

Proprioceptive recalibration arises slowly compared to reach adaptation

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Abstract When subjects reach in a novel visuomotor environment (e.g. while viewing a cursor representing their hand that is rotated from their hand's actual position), they typically adjust their movements (i.e. bring the cursor to the target), thus reducing reaching errors. Additionally, research has shown that reaching with altered visual feedback of the hand results in sensory changes, such that proprioceptive estimates of hand position are shifted in the direction of the visual feedback experienced (Cressman and Henriques in *J Neurophysiol* 102:3505–3518, 2009). This study looked to establish the time course of these sensory changes. Additionally, the time courses of implicit sensory and motor changes were compared. Subjects reached to a single visual target while seeing a cursor that was either aligned with their hand position (50 trials) or rotated 30° clockwise relative to their hand (150 trials). Reach errors and proprioceptive estimates of felt hand position were assessed following the aligned reach training trials and at seven different times during the rotated reach training trials by having subjects reach to the target without visual feedback, and provide estimates of their hand relative to a visual reference marker, respectively. Results revealed a shift in proprioceptive estimates throughout the rotated reach training trials; however, significant sensory changes were not observed until after 70 trials. In contrast, results showed a greater change in reaches after a limited number of reach training trials with the rotated cursor. These

findings suggest that proprioceptive recalibration arises more slowly than reach adaptation.

Keywords Reach adaptation · Proprioceptive recalibration · Time course · Motor learning

Introduction

When performing goal-directed reaches to objects in the environment, the central nervous system transforms visual and proprioceptive information about hand and target location into appropriate motor commands to move the hand to the desired location (Jeannerod 1988; Flanders et al. 1992; Desmurget et al. 1998). Although the visual and proprioceptive signals that indicate limb position are usually aligned, situations may arise in which the position at which one sees their hand differs from the position at which they feel their hand. When these signals conflict and one is reaching to a visual target, one tends to rely more on the visual estimate of the limb, rather than the actual or “felt” position. Thus, movements are corrected based on the visual estimate, such that a new mapping between visual input and motor output is learned (i.e. visuomotor adaptation; Krakauer et al. 1999; Sainburg and Wang 2002; Simani et al. 2007; Cressman and Henriques 2009). For example, if subjects train to reach to a visual target while viewing a cursor that is distorted (e.g. rotated or translated) relative to their hand's actual position, they initially produce deviated movements such that the cursor does not achieve the target. However, subjects rapidly learn to reach such that the cursor moves to the target. Moreover, when subjects reach in the absence of visual feedback, they continue to produce movements in the direction opposite to the visual distortion experienced. These persistent deviations in their

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movements reflect plastic changes (i.e. adaptation) in the motor system and are referred to as reach aftereffects (Martin et al. 1996; Krakauer et al. 1999, 2000; Baraduc and Wolpert 2002; Buch et al. 2003).

In addition to adaptation in the motor system, reaching with distorted visual feedback of the hand also results in changes to the sensory system. In particular, proprioceptive sense of felt hand position is recalibrated and shifted to match the visual representation of the hand experienced during the reach training trials (van Beers et al. 2002; Simani et al. 2007; Cressman and Henriques 2009). To assess sense of felt hand position after reaching in a virtual reality environment, Cressman and Henriques (2009) have devised a unique method that does not involve any goal-directed movements, such that subjects hand is moved to a goal location by a robot manipulandum. Subjects then indicate the position of their hand relative to a visual or proprioceptive reference marker, which only appears once the hand has arrived at its final position. Using this task, it has been demonstrated that, in general, subjects shift the position at which they feel their hand is aligned with a reference marker by about 20 % of the visuomotor distortion introduced (e.g. about 6° when a 30° hand-cursor distortion is introduced). This shift is in the same direction as the visual feedback experienced in the reach training trials, suggesting that it results from a recalibration of the proprioceptive sense of hand position in order to align it with the visual representation of the hand. Similar changes in felt hand position have been found across a wide range of experimental conditions, including: training hand (left or right), distortion type (rotated or translated cursor), distortion presentation (gradual or abrupt), reference marker (visual or proprioceptive), and age (young and older adults) (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Salomonczyk et al. 2011, 2012).

While it is well established that proprioceptive recalibration arises after reaching with distorted visual feedback of the hand, the time course of these sensory changes remains unclear. Thus, the main objective of this experiment was to look at how quickly sensory changes arise while reaching with distorted visual feedback of the hand. Additionally, the current design allowed us to compare sensory changes to motor changes over time. Previous work has shown that motor changes arise quickly. For example, adaptation to visuomotor distortions in virtual reality environments has been shown to occur within approximately 20 reach training trials when reaching to a single target (Krakauer et al. 2000; Kitago et al. 2013). However, previous studies showing rapid changes in the motor system have typically determined the time course of motor adaptation by examining changes in performance during trials in which the perturbation was still present (Krakauer et al. 1999, 2000, 2005; Buch et al. 2003; Mazzoni and Krakauer 2006; Yamamoto

et al. 2006; Neva and Henriques 2013) or using single interleaved “catch” trials in which the perturbation was suddenly removed (Benson et al. 2011). Changes in performance during training may involve explicit (i.e. strategic) rather than implicit adaptive processes and therefore may not reflect a measure of true motor adaptation (Weiner et al. 1983; Pisella et al. 2004; Redding et al. 2005). It is unclear whether implicit motor adaptation assessed through reach aftereffect trials (i.e. trials which are presented following training, in which subjects perform reaching movements in the absence of any perturbation) follows a similar time course and how these implicit changes compare to proprioceptive recalibration which arises implicitly in the absence of subjects awareness.

To establish the time course of proprioceptive recalibration and its relation to changes in reach adaptation over time, we measured and compared both proprioceptive recalibration and reach adaptation at eight time-points over the course of the experiment in which subjects trained to reach to a visual target with rotated visual feedback of the hand [i.e. a 30° clockwise (CW) cursor rotation]. Recently, Mattar et al. (2013) looked at the time courses of sensory and motor changes while subjects trained to reach in a velocity-dependent force field. Specifically, they had subjects perform a sensory estimation task six times during reach training trials in a velocity-dependent force field. They found that reach adaptation began earlier and occurred at a much greater rate during the initial trials, as compared to sensory changes. While these results provide initial insight into the time course of sensory changes in a motor learning paradigm, their sensory changes are associated with movement sense, rather than position sense (as assessed in the current study). Moreover, the time course of reach adaptation was assessed through trials in which the perturbation was still present. Thus, different results may be seen between their paradigm and the current paradigm due to differences in sensory coding for position versus movement sense (Allen and Proske 2006) and given that we used aftereffect trials to determine the time course of reach adaptation.

We hypothesized that changes in felt hand position would arise slowly over the course of the reach training trials, because the sensory system has been shown to be robust and resistant to change (Mattar et al. 2013). Additionally, we hypothesized that implicit reach adaptation would occur much earlier than proprioceptive recalibration and hence would have a greater rate of change.

Methods

Subjects

Twenty healthy, right-handed university students (5 females, 15 males; mean age = 21.2 years, SD = 2.2 years)

volunteered to participate in the following experiment. All subjects were verbally screened for history of sensory, neurological, and motor dysfunction. Subjects had normal or corrected-to-normal vision and were right-handed according to their responses on the modified version of the Edinburgh handedness inventory (mean score = 84 %, SD = 15 %; Oldfield 1971).

All subjects were naïve to the hypotheses and had never performed prior experiments that involved reaching with distorted visual feedback of the hand. This study was approved by the University of Ottawa's research ethics board, and all subjects provided informed consent before taking part in the experiment.

General experimental set-up

A side view of the experiment is illustrated in Fig. 1a. Subjects were seated in a height-adjustable chair in front of the experimental apparatus. The chair's height and distance from the apparatus were adjusted to ensure that subjects could comfortably see and reach to the visual target. Once adjusted, the chair remained in the same position for the entirety of the experiment. Subjects grasped the vertical handle of a two-joint robot manipulandum (BKIN technologies) with their right hand and made reaching movements to a visual target within a 70 cm by 36 cm workspace in the horizontal plane. Subjects started with their hand at a home position (white circle; 1 cm in diameter), which was aligned with their midline and was approximately 20 cm in front of their chests. Visual stimuli were projected from a downward facing computer monitor (EzSign model 47LD452B; refresh rate: 60 Hz; LG, Seoul, South Korea) onto a reflective surface that was aligned with the horizontal plane of the robot handle. The visual target (blue circle; 2 cm in diameter) appeared 15 cm and 45° CW from the home position relative to straight ahead. The room was dimmed and subjects were prevented from seeing their hands by a black cloth that was draped between the apparatus and their shoulders.

Procedure

The experiment was divided into 8 testing blocks. A breakdown of each testing block can be found in Fig. 2. Subjects completed the testing blocks in two testing sessions; they completed the first block in the first testing session and the next seven blocks in the second testing session. Depending on subjects' schedules, they either took a short break between sessions ($N = 18$, mean = 23.7 min, range = 11–30 min) or came back on a second day ($N = 2$, mean = 11 days, range = 8–14 days). The first session was just for familiarization purposes in order to get baseline results and did not influence performance in the second

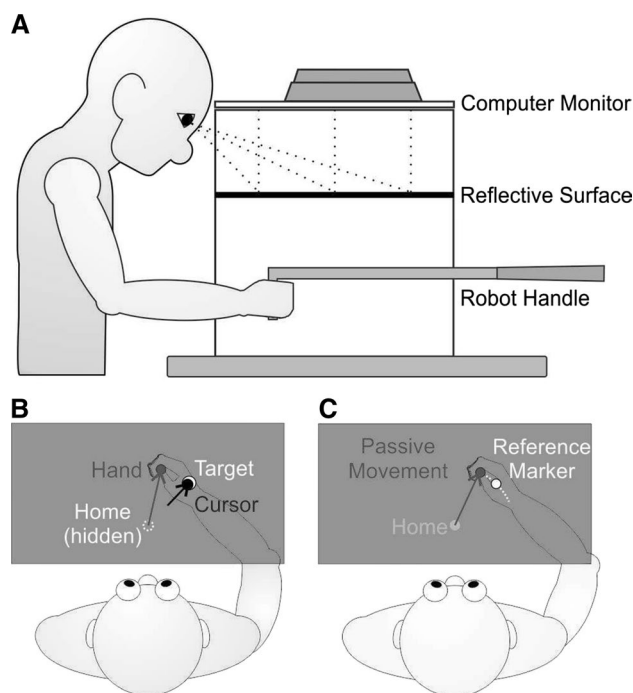


Fig. 1 Experimental apparatus. Side view of experimental apparatus (a). Top view and dimensions of experimental surface visible to subjects during the reach training (b) and proprioceptive estimation (c) tasks. **b** Visuomotor distortion introduced in the rotated reach training task. The home position was not shown to subjects (dotted white circle). In the rotated reach training trials, the cursor representing the hand's position (black circle, 1 cm in diameter; represented at the end of the black arrow) was rotated 30° CW relative to the actual position of the hand (represented by the dark grey arrow). The reach target (white circle, 2 cm in diameter) was located 15 cm and 45° CW from the home position relative to straight ahead. **c** For the proprioceptive estimation trials, the home position was only visible at the start of the movement (light grey circle, 1 cm in diameter). The reference marker (white circle, 1 cm in diameter) was located 15 cm and 45° CW from the home position relative to straight ahead. The hand was passively moved to a position along the white dotted line (shown for reference) using an adaptive staircase algorithm as described in the text

training session. Analyses showed that there were no differences in inter-subject variability between those who took short or long breaks between sessions. Within each block subjects performed three experimental tasks, which are outlined in more detail below. The blocks included sets of 50 (Block 1) aligned reach training trials, followed by 5 (Block 2), 5 (Block 3), 10 (Block 4), 20 (Block 5), 30 (Block 6), 30 (Block 7), and 50 (Block 8) rotated reach training trials. The number of reach training trials increased over blocks, allowing us to assess early changes in the sensory and motor systems with a high resolution and hence look for rapid changes, as have been shown to arise in the motor system (Krakauer et al. 2000; Kitago et al. 2013). Following the reach training trials, subjects completed 6 reach aftereffect trials (Time 1) followed by 50 proprioceptive estimate trials, and then an additional 6 reach

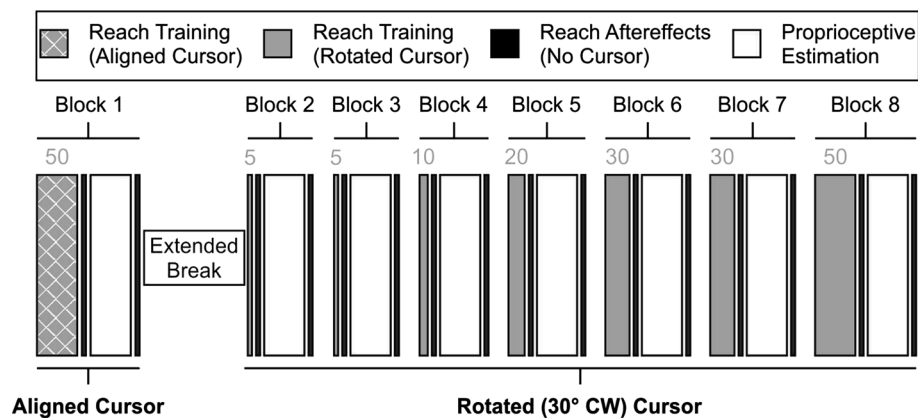


Fig. 2 Experimental design. A breakdown of the testing blocks completed within the experiment. Grey bars represent sets of reach training trials; the grey bar with the crossed pattern indicates trials in which the cursor was aligned with the hand, and the solid grey bars

indicate trials in which the cursor was rotated 30° CW relative to the hand. The grey numbers indicate the number of reach training trials within each block. Black bars represent sets of 6 aftereffects trials, and white bars represent sets of 50 proprioceptive estimate trials

aftereffect trials (Time 2). Thus, each subject completed a total of 200 reach training trials, 96 reach aftereffects trials, and 400 proprioceptive estimate trials over the course of the experiment with respect to a single target. Only one target/reference marker was included based on the time taken to complete the experiment (approximately 2 h in total).

Reach training task

Subjects grasped the robot handle with a comfortable but firm grip. After maintaining the hand at the home position for 500 ms, the visual target appeared 15 cm and 45° CW from the home position relative to straight ahead, so that it could be easily achieved. It is important to note that the home position was not displayed during these trials. Subjects were instructed to move as quickly and accurately as possible to the target while holding onto the robot handle. Visual feedback of the unseen hand was represented by a cursor (green circle; 1 cm in diameter). This cursor appeared as soon as the robot handle moved 7 cm outward from the home position, corresponding to a position where subjects tended to achieve peak velocity. Presenting the cursor at peak velocity allowed us to assess reaching performance in the reach training trials before subjects had an opportunity to correct their movements using visual feedback. In Block 1, the cursor was aligned with the actual position of the hand, and in all remaining blocks (Blocks 2–8), the cursor was rotated 30° CW relative to the hand (see Fig. 1b). The reach was considered complete once the centre of the green cursor had moved to within 0.5 cm of the target's centre. At this time, both the target and cursor were removed and the robot locked to a grooved path. This grooved path allowed subjects to actively guide their hand back to the home position via a direct linear route in the absence of visual feedback. If subjects attempted

to move outside of the grooved path, a very small 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 (Henriques and Soechting 2003). The position of the robot handle was recorded throughout all reaching tasks at a sampling rate of 1000 Hz and a spatial accuracy of 0.1 mm.

Reach aftereffects task

The reach aftereffects trials were used to determine how subjects reached (i.e. the extent of reach adaptation) as a result of the preceding reach training trials. Similar to the reach training task, subjects grasped the robot handle with a comfortable but firm grip. After maintaining their hand at the unseen home position for 500 ms, the visual target appeared 15 cm and 45° CW from the home position relative to straight ahead. Subjects were instructed to move as quickly and accurately as possible to the target while holding onto the robot handle. However, in this task, no visual feedback (i.e. no cursor) representing the hand was provided to subjects. Once the subjects had finished their reach (i.e. had maintained a final hand position for 1000 ms), the visual target disappeared and the trial was considered complete. The subject's hand was then guided back to the home position by a linear grooved path. Subjects completed two sets of aftereffect trials within each block: immediately following reach training trials (Time 1) and following the proprioceptive estimation trials mentioned below (Time 2).

Proprioceptive estimation task

The proprioceptive estimation trials were used to determine the position at which subjects perceived their unseen

hand was aligned with a visual reference marker. This task began with subjects grasping the robot handle at the home position. The position of the hand at the home position was indicated by displaying a white circle (1 cm in diameter) directly above the robot for 500 ms. After 500 ms, all visual feedback was removed, and the subject's hand was passively moved by the robot to a position somewhere along the white dotted line shown in Fig. 1c (note that the dotted white line in Fig. 1c was not visible to subjects). Research by Cameron et al. (2012) has found that passive, robot-assisted movements do not involve an active component, as demonstrated by a lack of EMG activity preceding movement onset during passive trials. Additionally, as visual feedback with regard to start or end positions was absent during these movements, subjects were not able to execute a planned movement in a particular direction (Cressman and Henriques 2009). The hand was moved by the robot according to a bell-shaped velocity profile, and the movement was 1 s in duration. The duration of the passive movement was based on average active movement times to the same target achieved by 3 subjects in a pilot study. Once the subject's hand reached its final position, a visual reference marker (yellow circle; 1 cm in diameter) appeared 15 cm and 45° CW from the home position relative to straight ahead (the same position as the visual target subjects reached to in the reach training task and reach aftereffects task). Subjects then made a two-alternative forced-choice judgement about the position of their hand, indicating whether they felt their hand was to the left or right of the visual reference marker along the dotted white line shown in Fig. 1c. There were no time constraints during this task, and subjects were encouraged to take as much time as they needed before giving their answer verbally to the experimenter. Once their response had been entered, the reference marker disappeared and the robot moved the hand back to the home position along the same route, with a 1-s movement duration.

The position of the hand relative to the reference marker was adjusted over trials using an adaptive staircase algorithm, according to a subject's responses (Kesten 1958; Treutwein 1995) as described by Cressman and Henriques (2009, 2010). Specifically, there were two staircases, a left and a right, which were adjusted independently and randomly interleaved. The left staircase started 20° CCW from the reference marker, and the right staircase started 20° CW from the reference marker. The position of the subject's hand relative to the reference marker was adjusted over trials according to their responses, such that the difference between hand locations in consecutive trials (i.e. step-size) decreased every time subjects reversed their pattern of responses within a particular staircase (i.e. from left to right or from right to left). Thus, subjects were tested more frequently at positions closest to their sensitivity threshold

between left and right. If subjects responded consistently, the two staircases converged at a point, representing the point at which they felt their hand was aligned with the visual reference marker (Cressman and Henriques 2009, 2010).

Data analyses

Proprioceptive estimates of hand position

To examine the time course of proprioceptive recalibration, we first determined the locations at which subjects felt their hands were aligned with a visual reference marker in each of the training blocks shown in Fig. 2. This location was determined by fitting a logistic function to each subject's responses during the corresponding proprioceptive estimation trials completed within the block. The point at which subjects responded "left" 50 % of the time (i.e. responded "left" and "right" equally often) represents their proprioceptive bias and provides a measure of subjects' accuracy of alignment of the hand with respect to the reference marker (i.e. the point at which subjects felt their hand was aligned with the reference marker). Additionally, we determined subjects' uncertainty by finding the difference between the values at which the probability of responding "left" was 25 and 75 %, which provides insight into subjects' precision.

Biases and uncertainty ranges were analysed in an 8 Block repeated-measures analysis of variance (RM ANOVA). Differences with a probability of less than 0.05 were considered significant and indicated that biases or uncertainty changed across block. Bonferroni post hoc tests were administered to find the locus of these differences for a set of pre-planned comparisons ($\alpha = 0.05$).

Reach adaptation

We determined angular reach errors at peak velocity (PV) in the reach training trials in order to determine whether subjects showed rapid changes in reaches when the distortion was still present as has been shown previously. As well, we analysed angular reach errors at both PV and movement endpoint (EP) in the no-cursor reach aftereffect trials to measure the time course of implicit motor changes after training with a rotated cursor. PV angular reach errors were defined as the angular difference between a movement vector (from the home position to the hand position at peak velocity) and a reference vector (joining the home position and the target). EP angular reach errors were defined as the angular difference between a movement vector (from the home position to the hand position at movement endpoint) and a reference vector (joining the home position and the target).

Given that reach aftereffects have been suggested to represent implicit motor adaptation, the following analyses are based on the no-cursor reach aftereffect trials. Performance in the training trials is provided for comparison purposes only. Average errors at EP and PV for each set of 6 reach aftereffect trials (i.e. trials completed at Time 1 or Time 2 within each block) were determined for each subject. To determine whether these average errors in the aftereffect trials at EP and PV followed a similar pattern across blocks, we first performed a 2 Error Score (EP vs. PV) \times 8 Block \times 2 Time (Time 1 vs. Time 2 relative to the proprioceptive estimate trials) RM ANOVA. Given that errors at peak velocity and movement endpoint reflect similar changes in reaches (i.e. ANOVA revealed no interaction between Error Score and Block [$F_{(7, 133)} = 1.233$, $p = 0.290$] or Error Score and Time [$F_{(1, 19)} = 0.063$, $p = 0.805$]), additional analyses were based on movement endpoint angular reach error as movement endpoint errors (1) were smaller than errors at peak velocity [$F_{(1, 19)} = 4.604$, $p = 0.045$] and therefore provide a more conservative error to compare with the smaller changes in proprioceptive biases, (2) avoid any angular deviations that arise during curved movements, and (3) are determined at a similar location as the proprioceptive biases.

We analysed changes in EP angular reach errors in an 8 Block \times 2 Time RM ANOVA. Differences with a probability of less than 0.05 were considered significant. Bonferroni post hoc tests were administered to find the locus of these differences for a set of pre-planned comparisons ($\alpha = 0.05$).

Relationship between proprioceptive estimation and reach adaptation

To examine the relationship between proprioceptive recalibration and reach adaptation, we compared average EP angular reach errors in the reach aftereffect trials at Time 1 and Time 2 to proprioceptive estimates using a 2 Measure (Reach Error at Time 1 or Time 2 vs. Proprioceptive Bias) \times 8 Block RM ANOVA.

To find differences in the rates of change for reach aftereffects (at Time 1 and Time 2) and proprioceptive biases, we fit exponential curves to the data using the curve fitting toolbox in MATLAB. The curves took the form of the following exponential function as used by Mattar et al. (2013):

$$\hat{y} = a \cdot [1 - (1 - b)^x] + c \quad (1)$$

such that y represents angular error, x represents the number of reach training trials completed just prior to the no-cursor reach aftereffect trials or proprioceptive estimates, a represents the scale of the change, b represents the rate of change, and c represents the vertical offset of the function (i.e. the initial deviation after training with the aligned

cursor). Rates of change were considered significantly different if their 95 % confidence intervals did not overlap. We also fit exponential curves to the reach training trials when (1) all reach training trials were included and (2) the first reach training trial of each set was removed, given the decay in reach errors seen at the start of each set of reach training trials or what Izawa et al. (2012) referred to as *forgetting*. This same forgetting can be seen in Fig. 4a of our results. In these analyses x represents the reach training trial number.

Control experiment

In the main experiment described above, subjects performed a set of reach aftereffect trials before and after the proprioceptive estimation trials within each block. The two sets of aftereffect trials were completed to see whether there was any change in reach errors after completing the proprioceptive estimation trials. As seen below, reach aftereffects decreased following the proprioceptive estimation trials. It is unclear whether this decrease in reach aftereffects was due to the proprioceptive estimation task itself, or the interval of time between sets of reach aftereffect trials. Thus, we performed a separate control study involving seven subjects (4 females, 3 males; mean age = 20.14 years, SD = 0.38 years). This study was identical to the main experiment except subjects did not perform proprioceptive estimation trials, but instead sat quietly holding on to the robot handle for 5 min between sets of reach aftereffect trials (the average time that it took subjects to complete a set of 50 proprioceptive estimation trials in the main experiment). To assess differences between the experiments, we performed a 2 Time (Time 1 vs. Time 2) \times 8 Block RM ANOVA, with Experiment as a between-subjects factor.

Results

Time course of proprioceptive recalibration

Proprioceptive estimates immediately following aligned reach training revealed an initial bias, such that subjects felt their hands were at the reference marker when they were shifted approximately 9.6° left of the reference marker. As shown in Fig. 3, proprioceptive estimates then shifted further to the left of this baseline estimate after training with rotated visual feedback of the hand. In fact, estimates shifted 8.8° more left of the baseline estimates after 150 reach training trials, as shown in Fig. 4c. In accordance with these observations, ANOVA revealed a significant effect of Block [$F_{(7, 133)} = 7.513$, $p < 0.001$], indicating that the position at which subjects felt that their hand was aligned with the visual reference marker changed over the

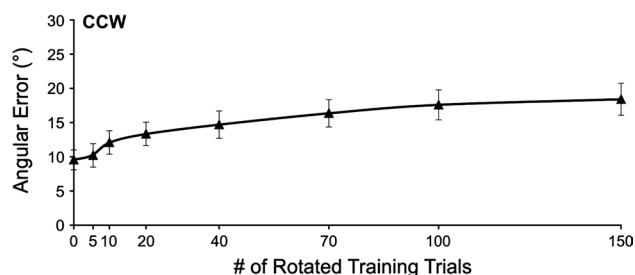
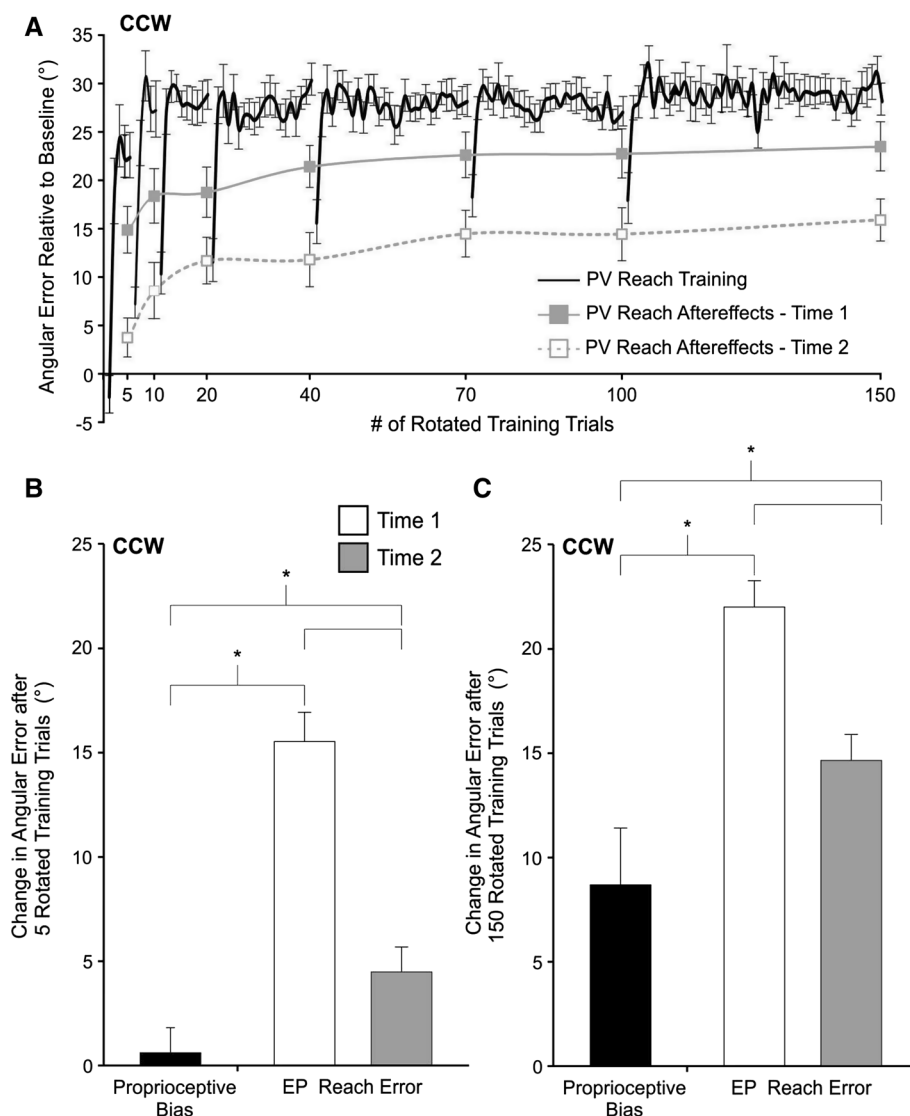


Fig. 3 Time course of changes in proprioceptive bias. Mean proprioceptive biases (i.e. felt hand position) represented as angular errors relative to the reference marker as a function of reach training trials with the 30° CW rotated cursor. The data point at 0 rotated training trials represents the proprioceptive bias following reach training with the aligned cursor (i.e. baseline)

Fig. 4 Time course of changes in angular reach error. **a** Mean angular reach errors (i.e. hand position) relative to the target during reach training trials and reach aftereffect trials. Mean PV angular reach errors for reach training trials completed with the rotated cursor relative to angular reach errors during reach training with an aligned cursor (*black lines*). Mean PV angular reach errors for reach aftereffect trials at Time 1 (*filled grey squares*) and Time 2 (*hollow squares*) are also displayed relative to errors achieved following training with an aligned cursor. **b, c** Mean changes in proprioceptive biases (*black bars*) and angular reach errors at movement endpoint (Time 1 *white bars*, Time 2 *grey bars*) following 5 reach training trials (**b**) and following 150 reach training trials (**c**) with the 30° CW rotated cursor relative to angular errors achieved following aligned reach training. Stars denote instances when data are significantly different ($p < 0.050$)



course of the reach training. In addition to demonstrating a change in proprioceptive bias over reach training trials, Fig. 3 also illustrates that this shift arose gradually over the course of the experiment, as the magnitude of the shift did not differ significantly between consecutive blocks. As shown in Fig. 4b, there were very little changes in proprioceptive bias after only 5 rotated training trials. However, post hoc analyses revealed that proprioceptive bias was significantly different from performance following the aligned training trials by Block 6, or following 70 rotated training trials. These results suggest that proprioceptive recalibration arises gradually over the course of reach training trials.

Subjects' levels of precision in estimating the location of their unseen hand were comparable after the aligned reach training trials and after all sets of rotated reach training

trials [$F_{(7, 133)} = 1.460, p = 0.187$]. The average uncertainty range across all blocks was 9° .

Time course of reach adaptation

Subjects reached such that their hand was to the left of the target after training with the aligned cursor (mean EP reach error = 3.1° , SD = 0.9°). To illustrate performance in the reach training trials with the rotated cursor, average angular error at PV for each reach training trial with the rotated cursor is plotted in Fig. 4a relative to average performance across the aligned training trials. As shown previously, we see that subjects quickly adapted to the cursor distortion within a few trials when reaching with the distortion (Krakauer et al. 2000). Additionally, mean angular reach errors in the no-cursor reach aftereffect trials are displayed in Fig. 4a following the aligned cursor reach training trials, and at the end of each of the 7 sets of rotated reach training trials. Specifically, in Fig. 4a, angular reach errors at PV are displayed before and after the proprioceptive estimation trials (at Time 1 and Time 2, respectively). From the reach training trials in Fig. 4a, we see that subjects quickly altered their movements when the distortion was present, but that performance decayed at the start of each set of reach training trials, following the proprioceptive estimates and aftereffect trials. Specifically, following training with rotated hand-cursor feedback, reach errors increased rapidly, such that subjects aimed significantly more to the left of the target after training with a rotated cursor compared to an aligned cursor [$F_{(7, 133)} = 63.718, p < 0.001$]. The total change in EP reach errors following 150 rotated reach training trials relative to baseline at Time 1 was 22.3° and at Time 2 was 14.7° , as shown in Fig. 4c. Analysis also revealed a significant interaction between Block and Time [$F_{(7, 133)} = 17.383, p < 0.001$]. Thus, we will consider changes in reaching performance at both Time 1 and Time 2 separately when discussing the remainder of our results.

As discussed above and shown in Fig. 4, reaching errors at Time 1 and Time 2 increased significantly over Block. ANOVA revealed a main effect of Block for errors at Time 1 [$F_{(7, 133)} = 67.752, p < 0.001$] and Time 2 [$F_{(7, 133)} = 36.952, p < 0.010$]. Post hoc analyses revealed that even though errors were smaller at Time 2 compared to Time 1, angular reach errors at Time 1 and Time 2 were both significantly greater relative to their respective baselines following Block 2 (i.e. after 5 reach training trials with the rotated hand-cursor feedback), indicating that changes in the motor system occurred very rapidly (see Fig. 4b). The time course of Time 1 angular reach errors showed a great initial increase which then plateaued at Block 5 (i.e. after 40 rotated cursor trials), such that there were no further significant changes across consecutive blocks. The time course of changes in angular reach errors

at Time 2 showed a smaller initial increase, with gradual increases until errors saturated following Block 6 (i.e. after 70 rotated cursor trials), and there were no more significant changes between consecutive blocks.

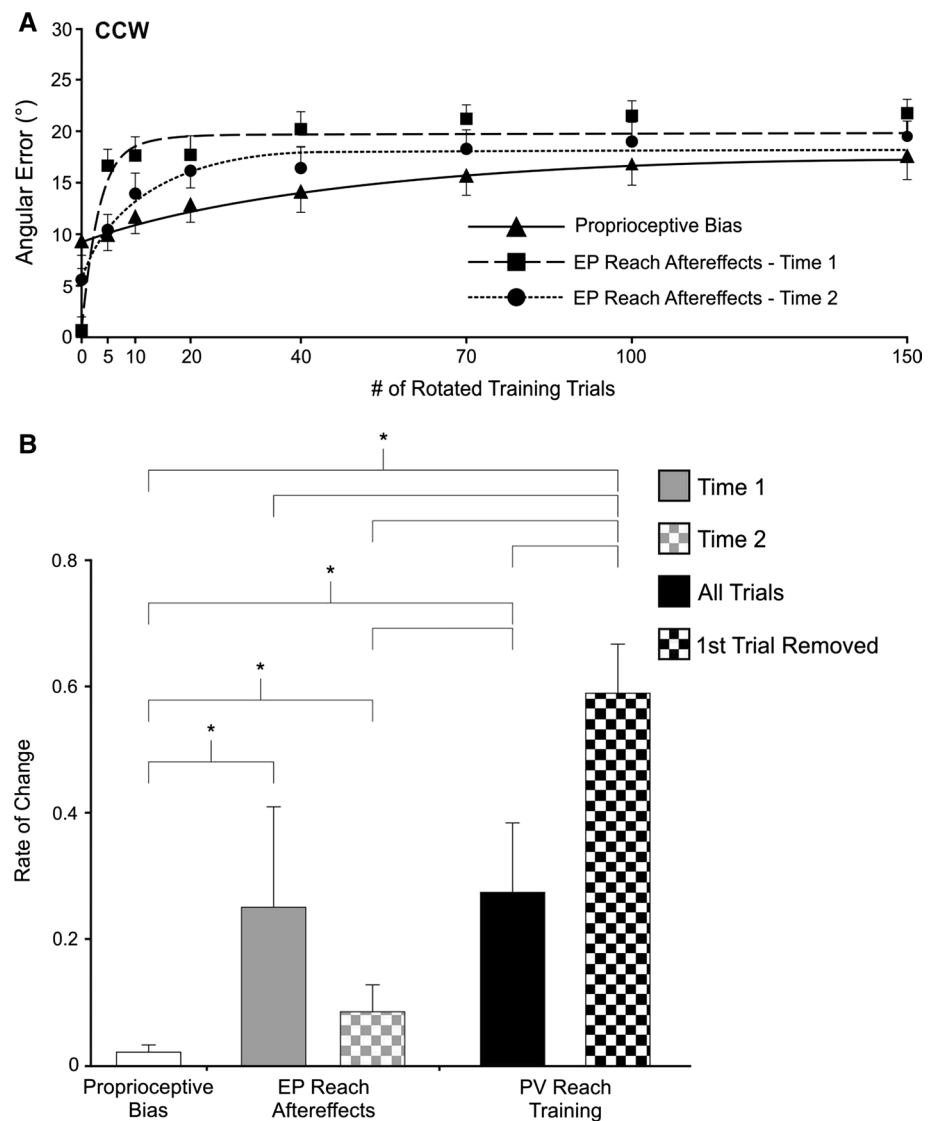
Comparison of proprioceptive recalibration and reach adaptation

Reaching errors at Time 1 and Time 2 compared to proprioceptive estimates across blocks of trials revealed significant interactions (Time 1: [$F_{(7, 133)} = 13.594, p < 0.001$] and Time 2: [$F_{(7, 133)} = 3.161, p < 0.010$]), suggesting that changes in reaches followed a different time course compared to changes in proprioceptive estimates. The changes over time are shown by the exponential curves fitted to the data (see Eq. 1) in Fig. 5a. Changes in reach error at Time 1 and Time 2 over blocks of training trials as well as proprioceptive bias were captured well by exponential curves, with r^2 values indicating that the curves accounted for 95.80 % (Reach errors at Time 1), 97.07 % (Reach errors at Time 2), and 98.70 % (Proprioceptive biases) of the variance of the curves. An exponential function yielded much better fits than using a linear function, which yielded r^2 values of 34.94 % (Reach errors at Time 1), 57.87 % (Reach errors at Time 2), and 83.88 % (Proprioceptive biases). From Fig. 5a, it is evident that reach adaptation assessed at both Time 1 and Time 2 arose much earlier than proprioceptive recalibration. This early increase in reach adaptation is reflected in the associated large rates of change (i.e. the slope or “b” term in Eq. 1) shown in Fig. 5b (Time 1 rate of change = 0.25, with the 95 % confidence interval ranging from 0.11 to 0.40, and Time 2 rate of change = 0.09, with the 95 % confidence interval ranging from 0.05 to 0.13). In contrast, proprioceptive estimates did not change as quickly (rate of change = 0.02, with the 95 % confidence interval ranging from 0.01 to 0.03) and the 95 % confidence intervals for the rates of change of reach adaptation do not overlap with the confidence interval for the rate of change of the proprioceptive bias. The rate of change of reach errors in the reach training trials is also displayed in Fig. 5b for comparison purposes when an exponential curve was fitted to (1) all reach training trials (rate of change = 0.28, with the 95 % confidence interval ranging from 0.18 to 0.38; $r^2 = 37.8$ %) and (2) trials in which the first trial of each set was excluded (rate of change = 0.60, with the 95 % confidence interval ranging from 0.52 to 0.67; $r^2 = 77.7$ %).

Control experiment

In the control experiment subjects sat quietly, holding onto the robot handle for 5 min in between sets of reach aftereffect trials. Figure 6 shows the difference in endpoint reaching errors between Time 1 and Time 2 in all 8

Fig. 5 Rates of sensory and motor changes. **a** Mean end-point (EP) angular reach errors (i.e. hand position relative to target position) at Time 1 (*squares*) and Time 2 (*circles*), as well as proprioceptive biases (*triangles*) as a function of training trials with the 30° CW rotated cursor. Data points at 0 rotated training trials reflect performance following training with an aligned cursor (i.e. baseline). *Smooth curves* indicate exponential fits to the data, according to Eq. 1. **b** Rates of change of the exponential functions for proprioceptive biases (*white bar*) and reach errors at movement endpoint (Time 1 *grey bar*, Time 2 *grey checkered bar*). Rates of change of exponential functions fit to the reach training trials shown in Fig. 4a are also provided with (*black bar*) and without (*black checkered bar*) the very first trial of each set included. Bars represent 95 % confidence intervals. Stars denote instances when the 95 % confidence intervals do not overlap



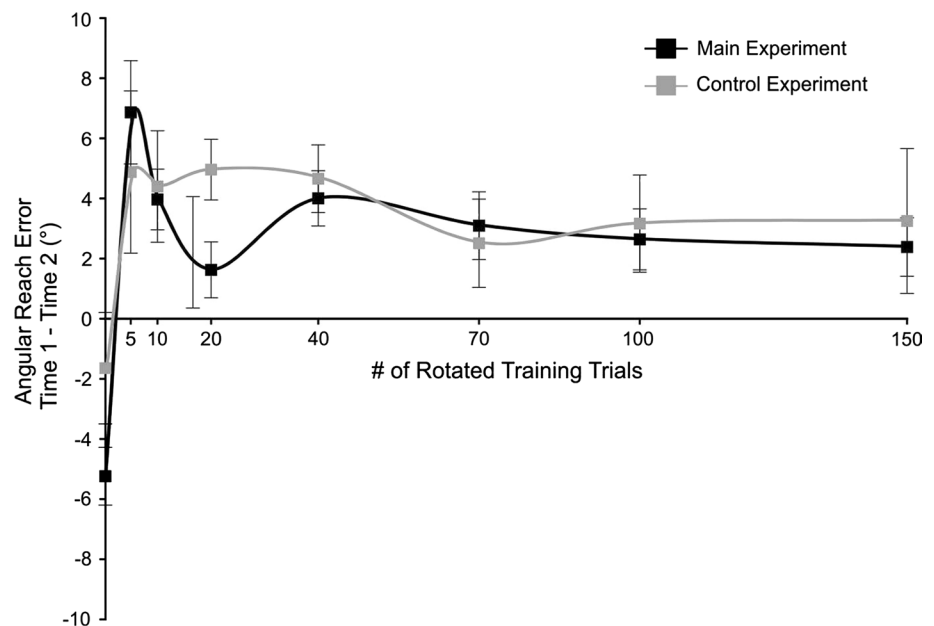
training blocks for both the Control and Main experiment discussed above. A 2 Time by 8 Block RM ANOVA with Experiment as a between-subjects factor revealed that there was no significant difference in reach aftereffects between experiment [$F_{(1, 25)} = 0.199$, $p = 0.660$], nor was there an interaction between Time and Experiment [$F_{(1, 25)} = 0.548$, $p = 0.466$]. In other words, the difference between reaching errors at Time 1 and Time 2 was not affected by whether subjects completed the proprioceptive estimation task, or merely held the robot handle for 5 min.

Discussion

The goal of the present experiment was to determine the time course for changes in the sensory system during visuomotor adaptation to a 30° CW cursor rotation. Additionally,

we were interested in comparing the time course of these implicit proprioceptive changes with implicit changes in the reach adaptation assessed through aftereffect trials. We found an overall change in proprioceptive bias of 8.8° following the 150 reach training trials, which corresponds to about 30 % of the magnitude of the visuomotor distortion. These changes were slow to arise and did not differ from baseline performance until after 70 training trials with the rotated cursor, after which we found no significant differences between consecutive blocks (i.e. the changes levelled off). In contrast, changes in reach aftereffects arose after only 5 training trials with the rotated cursor and continued to increase until errors of 22.3° and 14.7° were achieved, before (Time 1) and after (Time 2) the proprioceptive estimate trials, respectively. These rapid changes in the motor system versus slow changes in the sensory systems suggest that the visuomotor system is quicker to change than the sensory system, perhaps because we are much more often

Fig. 6 Differences in reach aftereffects at Time 1 and Time 2 for the main and control experiments. Mean change in movement endpoint angular reach errors between Time 1 and Time 2 as a function of training trials with the 30° CW rotated cursor. Data points at 0 rotated training trials reflect performance following training with an aligned cursor (i.e. baseline). In the main experiment (*black squares*), subjects completed the proprioceptive estimation trials between Time 1 and Time 2. In the control experiment (*grey squares*), subjects sat stationary while holding the robot handle for 5 min between Time 1 and Time 2



required to update our movements throughout our daily lives, rather than our sense of limb position.

Proprioceptive recalibration

Our data show a relatively large initial proprioceptive bias of about 9.6° to the left of the visual reference marker following reach training with an aligned cursor. We found that this initial bias was then shifted more leftwards following training with the rotated cursor, such that subjects recalibrated proprioception by approximately 9° following 70 reach training trials. The current data are consistent with previous studies from our laboratory which have found that proprioceptive estimates of hand position shift by about 25 % of the magnitude of the distortion when interleaved reach training trials are included between sets of proprioceptive estimates (Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012). Moreover, the current data extends this work by demonstrating that proprioceptive recalibration can saturate within 70 trials (at least when there is only one reach training target and reference marker). These results further suggest that, while the proprioceptive system is slow to change, no further changes are seen with additional training (e.g. another 80 trials).

Despite designing the experiment to try and introduce fast changes in the sensory system (e.g. by introducing the distortion abruptly and having only one reach training target and reference marker), the time course of proprioceptive changes found in the current study reflects a slow, gradual leftward shift in proprioceptive bias over the course of 70 training trials with the rotated cursor (rate of change = 0.0225). These changes were captured well by

the exponential curve shown in Eq. 1, such that the curve accounted for 98.70 % of the variance of the data. These results are consistent with work by Mattar et al. (2013) who assessed sense of hand motion rather than final hand position. Specifically, they showed that changes in the sensory system increased exponentially during reaches in a velocity-dependent force field (rate of change = 0.017), such that an exponential fit accounted for 93.3 % of the variance. Thus, proprioceptive changes appear to follow a relatively slow exponential increase after training with either a visual distortion or in a velocity-dependent force field.

In the present research, we discuss the observed changes in hand position as reflecting proprioceptive recalibration as opposed to visual recalibration based on our experimental manipulation and results across several previous studies. First, the current study only manipulated visual feedback of the hand position, rather than the entire workspace (as would occur in prism adaptation paradigms), which avoids recalibration of the visual system. Changes in felt hand positions have also been shown to be similar when subjects estimated the position of their hand relative to a proprioceptive reference marker (e.g. body midline) and a visual reference marker, suggesting that recalibration is independent of vision (Cressman and Henriques 2009; Clayton et al. 2014; Mostafa et al. 2014a). Moreover, shifts in proprioceptive estimates have also been shown when subjects reached to their unseen trained hand with the seen untrained hand (Clayton et al. 2014). Finally, if vision was recalibrated, we would expect changes in proprioceptive estimates to transfer between hands, which Mostafa et al. (2014b) have demonstrated does not occur.

Reach adaptation

We looked to compare our implicit sensory changes to implicit motor changes by examining the time course of reach errors in our reach aftereffect trials, which have been suggested to assess implicit adaptive motor processes as opposed to explicit, strategic processes (Weiner et al. 1983; Pisella et al. 2004; Redding et al. 2005). Additionally, we looked at the time course of adaptation in the reach training trials, which is likely influenced by a combination of implicit and explicit processes. We found that large changes in the motor system arose quickly in the reach training trials and aftereffect trials (e.g. 16.9° after 5 training trials with a 30° cursor rotation), which confirms previous findings which have found that reach performance returns to near baseline levels within 20 training trials with a 30° cursor rotation (Krakauer et al. 2000; Neva and Henriques 2013) and within 30 training trials with a 40° cursor rotation (Yamamoto et al. 2006). However, the rapid changes observed in the current study exhibited some decay, such that after approximately 5 min, reach aftereffects at Time 2 were only 5.1° (or 11.8° less than what was seen at Time 1) and performance at the start of each set of reach training trials differed from what was seen at the end of the previous set of reach training trials [as shown by Izawa et al. (2012) and Mattar et al. (2013)].

Changes in angular reach errors before (Time 1) and after (Time 2) proprioceptive estimate trials were well captured by exponential fits. Specifically, an exponential fit accounted for 95.80 and 97.07 % of the variance of EP reach errors at Time 1 and Time 2, respectively. Previous studies have also characterized motor adaptation to a visuomotor rotation (Krakauer et al. 1999, 2005) or a velocity-dependent force field (Smith et al. 2006; Mattar et al. 2013) as following exponential functions. However, these studies have typically looked at the rate of adaptation during training trials (i.e. trials when the perturbation is still present), such that explicit strategies could influence performance (Weiner et al. 1983; Pisella et al. 2004; Redding et al. 2005; Taylor and Ivry 2011; Taylor et al. 2014). On fitting an exponential function to our reach training trials, we found that it accounted for only 37.8 % of the variance of reach errors when all reach training trials were included in the analysis. However, when the first trial of each set of reach training trials was excluded from analysis, thus accounting for forgetting as suggested by Izawa et al. (2012), the fit was much better, accounting for 77.7 % of the variance of reach errors. Our study is one of the first to show that motor changes follow an exponential curve when motor learning is assessed through a reach aftereffect task, which removes the distortion completely.

Interestingly, the 95 % confidence interval for the reach training trials did not overlap with the aftereffect trials at Time 1 or Time 2 (as shown in Fig. 5b), when the first trial

was removed from each training block. Recently, reach adaptation to a visuomotor rotation has been suggested to also involve an explicit component, such that subjects consciously correct their movements to quickly bring the cursor to the target, and an implicit component which involves an error-based updating of an internal forward model (Benson et al. 2011; Taylor et al. 2014). The difference in results between our reach training trials and aftereffect trials may reflect the different contributions of explicit and implicit processes between the different types of trials.

We primarily assessed motor adaptation through aftereffect trials as they have been suggested to provide insight into more permanent and implicit motor changes, and hence potentially reflect changes observed in our proprioceptive estimate trials. Reach aftereffects assessed immediately following each set of reach training trials (Time 1) were greater than after a 5-min delay (Time 2) over the course of the experiment which was introduced by having subjects complete the proprioceptive estimation task. Specifically, reach aftereffect trials at Time 1 resulted in a greater overall magnitude of reach adaptation following all sets of training trials. This decay of reach adaptation was also observed in a control experiment in which we replaced the proprioceptive estimation task with a 5-min rest interval in which subjects sat stationary, gripping the robot handle. Thus, it appears that reach adaptation decays over a 5-min time interval, regardless of whether subjects are completing a perceptual task or resting quietly. Given that motor adaptation at Time 1 and Time 2 was assessed through aftereffect trials, differences in reach adaptation between the two time-points likely do not represent differences in strategic (explicit) versus implicit learning, but perhaps reflect differences in the contribution of a faster, labile component and a slower, temporally stable component of learning as put forth recently by Smith and colleagues (Hadjiosif and Smith 2013a, b; Miyamoto et al. 2014). Specifically, decreases in motor adaptation within a few aftereffect trials in Time 1 [as shown by Nourouzpour et al. 2015 and seen in the current data (not shown)] would reflect a decay of the faster, labile component, which has been shown to decay after about 16.5 s (Hadjiosif and Smith 2013a). We did not see a similar decay during aftereffect trials in Time 2 (as shown by a statistically greater mean standard deviation at Time 1 (9.99°) relative to Time 2 (8.80°); [$F_{(1, 19)} = 6.921, p = 0.016$]), as these likely involved a more temporally stable component of learning and hence may be a more accurate representation of long-term motor changes which result from an internal visuomotor remapping.

Comparison of proprioceptive recalibration and reach adaptation

Here we have shown that implicit changes in the sensory and motor systems arise with different time courses during

visuomotor adaptation. The motor system undergoes large, rapid changes after only 5 training trials with the rotated cursor. The sensory system, on the other hand, undergoes slower and more gradual changes, such that changes are not observed until after a number of training trials (e.g. 70 trials with the rotated cursor).

Cressman and Henriques (2010) have suggested that while sensory changes can result in changes in the motor system, they are not usually solely responsible for motor adaptation. Given the different time courses observed in the current study, even when a more stable measure of motor adaptation was used (i.e. aftereffects measured after a 5-min delay), our data support this suggestion. Specifically, we suggest that while sensory changes may partially contribute to motor adaptation, for the most part, proprioceptive recalibration and reach adaptation are driven by different error signals present during visuomotor adaptation. Specifically, reach adaptation may arise due to error-based learning, which involves the reduction of the difference between the predicted and sensory consequences of a subject's movements (i.e. reducing the difference between desired and actual performance; Tseng et al. 2007; Berniker and Kording 2008; Wei and Kording 2009). In contrast, proprioceptive recalibration may arise due to a cross-sensory error signal which depends on differences between visual and proprioceptive estimates of limb position (Cressman and Henriques 2010; Henriques and Cressman 2012; Salomonczyk et al. 2013; Henriques et al. 2014). From the results of the current study, it appears that it takes longer for the brain to resolve this sensory conflict and does not resolve it to the same extent as a visuomotor error signal.

Given that subjects reached to a single target, other learning mechanisms may have influenced the current results. For example, Diedrichsen and colleagues (2010) have attributed reach adaptation to use-dependent and error-based learning after showing that performing multiple movements in a particular direction (with no perturbation present) can result in reach aftereffects which are biased in the direction of the previously executed movements. It is unclear whether (and to what extent) sensory changes in the current study were influenced by use-dependent processes, as their role in proprioceptive recalibration is currently unknown. Thus, future research is required to determine the influence of use-dependent processes on proprioceptive recalibration.

Conclusion

In the current study, we found slow, gradual changes in the sensory system, which occurred later in time compared to changes in the motor system, even when implicit motor changes were assessed with aftereffect trials. Thus, the

visuomotor system appears to be quicker to change than the sensory system, perhaps because we are required to adjust our movements on a daily basis while interacting with a dynamic environment. The sensory system on the other hand is very rarely required to adapt, potentially leading to its resistance to change.

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