception, rather than a learned association between one's movements and sensory consequences. We have previously suggested that sensory recalibration may occur coincidentally, though separate from motor adaptation, as we have shown that changes in movements and sensory recalibration are uncorrelated (Cressman and Henriques 2009; Cressman et al. 2010; Salomonczyk et al. 2011, 2012). Indeed, Izawa et al. (2012) failed to observe a relationship between the perceptual and motor changes in their subjects. Moreover, in accordance with our suggestion, cerebellar patients have been shown to recalibrate proprioception such that proprioceptive estimates are shifted to match visual estimates of target positions in the absence (or lack) of motor adaptation (Block and Bastian 2012). In this task, subjects made reaching movements to visual and proprioceptive targets when visual and proprioceptive information were gradually misaligned. The authors found that following reach training, when endpoint feedback was not available, patients and controls realigned proprioceptive endpoints to the same extent; again, this realignment was independent of motor adaptation. Altogether, these findings indicate that the forward model may not have a role in realigning visual and proprioception, and instead suggest that proprioceptive recalibration may be used to update the state estimate for motor commands and thus lead to partial motor adaptation in some contexts.

For accurate and effective motor control, the CNS must consider the properties of the environment and objects we interact with, as well as our own effectors. This information is derived from sensory afferents. When faced with incongruence in sensory information (i.e. vision and proprioception), we have shown that the CNS recalibrates one sense to better match the other; in our case, proprioception is recalibrated to better align with visual estimates of hand position. Conversely, when an error in motor performance is experienced, the CNS may attribute these errors to internal misestimates (e.g. of effector location), but also to external or environmental causes. The CNS will then take into consideration both the updated body or effector percept and the adapted environmental percept when planning subsequent movements (Berniker and Kording 2012). In our present paradigm, subjects did not experience a performance error, and thus, we would not expect the environment percept to have been adapted. In other words, subsequent open-loop reach errors therefore reflected only an update in the body percept that did not increase with increasingly discrepant visuo-proprioceptive feedback. In contrast, subjects in our previous paradigms experienced both a cross-sensory discrepancy and motor performance errors, and subsequent open-loop reach errors could therefore have reflected a combination of the updated body and environment percepts that increased linearly with increasingly misaligned visual hand feedback. Thus, present findings suggest that proprioceptive recalibration may be used to update the state estimate for motor commands, resulting in motor adaptation in the absence of error-based learning. However, results suggest that the body percept or state estimate can only be updated to a certain extent, reflected by the saturation of proprioceptive recalibration and motor commands observed following exposure training with increasingly discrepant visuo-proprioceptive feedback.

In summary, these and other recent results suggest the need for a more comprehensive model of visuomotor learning that accounts for the role of visually driven proprioceptive recalibration in forming a new visuomotor mapping and subsequent use in movement planning, as well as the magnitude of the error signals that drive these motor and sensory changes.

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