

Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation

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ABSTRACT

Reaching with misaligned visual feedback of the hand leads to reach adaptation (motor recalibration) and also results in partial sensory recalibration, where proprioceptive estimates of hand position are changed in a way that is consistent with the visual distortion. The goal of the present study was to explore the relationship between changes in sensory and motor systems by examining these processes following (1) prolonged reach training and (2) training with increasing visuomotor distortions. To examine proprioceptive recalibration, we determined the position at which subjects felt their hand was aligned with a reference marker after completing three blocks of reach training trials with a cursor that was rotated 30° clockwise (CW) for all blocks, or with a visuomotor distortion that was increased incrementally across the training blocks up to 70° CW relative to actual hand motion. On average, subjects adapted their reaches by 16° and recalibrated their sense of felt hand position by 7° leftwards following the first block of reach training trials in which they reached with a cursor that was rotated 30° CW relative to the hand, compared to baseline values. There was no change in these values for the 30° training group across subsequent training blocks. However, subjects training with increasing levels of visuomotor distortion showed increased reach adaptation (up to 34° leftward movement aftereffects) and sensory recalibration (up to 15° leftwards). Analysis of motor and sensory changes following each training block did not reveal any significant correlations, suggesting that the processes underlying motor adaptation and proprioceptive recalibration occur simultaneously yet independently of each other.

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1. Introduction

When reaching to a target with misaligned visual feedback of the hand (i.e. reaching in a virtual reality environment or while wearing prism goggles), individuals adjust their movements in order for the visual representation of the hand to achieve the desired endpoint. Moreover, when the distortion is suddenly removed, reach errors referred to as aftereffects are observed, as subjects continue to make movements adapted to the distortion (Krakauer, Ghilardi, & Ghez, 1999; Krakauer, Pine, Ghilardi, & Ghez, 2000; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Redding & Wallace, 2000; Simani, McGuire, & Sabes, 2007). It has been suggested that in addition to this motor adaptation, proprioception is also recalibrated following reaches made with altered visual feedback. This proposal is based on changes in reaches observed when subjects are required to reach

to visual and proprioceptive targets with their adapted hand following prism exposure (Harris, 1963; Hay & Pick, 1966; Redding & Wallace, 2000) and visuomotor adaptation, in which visual feedback of the hand position was displaced (Simani et al., 2007; van Beers, Wolpert, & Haggard, 2002). While subjects' reaches are altered after reaching with altered visual feedback of the hand, it is unclear whether these changes reflect proprioceptive recalibration per se. Given that subjects moved their adapted arm, errors may better reflect motor adaptation than cross-sensory recalibration (i.e. changes to the motor system rather than sensory changes). To avoid this potential motor confound, Henriques and colleagues (Cressman & Henriques, 2009, 2010; Cressman, Salomonczyk, & Henriques, 2010) and Ostry, Darainy, Mattar, Wong, and Gribble (2010) have recently designed novel perceptual tasks to examine proprioceptive recalibration. In these tasks subjects estimate the position of their hand with respect to a visual or proprioceptive (i.e. body midline) reference marker and hence do not perform any goal-directed movements with the adapted hand.

Results using this proprioceptive estimation task reveal that proprioceptive estimates of hand position are significantly shifted

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in the direction of motor adaptation after subjects reach with visual or force perturbations applied to the hand. Moreover, these changes in felt hand position do not differ in magnitude when estimates of hand position following visuomotor adaptation are made relative to visual or proprioceptive references (Cressman & Henriques, 2009), suggesting that these misestimates are due to recalibration of proprioception rather than any change in the visual percept. As additional support for the recalibration of proprioception, we have shown that changes in felt hand position do not transfer between limbs following visuomotor adaptation (Salomonczyk, Henriques, & Cressman, 2010). Specifically, if the visual representation of space had been recalibrated, we expect that changes in sensory alignment would have been present in both the trained and untrained hand, which we did not observe.

We have found that proprioceptive recalibration is a robust process that occurs along with motor changes under a variety of contexts, including when the hand is passively or actively displaced, when the visuomotor distortion is gradually or abruptly introduced, following training with a rotated or translated cursor, using either the left or right hand, and in both young and older adults (Cressman & Henriques, 2009; Cressman et al., 2010; Salomonczyk et al., 2010). While sensory changes are also observed in conjunction with motor changes following dynamic learning (Ostry et al., 2010) these changes are slightly smaller than those observed following visuomotor rotation training (11% vs. 33% of the deviation of the accompanying movement aftereffects). Surprisingly, we also found similar changes in felt hand position even in the absence of visuomotor adaptation training trials. In this task, subjects were merely exposed to a sensory discrepancy between visual and proprioceptive signals while their hand was passively moved by a robot and they viewed a cursor that simultaneously travelled directly to the target (Cressman & Henriques, 2010). Because no goal-directed reach training was involved and no motor commands were generated, the sensorimotor error signal was eliminated and subjects experienced only a cross-sensory error signal derived from the discrepancy between visual and proprioceptive feedback. In addition to recalibrating proprioception, this cross-sensory error signal was sufficient to produce significant movement aftereffects when subjects were asked to reach to targets with no visual feedback. While these aftereffects were only one third of the magnitude reported in previous studies where subjects could use the additional sensorimotor error signal to adapt their reaches (i.e. 20% vs. 60% of the 30° visuomotor distortion; Cressman & Henriques, 2009), they were similar in magnitude to and correlated with the changes in proprioception. Given that movement aftereffects produced following cross-sensory discrepancy exposure were almost two thirds smaller than those produced following visuomotor adaptation learning trials, the larger aftereffects following visuomotor adaptation may be due to additional changes exclusive to the motor system derived from the sensorimotor error signal.

Based on these previous results, it is possible that motor and sensory recalibration following sensorimotor learning rely on different training signals. As with visual processing (Goodale & Milner, 1992; Milner & Goodale, 1995), separate cortical areas have been suggested to be involved in action-oriented proprioceptive processing (the posterior parietal cortex) vs. perception oriented proprioceptive processing (the insula; Dijkerman & de Haan, 2007). Thus, perhaps the separate streams may be differentially involved in realigning proprioceptive and visual feedback of the hand and for providing a unified estimate of hand position for feedforward motor control. To study the relationship between motor and sensory changes, we sought to examine these processes following (1) prolonged reach training and (2) training with increasing levels of visuomotor distortion. While proprioceptive recalibration occurs under a variety of contexts following motor learning, it is unclear

if proprioceptive recalibration saturates in the same manner as movement aftereffects (as found by Krakauer, Ghez, and Ghilardi (2005) and Wong and Henriques (2009)) or whether prolonged training would lead to increased proprioceptive recalibration. For example, although we found proprioceptive recalibration to be much smaller than movement aftereffects following over 200 visuomotor adaptation trials (Cressman & Henriques, 2009), it is possible that proprioceptive recalibration requires more training in order to attain levels equivalent to those for motor adaptation. Based on previous findings demonstrating that the magnitude of the distortion affects motor learning (Abeele & Bock, 2001; Kagerer, Contreras-Vidal, & Stelmach, 1997), we also examined whether adaptation to increasing distortions (and thus exposure to increasing sensorimotor error signals) would result in sensory changes consistent with those of the motor system. To address these questions, we used the same technique for measuring hand proprioception following visuomotor adaptation to a rotated cursor as described by Henriques and colleagues (Cressman & Henriques, 2009, 2010; Cressman et al., 2010; Salomonczyk et al., 2010).

2. Methods

2.1. Subjects

Twenty-three right-handed young adults (mean age = 22.58, SD = 4.09, 14 female) were recruited from York University and volunteered to participate in the experiments described below. 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 30° ($n = 10$) or 70° ($n = 13$) training groups. All subjects provided informed consent in accordance with the ethical guidelines set by the York University Human Participants Review Sub-Committee.

2.2. General experimental setup

A side view of the set up is provided in Fig. 1A. Subjects were seated in a height adjustable chair so that they could comfortably see and reach to all target and reference 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 510 N, refresh rate 72 Hz) installed 17 cm above the robot onto a reflective surface. The reflective surface was opaque and positioned so that images displayed on the monitor appeared to lie in the same horizontal plane as that of the robot handle. 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.

2.3. General procedure

The experiment consisted of two separate testing sessions completed on two testing days. Each testing session involved two tasks (comprising one block) and on the second day of testing these tasks were repeated three times (Fig. 2). On the first testing day subjects completed the reaching trials outlined below while seeing a cursor that was veridical, or aligned, with their 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. The misaligned cursor was rotated 30°, 50° or 70° clockwise (CW) relative to the actual hand position and was represented by a green disc 1 cm in diameter (white circle, Fig. 1B). The 30° training group completed all three blocks of the second session with a 30° rotated cursor, while the 70° training group completed the first block of the second session with a 30° rotated cursor, the second block with a 50° rotated cursor, and the third block with a 70° rotated cursor. For both groups, the 30° rotation was introduced gradually such that on the first trial the cursor was rotated 0.75° clockwise (CW) with respect to the hand. The rotation then increased by 0.75° each trial, until the full distortion was achieved. For the 70° training group, the cursor distortion in the 50° and 70° blocks was again introduced gradually by 0.75°/trial, starting from the rotation of the previous block (i.e. in block two the distortion was introduced at 30.75°, and increased by 0.75° per trial up to 50°; in block three the distortion was introduced at 50.75°, and increased by 0.75° per trial up to 70°).

2.3.1. Task 1: reach training and motor adaptation

While grasping the robot manipulandum with the right hand, subjects were instructed to reach to a visual target (yellow circle, 1 cm in diameter) as quickly and accurately as possible while viewing either an aligned (first testing day) or misaligned (second testing day) cursor that moved with their hand. The reach targets were located radially 10 cm from the home position at 5 and 30° left (CCW) and right

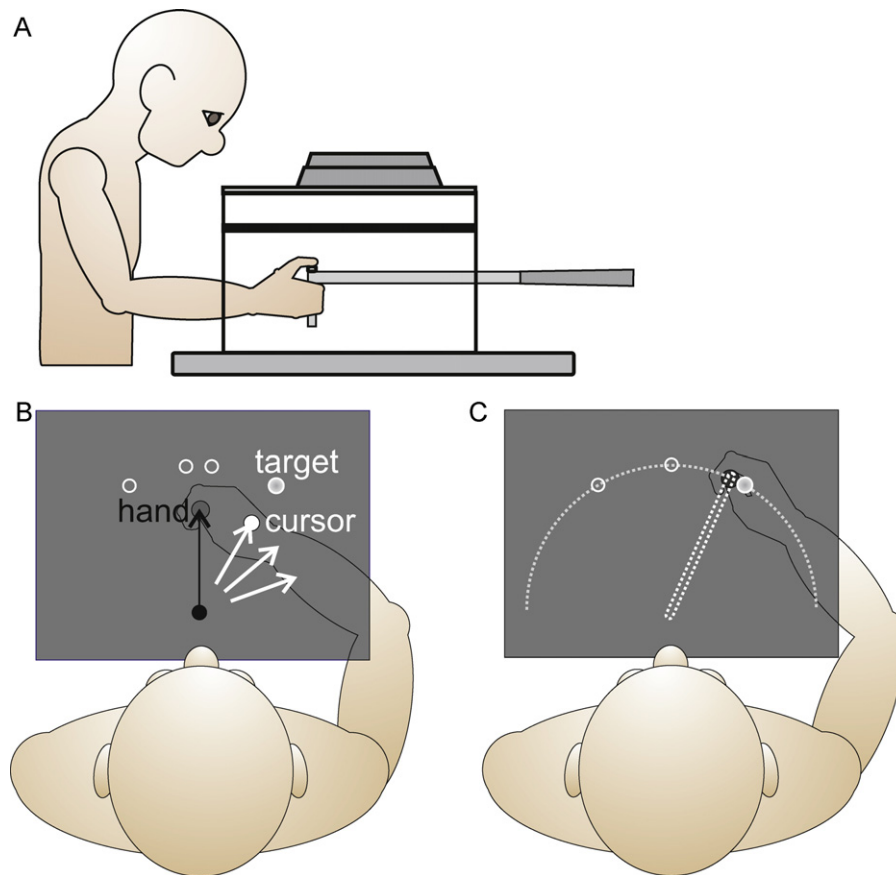


Fig. 1. Experimental setup and design. (A) Side view of the experimental setup. (B and C) Top view of the experimental surface visible to subjects. (B) Visuomotor distortion introduced in the rotated Reach Training Task. The 1 cm green cursor (representing the hand) was rotated 30° clockwise with respect to the actual hand location (white disk) during the first rotation training block and increased to 50° and 70° for the second and third rotation training blocks, respectively for the 70° training group. Reach targets (white rings) 1 cm in size were located 10 cm from the home position (black circle) at 5° and 30° left and right of body midline. (C) In the proprioceptive estimate task, subjects actively pushed their hand out 10 cm along a constrained linear path (depicted by the rectangle) from the home position and judged the position of their hand with respect to a reference marker. Reference markers (white rings) were located at 0° and 30° left and right of midline.

(CW) of centre (white rings in Fig. 1B). The home position was located approximately 40 cm in front of subjects, in line with 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 disappeared and subjects moved their hands back to the home position along a linear route in the absence of visual feedback. If subjects attempted to move outside of the established linear 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 grooved wall (Cressman & Henriques, 2009, 2010; Cressman et al., 2010; Henriques & Soechting, 2003; Jones, Cressman, & Henriques, 2010). The order of the reach trials was pseudo-randomized such that subjects reached once to 3 of the reach targets, specifically the two peripheral targets and one of the pair of peri-central (5°) targets, before any target was repeated. Subjects completed 99 reach trials (box 1, Fig. 2).

After completing the 99 reach training trials, subjects immediately completed 12 aiming movements, 3 reaches to each of 4 reach targets (i.e. both outer targets and the two peri-central targets), without the cursor (box 2, Fig. 2). These trials were included to measure aftereffect reach errors to ensure that subjects had adapted their reaches in response to the misaligned cursor on the second testing day. On these trials subjects were instructed to aim to a target and hold their end position. Once this end position had been maintained for 500 ms, the visual target disappeared and the trial was considered complete. Subjects were guided back to the home position by a linear grooved path. The position of the robot manipulandum was recorded throughout all reaching trials at a sampling rate of 50 Hz and a spatial accuracy of 0.1 mm.

2.3.2. Task 2: proprioceptive estimate trials + reach trials

In this task, proprioceptive estimates and reach trials (boxes 3–5 in Fig. 2) were systematically interleaved. Subjects began by completing an additional 12 reaching trials with an aligned (first testing day) or misaligned (second testing day) cursor (box 3). Subjects reached once to 3 of the reach targets, specifically the two peripheral targets and one of the pair of peri-central (5°) targets, before any target was

repeated. These reaches were then immediately followed by interleaving sets of 15 proprioceptive estimate trials (box 4) and 6 reaching trials (box 5). A proprioceptive estimate trial began with the subject grasping the robot manipulandum at the home position. The position of the hand at the home position 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 10 cm in length (as described previously, rectangle in Fig. 1C). On all trials, once the hand reached the end of the path (along the dotted arc in Fig. 1C) a reference marker located at 0°, 30° left (CCW) or 30° right (CW) of centre (white rings, Fig. 1C) appeared 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 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). The test sequence of 15 proprioceptive estimates followed by 6 reaches was completed 10 times, for a total of 222 trials (150 proprioceptive estimate trials (50 at each reference marker) + 72 reach trials).

Subjects completed 15 final no cursor reaches (box 6, Fig. 2) immediately after completing the proprioceptive estimate + reach task in order to ensure that they were still reaching in a similar manner as before the proprioceptive estimate trials. These reaches were carried out like the previous 12 no cursor reach trials (box 2 in Fig. 2) but now all 5 reach targets and reference marker positions were presented.

2.4. Data analysis

2.4.1. Motor adaptation

We analyzed reaching errors (i.e. aftereffects) made in the no-cursor reach trials to (1) determine if subjects adapted their reaches after aiming with a misaligned

Aligned Cursor

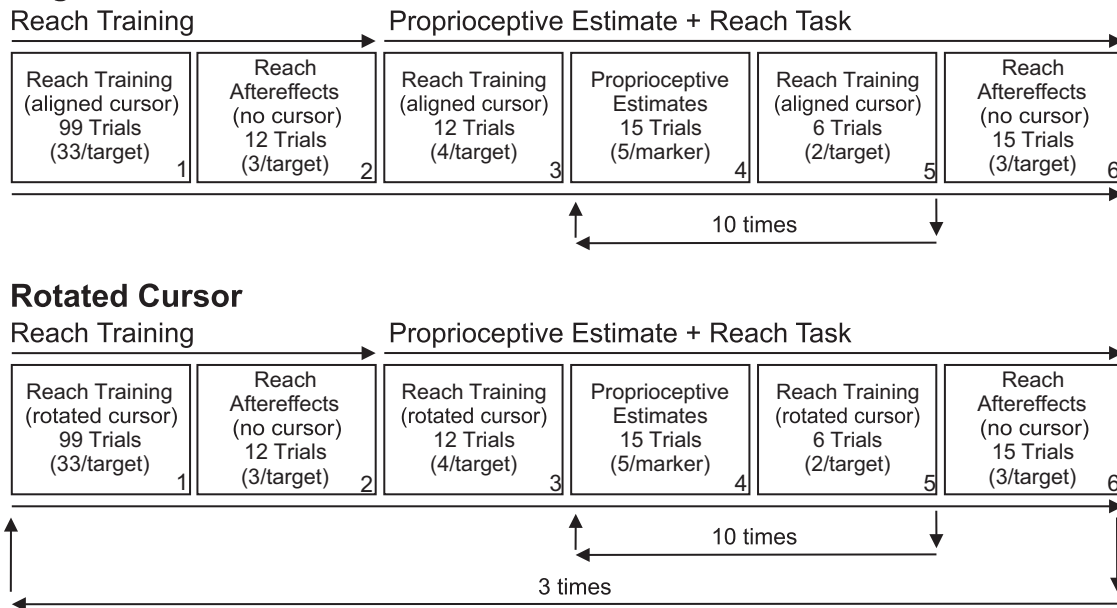


Fig. 2. Breakdown of the testing sessions within the experiment. In the first testing session (top row) subjects reached with an aligned cursor that accurately represented the position of their hand in the reach training trials. In the second testing session (bottom row), subjects first reached with a misaligned cursor that was rotated 30° clockwise with respect to the actual hand location during the reach training trials (first rotated block). Subjects then completed two more training blocks during which time the cursor was rotated 30° or 50° (second rotated block) and 30° or 70° (third rotated block). After completing 99 reach training trials with an aligned (top row) or misaligned cursor (bottom row), subjects next reached to each of four reach targets (the two outer targets and the two inner targets), 3 times each without a cursor in order to assess motor adaptation (reach aftereffects trials, Box 2 in top and bottom rows). Subjects then completed 12 reaches to the reach targets with the cursor present (Box 3). This was followed by 10 sets of 15 proprioceptive estimate trials (Box 4) and 6 visually guided reaches (Box 5) for a total of 150 proprioceptive estimate and 60 reach trials. Following this, subjects reached to all targets and reference markers 3 times without a cursor in order to assess maintenance of reach aftereffects (Box 6). In the first testing session, subjects only completed one block of training trials with aligned visual feedback of the hand. In the second testing session, subjects completed three training blocks with misaligned visual feedback of the hand.

cursor and (2) ensure that subjects maintained adaptation across the proprioceptive estimate and reach 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). Reach errors at peak velocity (PV) were defined in a similar manner. In particular, reach errors at PV were defined as the angular difference between a movement vector at peak velocity and a reference vector. To determine if subjects had indeed adapted their reaches, we analyzed mean endpoint aftereffects and aftereffects at peak velocity separately using a RM-ANOVA with 2 Training Group (30° group vs. 70° group) × 4 Visual Feedback Block (aligned feedback vs. first block of rotated feedback (30°) vs. second block of rotated feedback (30° or 50°) vs. third block of rotated feedback (30° or 70°)) × 2 Time (trials completed following reach training vs. trials completed following the proprioceptive estimate and reach trials) factors. Training Group was a between-group factor while Visual Feedback Block and Time were within-group factors. Tukey's Honestly Significant Difference (HSD) post hoc tests were administered to determine the locus of these differences ($\alpha = .05$). In addition to revealing if subjects adapted their reaches in response to the visuomotor distortion and maintained this level of adaptation across the testing session, this analysis allowed us to determine if reach adaptation increased with increasing practice and/or distortion following visuomotor learning.

2.4.2. Proprioceptive estimates of hand position

To examine the influence of prolonged reach training and the magnitude of visuomotor distortion on changes in proprioceptive recalibration, we determined the locations at which subjects felt their hands were aligned with the reference markers. This location was determined by fitting a logistic function (solid black line, Fig. 3B) to each subject's responses (Fig. 3A) for each reference marker in each testing session. The point of responding "left" 50% of the time (i.e. responding "left" and "right" equally often) represents bias (Cressman & Henriques, 2009, 2010; Jones et al., 2010). 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% (dashed grey lines, Fig. 3B). 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 two proprioceptive estimates (less than 1% of total estimates) were excluded.

Biases and uncertainty ranges were analyzed in a 2 Training Group (30° group vs. 70° group) × 4 Block (aligned feedback vs. first block of rotated feedback (30°) vs. second block of rotated feedback (30° or 50°) vs. third block of rotated feedback

(30° or 70°)) × Marker Location (0° vs. 30° CW vs. 30° CCW) RM-ANOVA. Differences with a probability of less than .05 were considered to be significant. Tukey's Honestly Significant Difference (HSD) post hoc tests were administered to determine the locus of these differences ($\alpha = .05$).

3. Results

3.1. Motor adaptation

Across groups, subjects reached to the targets with an average movement time of $1.95 \pm .93$ s (SD) and an average peak velocity of $16.4 \text{ cm/s} \pm 5.9 \text{ cm/s}$ (SD) when no visual feedback of the hand was provided. Mean reach endpoint errors (i.e. aftereffects) for these no-cursor trials following training with an aligned cursor were on average 0.75° to the right of the target. These small reaching errors suggest that all subjects were able to accurately reach to a target even without any visual feedback of their hand position. Mean aftereffects following training with misaligned visual feedback of the hand are displayed in Fig. 4. In this figure we see that after training with a rotated cursor, endpoint errors deviated significantly more leftwards of the target ($F(3,63) = 78.104, p < .001$) for both training groups. Following the first block of 30° rotated cursor feedback training, reaching movements deviated on average 16° leftwards for all subjects compared to aftereffects following aligned training. The training groups then differed on subsequent training blocks ($F(3,63) = 10.445, p < .001$). Specifically, aftereffects for those subjects that trained with a 30° cursor rotation (white bars in Fig. 4) remained constant and did not differ significantly with successive blocks of training ($p > .05$ for all contrasts). In contrast, aftereffects for subjects that trained with a 50° and 70° rotation in rotated training Blocks 2 and 3 respectively (filled bars), increased to 27.6° and 33.8° respectively compared to training with an aligned cursor ($p < .001$). For the 70° training group, aftereffects follow-

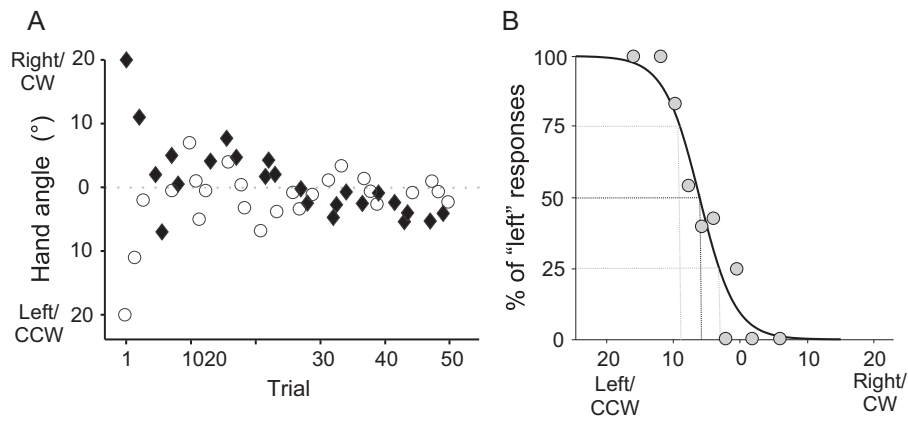


Fig. 3. Angular position of the hand during proprioceptive estimate trials and percentage of left responses for a single subject when the 0° visual reference marker was displayed. (A) The left (white circles) and right (black diamonds) staircases began with the subject's hand deviated by 20° from the reference marker (dashed line) and gradually converged over trials. (B) A logistic function was fitted to the response data to define bias and uncertainty, where bias is the probability of responding left 50% of the time (dashed black line) and uncertainty is the difference between the values at which the probability of responding left was 25 and 75% (dashed grey lines).

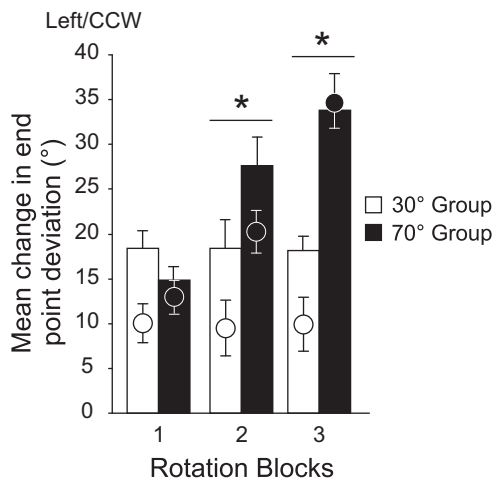


Fig. 4. Aftereffects following training with misaligned visual feedback of the hand. Endpoint errors were calculated by subtracting angular reach endpoint errors in the no cursor reach trials after training with an aligned cursor from errors completed in the no cursor reach trials after training with a rotated cursor. Errors at peak velocity were calculated by subtracting angular reach errors at peak velocity in the no cursor reach trials after training with an aligned cursor from errors completed in the no cursor reach trials after training with a rotated cursor. Errors at reach endpoint (bars) and at peak velocity (circles) averaged across targets and subjects for the 30° training group (open symbols) and the 70° training group (filled symbols) are shown for the no cursor reaches completed after the three consecutive rotated training blocks of trials. Asterisks indicate significant group differences ($p < .05$). Error bars reflect standard error of the mean.

ing each training block differed significantly from the previous block (aligned block 1 vs. rotated block 1, $p < .001$; rotated block 1 vs. rotated block 2, $p < .001$, rotated block 2 vs. rotated block 3, $p = .006$). For both groups, aftereffects following reach training trials did not differ from aftereffects following proprioceptive estimates ($F(1,21) < 1$). Thus, results from the 70° training group indicate that as the magnitude of the distortion of the visual cursor feedback became greater, so too did motor adaptation. However, the relative proportion of aftereffects was consistent for each training block and on average represented 51% of the visuomotor distortion: a one-way ANOVA revealed no differences between blocks ($F(2,38) < 1$, $p = .654$; 70° group: first rotated block, $\bar{x} = 49\%$, $SD = 19.38$; second rotated block, $\bar{x} = 55\%$, $SD = 22.82$; third rotated block, $\bar{x} = 48\%$, $SD = 21.41$). As well, subjects in the 30° training group maintained a reach adaptation level of 61% of the visuomotor distortion across all training blocks, similar to that of the 70° training group (30°

group: first rotated block $\bar{x} = 60\%$, $SD = 24.78$; second rotated block, $\bar{x} = 63\%$, $SD = 23.47$; third rotated block, $\bar{x} = 60\%$, $SD = 17.04$). Reach errors at peak velocity followed the same pattern of results as the reach endpoints described above, consistent with previous work from our lab suggesting that deviations at endpoint and peak velocity are comparable (Wong & Henriques, 2009).

3.2. Proprioceptive recalibration

3.2.1. Bias

Fig. 5A displays mean proprioceptive biases at all three reference marker locations (circles) for both the 30° (top panel) and 70° training groups (bottom panel). The diamonds indicate biases following training with an aligned cursor, while the three sets of triangles indicate biases following the three training blocks with a rotated cursor (white = 1st block, grey = 2nd block, black = 3rd block). For both groups of subjects we see that, on average, estimates of unseen hand location were slightly biased to the left after reaching with an aligned cursor. In fact, the mean bias collapsed across all subjects and reference markers was 5.1° left of the reference marker (previous studies in our lab have shown that this is merely a hand bias, Jones et al., 2010). More importantly however, following reach training with misaligned cursor feedback of the hand, biases were shifted further left for both training groups. Fig. 5B displays the mean changes in bias following visuomotor adaptation training. Following training with a 30° rotated cursor, biases were shifted on average 7.3° more leftwards for all subjects compared to estimates following training with an aligned cursor ($F(3,63) = 42.39$, $p < .001$). However, the training groups differed on subsequent blocks ($F(3,63) = 4.771$, $p = .005$). Similar to the aftereffects errors discussed above, biases for the 30° training group did not change across successive blocks of reach training trials with a cursor rotated 30° CW with respect to the hand ($p > .05$ for all contrasts). Moreover, the average biases for the 70° training group following training with a 50° and 70° rotated cursor increased leftwards by 12.2° and 14.7° respectively, relative to performance following training with an aligned cursor. For the 70° training group, changes in bias following each rotated training block were different from the previous block (rotated block 1 vs. 2, $p = .001$; block 2 vs. 3, $p = .048$). Changes in bias were similar across all reference marker locations ($F(2,42) < 1$ for both groups). Thus, as the magnitude of the visuomotor distortion became greater, so too did proprioceptive recalibration. However, the relative proportion of changes in bias for the 70° training group were consistent for each training block and on average represented 24% of the visuomotor

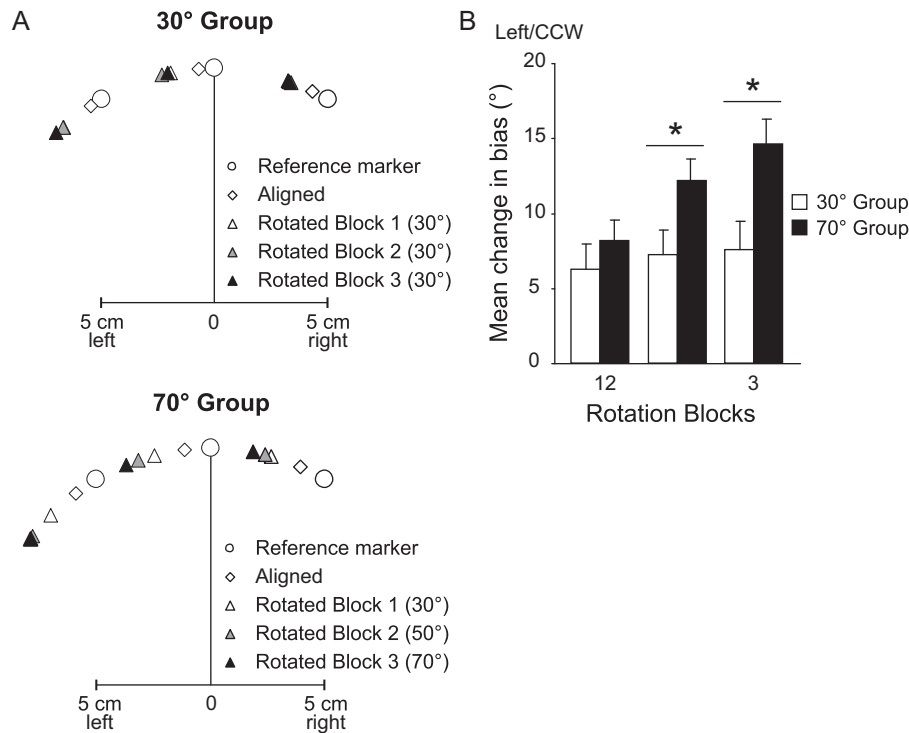


Fig. 5. Proprioceptive biases following training with aligned and misaligned visual feedback of the hand. (A) Mean 2-D proprioceptive biases following training with an aligned (diamonds) or misaligned (after the first rotated block: white triangles; second rotated block: grey triangles; third rotated block: black triangles) cursor for subjects in the 30° (upper panel) and 70° (lower panel) training groups. The actual reference marker positions are represented as circles. (B) Mean changes in biases after training with a misaligned cursor compared to an aligned cursor were averaged across reference markers for the 30° (open bars) and 70° (filled bars) training groups. Asterisks indicate significant group differences ($p < .05$). Error bars reflect standard error of the mean.

distortion (first rotated block, $\bar{x} = 26\%$, $SD = 18.04$; second rotated block, $\bar{x} = 24\%$, $SD = 10.10$; third rotated block, $\bar{x} = 21\%$, $SD = 9.32$). Subjects in the 30° training group also maintained a change in bias equivalent to 28% of the visuomotor distortion across all training blocks consistent with that of 70° training group (first rotated block $\bar{x} = 29\%$, $SD = 20.22$; second rotated block, $\bar{x} = 29\%$, $SD = 19.18$; third rotated block, $\bar{x} = 26\%$, $SD = 15.93$).

3.2.2. Uncertainty

Fig. 6 depicts the magnitude of the uncertainty ranges for both the 30° (white bars) and 70° (filled bars) training groups follow-

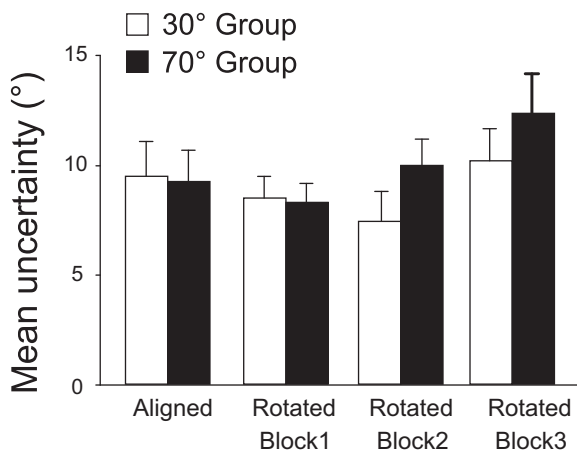


Fig. 6. Magnitude of the uncertainty ranges in the proprioceptive estimate trials were averaged across subjects and reference marker positions following reach training with an aligned cursor or with a misaligned cursor (after rotated training block 1, 2 and 3) for subjects in the 30° (open bars) and 70° (filled bars) training groups. Error bars reflect standard error of the mean.

ing reaches with an aligned and misaligned cursor. Uncertainty levels were on average 9.5° for each reference marker. Subjects' levels of precision in estimating the location of their unseen hand were comparable after reach training with aligned and misaligned cursor feedback ($F(3,63) = 2.455$, $p = .071$). While no overall differences were observed between groups ($F(1,21) < 1$) or reference marker locations ($F(2,42) = 2.26$, $p = .117$), a significant interaction was observed, wherein subjects in the 70° training group demonstrated greater precision (7.8°) when estimating hand position relative to the centre reference marker compared with the markers located 30° left and right of centre (12° and 10.2°, respectively; $F(2,42) = 4.423$, $p = .018$). No other differences were observed.

3.3. Motor adaptation vs. proprioceptive recalibration

Fig. 7A displays mean changes in bias and aftereffects following training with a misaligned cursor compared to an aligned cursor. From this figure we see that subjects adapted their reaches and recalibrated proprioception, and that proprioceptive recalibration was less than reach adaptation for both groups of subjects across all training blocks. In fact, on average, both groups of subjects recalibrated proprioception by roughly 45% of the movement aftereffects achieved on all training blocks. Furthermore, from Fig. 7A we see that the 70° training group demonstrated a continual increase in changes in bias and aftereffects following training with an increasing visuomotor distortion, while the 30° training group did not show any changes in either bias or aftereffects following repeated training with a 30° cursor rotation.

From Fig. 7A it appears that the magnitude of proprioceptive recalibration increased coincidentally with increasing aftereffects. In Fig. 7B and C we plot the changes in proprioceptive recalibration and reach adaptation as a percentage of the visuomotor distortion for the 30° training group and 70° group, respectively. We found no

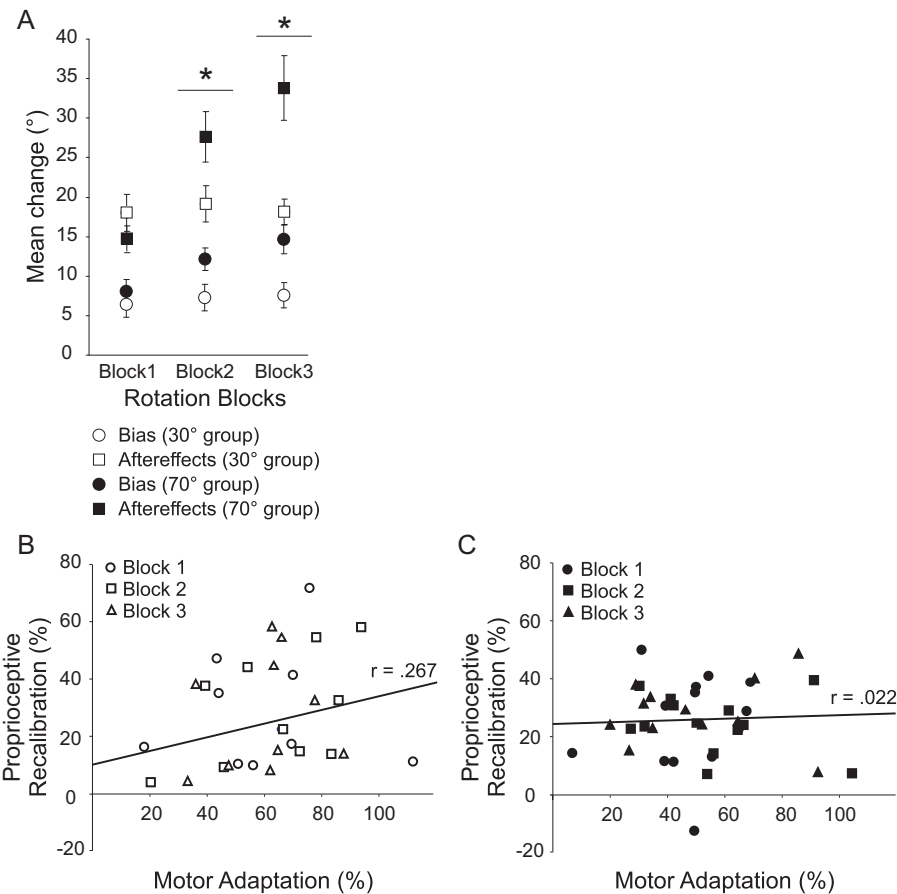


Fig. 7. Comparison between changes in bias and aftereffects across the two training groups. (A) Angular changes in bias (circles) and aftereffects (squares), averaged across subjects and locations, following reach training with misaligned visual feedback of the hand in the three training blocks are shown for subjects in the 30° (open symbols) and 70° (filled symbols) training groups. Asterisks indicate significant group differences ($p < .05$). Error bars reflect standard error of the mean. (B and C) Changes in sensory and motor recalibration as a percentage of the visuomotor distortion introduced during each training block for subjects in the 30° training group (B) and 70° training group (C) following rotated blocks 1 (circles), 2 (squares) and 3 (triangles). Each symbol represents the percentage change in bias and % change in aftereffects averaged across marker and target locations for each subject. Solid line indicates the line of best fit for all data points.

significant relationship between the magnitude of proprioceptive recalibration and the extent of aftereffects (when expressed as a percentage of the visuomotor distortion) for either the 30° training group, Fig. 7B: $\beta_1 = .225$, $p = .154$, or for the 70° training group, Fig. 7C: $\beta_1 = .026$, $p = .896$; or when values from all subjects and all blocks of trials were included in the analysis ($\beta_1 = .123$, $p = .154$). Likewise, individual analyses of each training block for both groups of subjects did not reveal any significant relationships between the percentage of proprioceptive recalibration and reach adaptation achieved (30° training group: first rotated block, $\beta_1 = .026$, $p = .931$; second rotated block, $\beta_1 = .397$, $p = .155$; third rotated block, $\beta_1 = .313$, $p = .344$; 70° training group: first rotated block, $\beta_1 = .306$, $p = .272$; second rotated block, $\beta_1 = -.118$, $p = .378$; third rotated block, $\beta_1 = -.087$, $p = .514$). Given that these coincident sensory and motor changes were not correlated, we hypothesized that the trend of increasing proprioceptive recalibration with increasing reach adaptation in the 70° training group, as shown in Fig. 7A, was due to the size of the error signal. To determine if the magnitude of the visuomotor distortion was driving these changes, we analyzed the actual mean changes in bias (in degrees) of the 70° training group (as these subjects experienced an increase in the visuomotor distortion) in a regression in which actual changes in aftereffects (in degrees) and magnitude of the visuomotor distortion were used as predictor variables. While the overall correlation was significant ($F(2,36) = 4.67$, $p = .019$), it was only the magnitude of the visuomotor distortion that was a significant predictor of the changes in bias ($\beta_1 = .193$, $p = .007$). Changes in aftereffects did not significantly

predict changes in bias for this training group ($\beta_2 = -.057$, $p = .494$) or when all subjects were included in analyses ($\beta_2 = .021$, $p = .499$).

Finally, to compare the relationship between sensory and motor recalibration across the 2 groups of subjects and training blocks, we divided the actual change in bias by the change in aftereffects for each subject following all three rotated feedback training blocks to derive a ratio of sensory to motor recalibration. We then subjected these values to a 2 Group (30° training group vs. 70° training group) \times 3 Block (first block of rotated feedback (30°) vs. second block of rotated feedback (30° or 50°) vs. third block of rotated feedback (30° or 70°)) RM-ANOVA to determine if these ratios remained consistent across training blocks. No significant differences between blocks ($F(2,42) = 1.92$, $p = .174$) or groups ($F(1,21) < 1$) were observed. Thus, the proportion of sensory to motor recalibration remained consistent across blocks for both groups. Altogether these findings indicate that while the relationship between sensory and motor recalibration remains constant following prolonged training or reaching with a greater visuomotor distortion, results suggest that these two processes may be independent and due to two separate adaptation processes.

4. Discussion

The goal of the present study was to examine the relationship between changes in sensory and motor systems following visuomotor adaptation. To do so we asked if prolonged reach training with distorted visual feedback of the hand or training with an increas-

ing visuomotor distortion leads to increased motor adaptation and proprioceptive recalibration. Subjects completed one block of reach training trials with an aligned cursor and three blocks of reach training with a misaligned cursor that (a) was rotated 30° clockwise relative to the subject's unseen hand for all three blocks, or (b) was incrementally rotated 30°, 50° and 70° clockwise across three subsequent training blocks. After each training block we assessed reach adaptation and sense of felt hand position. We found that following initial training to a cursor rotated 30° CW with respect to the hand, subjects adapted their reaches by 16° or approximately 55% of the distortion compared to when they reached with aligned visual feedback of the hand. Subjects also shifted the position at which they felt their hand was aligned with a reference marker leftwards by 7° or roughly one quarter of the visuomotor distortion. Prolonged reach training with a 30° rotation did not lead to any further motor adaptation or proprioceptive recalibration, suggesting that both motor recalibration and sensory recalibration saturated within the first 100 trials of reach training. Conversely, reach adaptation increased to 28° and 34° following training with a 50° and 70° cursor rotation, respectively, while changes in bias increased to 12° and 15° following the same rotations. Overall, the magnitude of proprioceptive recalibration was approximately 45% of the observed reach adaptation across all conditions for both groups.

The magnitude of the visuomotor distortion was correlated with both changes in proprioceptive bias and movement aftereffects; however, no relationship between these sensory and motor changes was observed overall or within training blocks. In contrast to changes in proprioceptive biases and movement aftereffects, the precision of subjects' estimates of hand position did not change across training blocks. Thus subjects responded in a similar manner regardless of the magnitude of the distortion or the number of reach training trials completed. In accordance with these findings, Cressman et al. (2010) also found that uncertainty in felt hand position remained consistent across training sessions and hence was not related to changes in proprioceptive bias and reach aftereffects in both young and older adults. Taken together, these findings suggest that the size of the distortion has a similar effect on both sensory and motor changes but does not affect the precision of subjects' estimates of hand position.

Following the first block of learning trials and throughout subsequent blocks, subjects in both groups began to feel their hand near the position that it was visually represented by a cursor. In the current study, this was demonstrated by asking subjects to estimate the location of their unseen hand with respect to a visual reference marker. Previous work has also shown recalibration of felt sense of hand position with respect to an internal reference as defined by the subjects' body midline (Cressman & Henriques, 2009). Moreover, this recalibration was not different from recalibration observed when a visual reference marker was displayed at the same location. These results strongly suggest that proprioception is recalibrated following visuomotor adaptation such that proprioceptive estimates of hand position are shifted to match the visual percept of hand position. Furthermore, given that proprioceptive recalibration failed to transfer from the trained hand to the untrained hand following visuomotor adaptation training (Salomonczyk et al., 2010) provides additional evidence that our method assesses proprioceptive recalibration rather than a visual shift, or combination of the two.

4.1. The influence of reach training

While more extensive training has been hypothesized to contribute to greater perceptual changes (Ostry et al., 2010), we found that this was not the case. Changes in bias and aftereffects after subsequent training trials with the same distortion were no larger than those following the first block of training with misaligned

visual feedback of the hand. This is consistent with reach adaptation findings from Krakauer et al. (2005), who showed that prolonged training with a cursor that was rotated with respect to the hand did not result in an increase in the magnitude of motor adaptation. Based on their findings, Krakauer et al. suggested that motor learning saturates within the first block of reach training. Results from our lab (Wong & Henriques, 2009) also indicate that prolonged training over subsequent testing days does not result in increased motor learning as we found no differences between aftereffects following an initial day of reach training (250 trials) and subsequent testing days in which 750 additional trials were performed.

Several authors have suggested a multi-rate model of motor learning wherein one system is highly sensitive to error but learning is rapidly forgotten, while the other system is less sensitive to error but retains learning much more robustly (Kording, Tenenbaum, & Shadmehr, 2007; Shadmehr, Smith, & Krakauer, 2010; Smith, Ghazizadeh, & Shadmehr, 2006). The latter slow-learning process is associated with long-term stable motor changes in the effector (Criscimagna-Hemminger & Shadmehr, 2008), likely because errors that drive this long-term slow learning may be attributed to more long-lasting changes in the plant or effector, like those resulting from fatigue, damage or development. For example, errors due to growth of the arm during childhood would require a more enduring change in estimating the state of the plant than those errors produced when using a new tool. Since sensory information like proprioception are critical for state estimates, it may be that changes in proprioceptive estimates or proprioceptive recalibration may be associated more with a slower learning process than those that lead to changes in movements (aftereffects) which tend to be greater in magnitude. However, further studies are necessary to properly test this possibility. So far, the multi-rate model of motor learning has not been explored for visuomotor adaptation, only for saccade adaptation and force-field learning.

4.2. Mechanisms contributing to motor adaptation and proprioceptive recalibration

Results from our lab do indicate that learning rates during closed loop reaches are dependent on the magnitude of the visuomotor distortion (Balitsky-Thompson & Henriques, 2010; Dionne & Henriques, 2008). The increase in aftereffects or deviations in open loop reaches and the increase in bias observed in the present study were systematically shown to be related to the magnitude of the visuomotor distortion, suggesting that changes in the sensory and motor systems are tied directly to the magnitude of the distortion rather than practice. Consistent with previous work from our lab (Cressman & Henriques, 2009; Cressman et al., 2010; Salomonczyk et al., 2010), sensory and motor changes were not significantly correlated, suggesting that these changes arose via coincident yet separate mechanisms. Differences in changes in sensory and motor systems could arise due to the source of error signals used to generate adaptive responses in the two systems. Sensory prediction errors, or the difference between the actual sensory feedback and expected sensory feedback for a given motor command, are considered to be the predominant error signal driving motor adaptation (Miall & Wolpert, 1996; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). While previous studies suggest that this error signal also contributes to changes in proprioception (Simani et al., 2007; van Beers et al., 2002), studies from our lab have shown that a cross-sensory error signal (visual-proprioceptive discrepancy) is sufficient and more likely to be responsible for updating proprioceptive estimates of hand position (Cressman & Henriques, 2010). As well, this cross-sensory error signal may even be partially responsible for changes in movements following visuomotor adaptation. To investigate the role of cross-sensory error signals in both sensory and motor recalibration, Cressman and Henriques

(2010) eliminated sensory prediction errors by having a robot manipulandum passively guide subjects' hands while they viewed a cursor rotated 30° CW with respect to their hand move directly to a target (i.e. the cursor moved to target so there was no discrepancy in desired/predicted and actual movement). Following exposure to this cross-sensory discrepancy between seen and felt hand movement, proprioceptive estimates of the hand were shifted in the direction of the distortion and by the same magnitude as that produced following adaptation to a visuomotor rotation of 30° CW when subjects actively and voluntarily directed their reaches toward the target (Cressman & Henriques, 2009). Moreover, when subjects reached to the same targets following exposure to this cross-sensory discrepancy, their open-loop reaches were also significantly deviated. However, these aftereffects were only about a third of the size of aftereffects typically following adaptation. Indeed, the aftereffects in this study were about the same size as, and were significantly correlated with, proprioceptive misestimates of hand position. This is in contrast to the lack of correlation between aftereffects and proprioceptive recalibration following visuomotor adaptation reported previously (Cressman & Henriques, 2009) and in the present study. Thus, aftereffects following mere exposure to cross-sensory discrepancy may be due to a change in felt hand position rather than any real motor recalibration and sensory prediction errors may not be the only training signal responsible for motor recalibration (i.e., movement aftereffects) produced during visuomotor adaptation. In the present study we explored how the magnitude of the distortion would affect proprioceptive recalibration and motor adaptation. In previous research, the magnitude of the distortion (and thus the sensory prediction error signal) has been shown to affect motor learning (Abeele & Bock, 2001; Kagerer et al., 1997). Here, we observed that an increase in the magnitude of a visuomotor distortion resulted in proportional increases to both proprioceptive and motor recalibration. These results suggest that the magnitude of the cross-sensory error signal gives rise to changes in proprioception directly.

Like in our previous studies, a visual cue indicated the initial start position of the hand for the proprioceptive estimation trials so that we could ensure that our observed changes in proprioceptive estimates were not due to a drift in proprioception (Brown, Rosenbaum, & Sainburg, 2003). Given that subjects were provided with a visual representation of their hand position at the beginning of these estimation trials, it is possible that this cue may also have been used to recalibrate proprioceptive estimates of hand position (this time to a visually aligned location) and minimize the proprioceptive bias which was measured at the endpoint of the movement trajectory located 10 cm away, thus reducing the overall changes in felt hand position following visuomotor adaptation. Nonetheless, we did find a significant change in proprioceptive estimate of hand position. While the role of this initial visual hand feedback on proprioceptive recalibration remains to be determined, the results of the present study provide valuable insight into how the size of the visuomotor distortion and the length of training affect both sensory and motor changes.

4.3. Vision and proprioception

Both vision and proprioception have been shown to play integral roles in sensorimotor adaptation (Simani et al., 2007; van Beers et al., 2002). Sensory information from these modalities may be processed in a similar manner within the brain as it has been suggested that both visual (Goodale & Milner, 1992; Milner & Goodale, 1995) and proprioceptive signals (Dijkerman & de Haan, 2007) are processed within two distinct streams – dependent on whether the information is to be used to guide action or for perception. Furthermore, Dijkerman and de Haan suggest that the two proprioceptive processing streams may even be represented in different

areas of the brain such that action-oriented processing occurs in the posterior parietal cortex (PPC) and perception-oriented processing occurs in the insula as well as the PPC. The processing of proprioception necessary for re-aligning proprioceptive and visual feedback of the hand (i.e. resolving the cross-sensory error signal) may therefore be separate from the processing of proprioception necessary for providing a unified estimate of hand position for feed-forward motor control (i.e. resolving the sensory prediction error signal). This segregated processing could explain how sensory and motor recalibration could arise as two related yet distinct processes in the brain. Further evidence for the possibility of distinct processes comes from findings of visuomotor adaptation in deaf-fingered individuals who have been shown to adapt their reaches following reaching with misaligned visual feedback of the hand (Bernier, Chua, Bard, & Franks, 2006; Ingram et al., 2000).

Proprioceptive recalibration may arise because the central nervous system requires a unified estimate of hand position for motor control. Previous research has shown that motor performance is better when one has access to information from multiple sensory modalities compared to a single one, even though vision and proprioception sometimes provide naturally conflicting information (van Beers et al., 2002). Thus, one way for the brain to resolve conflicting information in order to provide a unified estimate is to recalibrate one sense so it better matches the other. In the present case, proprioception is recalibrated to match visual estimates of hand position.

4.4. Conclusions

While the precise relationship between cross-sensory error and sensory prediction error signals on reach adaptation and proprioceptive recalibration remains to be determined, our results provide further evidence of sensory plasticity after learning to reach with misaligned visual feedback of the hand. Our method of assessing proprioceptive recalibration allows us to examine the influence of cross-sensory recalibration processes directly, independent of motor adaptation. With our method, proprioceptive recalibration has been observed in a variety of contexts, including following learning with translated and rotated cursor distortions (Cressman & Henriques, 2009, 2010) and force field perturbation (Ostry et al., 2010) when estimating the position of the hand relative to both proprioceptive and visual stimuli (Cressman & Henriques, 2009), following adaptation of both the left and right hands (Salomonczyk et al., 2010), across the lifespan (Cressman et al., 2010), and following prolonged reach training and training to increased distortions. With our method, we possess the requisite tools to investigate the role of distinct error signals in motor and sensory plasticity and with further studies we hope to gain insight into the contribution of these signals to recalibration processes. At present, results indicate that the magnitude of the visuomotor rotation predicts the magnitude of sensory and motor changes following adaptation.

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