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Sensory Recalibration of Hand Position Following Visuomotor Adaptation

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Cressman EK, Henriques DYP. Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102: 3505–3518, 2009. First published October 14, 2009; doi:10.1152/jn.00514.2009. Goal-directed reaches are rapidly adapted following exposure to misaligned visual feedback of the hand. It has been suggested that these changes in reaches result in sensory recalibration (i.e., realigning proprioceptive estimates of hand position to match the visual estimates). In the current study we tested whether visuomotor adaptation results in recalibration of hand proprioception by comparing subjects' estimates of the position at which they felt their hand was aligned with a reference marker (visual or proprioceptive) before and after aiming with a misaligned cursor. The misaligned cursor was either translated or rotated to the right of the actual hand location. On the estimation trials, we did not allow subjects to freely move their hands into position. Instead, a robot manipulandum either passively positioned the hand (*experiments* 1 and 2) or subjects moved their hand along a robot-generated constrained pathway (*experiments* 3 and 4). We found that regardless of experimental manipulation, subjects' proprioceptive estimates of hand position were more biased to the left after visuomotor adaptation. The leftward shift in subjects' estimates was in the same direction and one third of the magnitude of the adapted movement. This suggests that in addition to recalibrating the sensorimotor transformations underlying reaching movements, visuomotor adaptation results in partial proprioceptive recalibration.

INTRODUCTION

When reaching to a visual target we combine visual information regarding target location and hand position with limb proprioceptive information, to compute the motor error needed to produce a correct motor command (e.g., Jeannerod 1988). Typically, visual and proprioceptive estimates are aligned, such that one feels the hand is at the same position at which one sees it. However, situations arise in which these sensory signals conflict (e.g., when looking through a microscope or in a mirror). In cases when sensory cues conflict and one is reaching to a visual target, one tends to rely more on the visual estimate of the hand than on the actual or felt position. Thus movements are adjusted in accordance with the seen position of the hand and one learns a new visuomotor mapping (visuomotor adaptation). For example, if a cursor is shifted rightwards relative to the actual hand location, subjects adjust their reaches, aiming to the left of the intended target to bring the cursor onto the target (Baraduc and Wolpert 2002; Ghahramani et al. 1996; Magescas and Prablanc 2006; Simani et al. 2007; Vetter et al. 1999).

It is currently unclear how the brain deals with these conflicting sensory signals. One possibility is that vision merely overrules the proprioceptive sense of the hand position during visuomotor adaptation. On the other hand, perhaps reaching with altered visual feedback of the hand causes proprioception to be recalibrated such that subjects begin to feel their hand is at the same location at which they see it. In an attempt to address this issue, previous work has typically asked subjects to reach to visual and proprioceptive targets with their *adapted* hand following visuomotor adaptation (Simani et al. 2007; van Beers et al. 2002). Although subjects' reaches were altered following visuomotor adaptation, it is unclear whether these changes reflect intersensory recalibration per se. Subjects were allowed to freely move their adapted arm. Thus errors in reaches could have arisen due to subjects using the adapted sensorimotor mapping.

Given the possibility that reaching tasks may engage adapted sensorimotor mappings, Henriques and colleagues (Malfait et al. 2008; Wong and Henriques 2009) have recently attempted to assess proprioceptive recalibration in perceptual, nonreaching tasks. In their paradigms, subjects were required to report on the shape that the hand had traversed or hand-path geometry relative to a reference following visuomotor adaptation. Although these tasks do not directly assess changes in sense of the hand position, they do provide some insight into proprioceptive recalibration. Specifically, based on the differences in results between the two paradigms, it appears that proprioceptive recalibration may be dependent on the visuomotor distortion introduced and/or how subjects position their hand during the perceptual estimates. For example, Malfait et al. (2008) found evidence for proprioceptive recalibration in a task in which subjects reported whether the path that the hand was *passively* moved through matched a square path that a cursor traced out. This task was completed after subjects were exposed to a *translated* cursor when tracking a moving dot with their hand and learned to trace a rectangular path to guide the cursor around a square. In contrast to these results, Wong and Henriques (2009) found no changes in subjects' sense of hand direction after they were exposed to a *rotated* cursor in an aiming task and *actively* pushed the robot into position during the proprioceptive estimates.

In the current task, we wanted to determine whether the sense of hand *position* was recalibrated following visuomotor adaptation in a reaching task. To do this, we modified the perceptual paradigms of Malfait et al. (2008) and Wong and Henriques (2009) and determined the position at which subjects perceived their unseen hand was aligned with reference markers in a task that did not allow subjects to reach, aim, align—or otherwise freely move—their adapted hand. In contrast to previous studies, our reference markers consisted of both visual and proprioceptive cues. Given the differences obtained between Malfait et al. (2008) and Wong and Henriques (2009), we used a robot manipulandum to either passively position the hand (*experiments* 1 and 2) or generate a constrained pathway along which subjects moved their hand (*experiments* 3 and 4). Once the hand reached the end of the path, a reference marker appeared and subjects reported whether their unseen hand was left or right of the reference marker.

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Because the reference markers varied in location and did not appear until the hand was at the final test location, we are confident that we assessed proprioception in a task where subjects could not plan the direction or extent of their arm movement, like they could if they had been allowed to freely move their hand.

Subjects estimated the positions of their hands after reaching with a veridical cursor (baseline condition) and after adapting their reaches to a misaligned cursor. Based on the discrepancy between the findings of Malfait et al. (2008) and Wong and Henriques (2009), we manipulated the visuomotor distortion introduced during the misaligned reaching trials in addition to the manner by which subjects positioned their hand in the proprioceptive estimation trials. Similar to the study by Malfait et al. (2008), we introduced a constant directional discrepancy between the hand and the visual cursor by translating the cursor 4 cm to the right of the hand in *experiments* 1 and 3. In *experiments* 2 and 4, we rotated the cursor 30° clockwise (CW) with respect to the hand, as done by Wong and Henriques (2009). If learning to reach with a misaligned cursor results in proprioceptive recalibration, then subjects' perceptions of hand location should shift so that they are aligned with the cursor they saw during the misaligned visually guided reaches. In other words, when subjects adapt their reaches to a rightward-shifted cursor, their proprioceptive sense of hand position should also shift rightward relative to their sense of hand position after reaching with a veridical cursor. This rightward shift in sense of hand position would result in the subjects' hands having to be shifted more to the left of a reference marker for them to perceive that the unseen hand was at the same location as that of the reference. On the other hand, if we find no systematic difference in hand-reference marker alignment estimates following visuomotor adaptation to a misaligned cursor compared with training with a veridical cursor, this would suggest that visuomotor adaptation does not lead to (or require) intersensory remapping.

METHODS

Subjects

In total, 28 healthy, right-handed university students (mean age = 21.0 yr, SD 1.9 yr) volunteered to participate in one or more of the experiments described in the following text. All subjects were prescreened verbally for self-reported handedness and history of visual, neurological, and/or motor dysfunction. The one subject who reported using both right and left hands for various activities completed the 32-item Waterloo Handedness Questionnaire (Steenhuis and Bryden 1989) and was designated as right-handed. All subjects gave informed consent and the study was conducted in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee. Table 1 provides a breakdown of the number of subjects who completed each experiment and an overview of the tasks included within each of the four experiments.

General experimental setup

A side view of the setup is illustrated in Fig. 1*A*. Subjects were seated at a table in a chair whose distance and height from the table were adjusted to ensure that subjects could comfortably see and reach to all target positions. Once the chair was adjusted it remained in the same position for all experimental sessions. Subjects were instructed to grasp the vertical handle of a two-joint robot manipulandum (Interactive Motion Technologies) with their right hand, such that their thumb was positioned on a top marker (1.4 cm in diameter). Visual stimuli were projected from a monitor (SyncMaster model 510N; refresh rate: 72 Hz; Samsung, Brisbane, CA) installed 17 cm above the robot and viewed by subjects as a reflected image. 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 right hand was blocked by the reflective surface and a black cloth draped between the experimental setup and the subjects' right shoulders.

Procedure

We conducted a series of four experiments to determine the conditions under which visuomotor adaptation leads to proprioceptive recalibration. Across these experiments, we varied the visuomotor distortion introduced during the reach training trials (translated vs. rotated cursor) and the proprioceptive signals available during assessment of proprioceptive recalibration (passive vs. active hand-positioning task). Table 1 and Fig. 2 provide a general overview of the experimental sessions in each of the experiments. We will begin by outlining *experiment* 1 in detail and then highlight changes in the subsequent protocols.

TABLE 1. *Breakdown of experiment sessions and subjects*

Experiment	Number of Subjects	Session Number	Visual Feedback of the Hand	Number of Reference Markers	Center Reference Marker Modality
Experiment 1:					
Passive translation	11	1	Aligned cursor	6 peripheral, 1 center	Proprioceptive
		2	Aligned cursor	6 peripheral, 1 center	Visual
		3	Translated cursor	6 peripheral, 1 center	Proprioceptive
		4	Translated cursor	6 peripheral, 1 center	Visual
Experiment 2:					
Passive rotation	16	1	Aligned cursor	6 peripheral, 1 center	Proprioceptive
		2	Aligned cursor	6 peripheral, 1 center	Visual
		3	Rotated cursor	6 peripheral, 1 center	Proprioceptive
		4	Rotated cursor	6 peripheral, 1 center	Visual
Experiment: 3					
Active translation	10	1	Aligned cursor	4 peripheral, 2 center	Proprioceptive + visual
		2	Translated cursor	4 peripheral, 2 center	Proprioceptive + visual
Experiment 4:					
Active rotation	10	1	Aligned cursor	4 peripheral, 2 center	Proprioceptive + visual
		2	Rotated cursor	4 peripheral, 2 center	Proprioceptive + visual

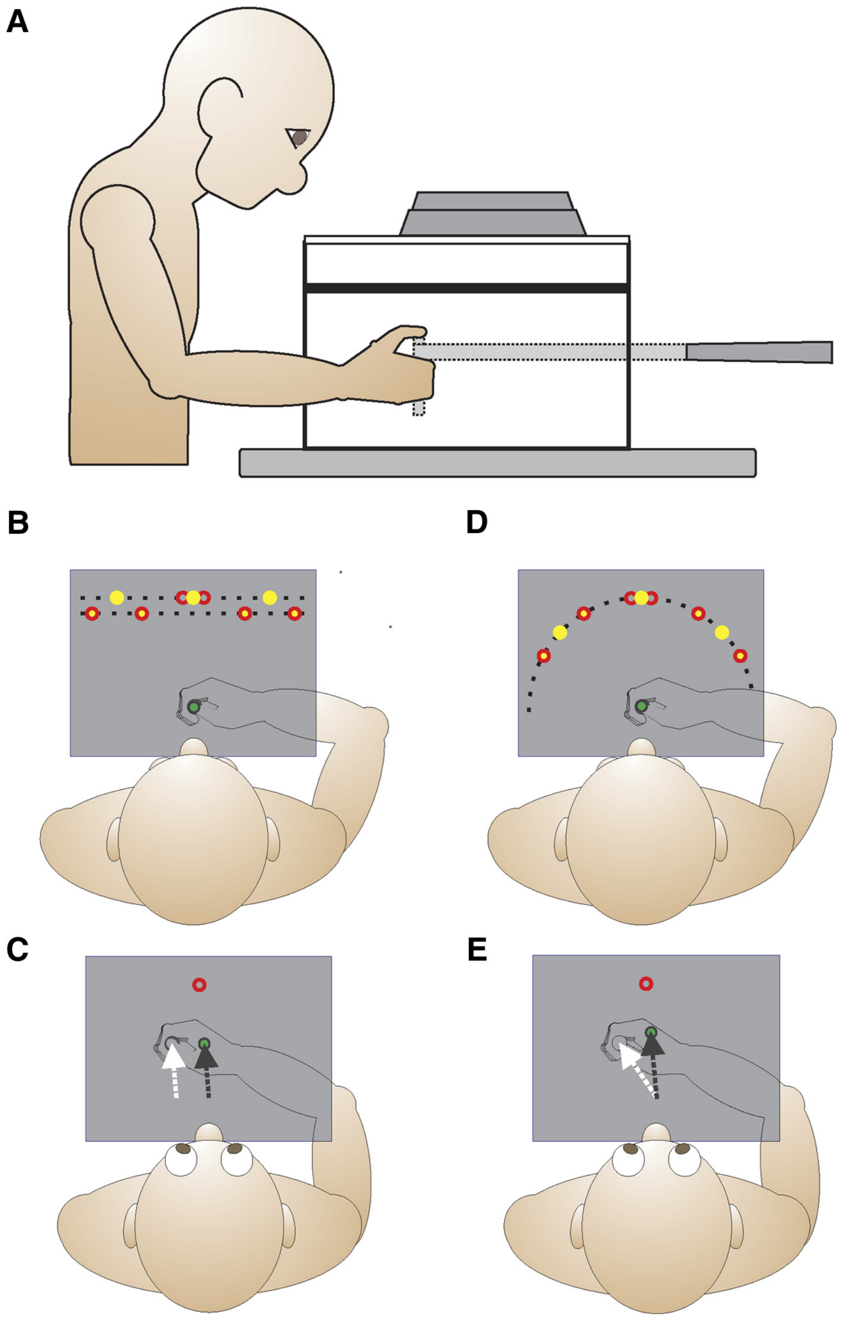

FIG. 1. Experimental setup and design. *A*: side view of the experimental setup. *B*: top view of experimental surface visible to subjects in the translated *experiments* 1 and 3. The center home position was represented by a 1-cm green circle and was located about 20 cm in front of subjects' chests. Targets were located along 2 lines (8.66 and 10 cm in front of the home position) and were 1 cm in diameter. Alignment reference markers are indicated by solid yellow circles, located 5, 7.5, and 10 cm left and right of the 0 cm or center-reference marker (aligned with the body midline). Note that in *experiment* 3, the 10 cm left and rightward reference markers were not included in the proprioceptive estimation task. Reach targets, located 0.9, 5, and 10 cm left and right of center, are outlined in red. *C*: visuomotor distortion introduced in the translated-reach training task. The start position for the hand was shifted during the translated-reach training task so that the hand began its reaching movements 4 cm to the left of the home position. This shift ensured that the green cursor (representing the hand) appeared to come from a central position. *D*: targets presented in the rotated *experiments* 2 and 4. Alignment reference markers are indicated by solid yellow circles and are located 30, 45, and 60° counterclockwise (CCW, *left*) and clockwise (CW, *right*) of the 0° center-reference marker. Note that in *experiment* 3, the 60° reference markers were not included in the alignment task. Reach targets are located 5, 30, and 60° on either side of center and are outlined in red. All targets were located along a circle arc at a distance of 10 cm from the home position. *E*: visuomotor distortion introduced in the rotated-reach training task. The green cursor (representing the hand) was rotated 30° CW with respect to the actual hand location during the rotated-reach training task. Note that the black dotted lines shown in *B* and *C* are provided as references. They indicate the arrangement of the reach targets and reference markers and illustrate potential positions that the hand could have been moved to during the proprioceptive estimate trials.

Experiment 1: passive translation

STIMULUS DISPLAY. *Reach targets.* There were six reach targets represented by 1-cm-diameter yellow disks. The reach targets were located 0.9, 5, and 10 cm to the left and right of center, with the 5 and 10 cm targets located 8.66 cm in front of the home position and the 0.9 cm targets located 10 cm in front of the home position (red open circles, Fig. 1*B*). These target positions were chosen to overlap with the targets in *experiment* 2, described in the following text, as much as possible.

Proprioceptive reference markers. There were seven alignment reference markers, located along two lines, 8.66 or 10 cm, in front of the home position (yellow circles, Fig. 1*B*). One reference marker was located 10 cm directly in front of the home position (0 cm) and represented visually (yellow disk, 1 cm in diameter) or proprioceptively. This proprioceptive marker position was based on an internal representation of body midline. Additional visual reference markers were located 5 and 10 cm to the left and right of the 0 cm center reference marker, 8.66 cm in front of the home position. Two final reference markers were located 7.5 cm to the left and right of the 0 cm center reference marker, 10 cm in front of the home position in *experiment* 1.

Testing sessions 1 and 2: reach training with veridical cursor, baseline performance

REACH TRAINING TASK. Subjects began by completing a reach training task (first box in Fig. 2*A*). A reach trial began with subjects grasping the robot manipulandum with a comfortable but firm grip. The robot was positioned at a home position located about 20 cm in front of subjects' chests and aligned with their midline. In contrast to the proprioceptive estimate trials discussed in the following text, the home position was not illuminated in the reach trials. After maintain-

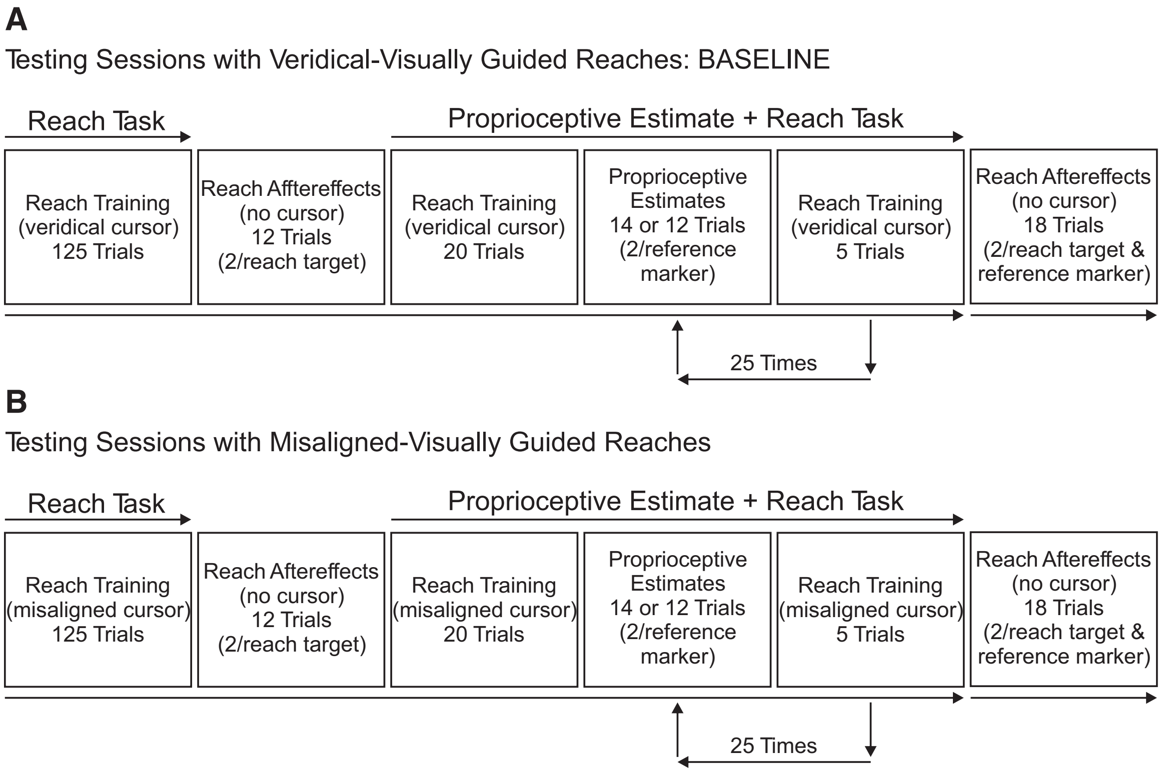

FIG. 2. Breakdown of the testing sessions within each experiment. *A*: testing session(s) run during the first half of each experiment, which provided baseline measures of performance. Subjects began a testing session by reaching to visual targets while a cursor accurately represented the location of their hands (box 1). After completing 125 visually guided reach trials, subjects next reached to each of the 6 reach targets twice without a cursor, to assess visuomotor adaptation (reach aftereffect trials, box 2). Subjects then completed 20 reaches to the reach targets with the cursor present (box 3). This was followed by 25 sets of either 14 (*experiments* 1 and 2) or 12 (*experiments* 3 and 4) proprioceptive estimates (box 4) and 5 visually guided reaches (box 5). After completing the proprioceptive estimate + reach task, subjects completed 18 reaches without the cursor, 2 reaches to all 9 target/reference-marker positions (box 6). *B*: testing session(s) run during the second half of the experiment, where the cursor was misaligned from the actual hand location during the visually guided reaching trials (boxes 1, 3, and 5). In *experiments* 1 and 3, the cursor was shifted 4 cm rightward with respect to the hand, whereas in *experiments* 2 and 4, the cursor was rotated 30° CW with respect to the hand. In *experiments* 1 and 2, subjects completed 2 testing sessions when the cursor was veridical and 2 testing sessions when it was misaligned with respect to the actual hand location. In *experiments* 3 and 4, subjects completed one testing session when the veridical cursor was presented during reach training and one when a misaligned cursor was displayed during reach training.

ing the hand at the home position for 300 ms, one of the six reach targets would appear. Subjects were instructed to move as quickly and accurately as possible to the target while gripping the handle of the free-moving robot manipulandum. The position of the unseen hand was represented by a cursor (1-cm green disk, shown in Fig. 1*C*) and appeared as soon as the robot handle had moved 4 cm outward from the home position. The reach was considered complete when the center of the cursor had moved to within 0.5 cm of the target's center. At that point, both the target and cursor were removed and the robot was locked to a grooved path. This grooved path guided subjects back to the home position by a direct linear route in the absence of visual feedback. If subjects attempted to move outside of the established path, a resistance force [proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s)] was generated perpendicular to the grooved wall (Henriques and Soechting 2003).

The order of the reach trials was pseudorandomized such that subjects reached once to five of the reach targets, specifically the four peripheral targets and one of the pair of pericentral (0.9 cm) targets, before any target was repeated. Thus although subjects never reached to a central target in this task, for each set of five reaches they did move their hand to a near-central location. Subjects completed 125 reach trials.

REACH AFTEREFFECTS. After completing the reach training task, subjects immediately completed 12 aiming movements, 2 reaches to each of the 6 reach targets, without the cursor (second box in Fig. 2*A*). These reach aftereffect trials were included to measure errors in subjects' reaches and establish that subjects had adapted their reaches in response to the misaligned cursor in testing sessions 3 and 4 (i.e., visuomotor adaptation). 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.

PROPRIOCEPTIVE ESTIMATE + REACH TASK. Subjects were provided with the opportunity to take a short break before beginning the following task. The majority of subjects opted to begin the proprioceptive estimate + reach task immediately after the reach aftereffect trials. In this task, proprioceptive estimates and reach trials (boxes 3–5 in Fig. 2*A*) were systematically interleaved. Subjects began by completing an additional 20 reaching trials with a veridical cursor (box 3). These reaches were then immediately followed by interleaving sets of 14 proprioceptive estimate trials (box 4) and 5 reaching trials (box 5). The test sequence of 14 proprioceptive estimates followed by 5 reaches was completed 25 times, for a total of 475 trials [350 proprioceptive estimate trials (50 at each target) + 125 reach trials].

In the proprioceptive estimate trials (box 4 in Fig. 2*A*), we determined the position at which subjects perceived their unseen hand was aligned with the seven reference markers. A proprioceptive estimate trial began with subjects grasping the robot manipulandum that was positioned at the home position. The position of the hand was indicated by displaying a 1 cm diameter green circle directly above the robot for 500 ms (Fig. 1*B*, green circle). After 500 ms the home position reference was removed and the hand was passively moved outward, such that the robot positioned the hand somewhere along the dashed black lines shown in Fig. 1*B*. The robot moved the hand with a bell-shaped velocity profile such that an average speed of 30 cm/s was achieved. All movements took 400 ms to complete. Once the hand reached its final position (i.e., was within 0.5 cm of the desired location), a reference marker appeared. Subjects then made a two-alternative forced-choice judgment about the position of their hand, indicating whether their hand was left or right of the reference marker. There were no time constraints during the task and subjects were encouraged to take as long as they needed before pressing a left or right key to indicate whether they felt their hand was to the left or to the right of the reference marker, respectively. After entering a response, the reference marker disappeared and the robot moved the hand directly back to the home position.

We ran separate sessions (sessions 1 and 2), in counterbalanced order across subjects, when the center reference marker was proprioceptive and visual (first two rows of Table 1). On trials in which the proprioceptive reference marker was presented, a subject's hand moved outward like all other trials. However, once the hand achieved its final position, instead of a visual reference marker appearing, a beep sounded and subjects indicated whether their hand was to the left or right of their body midline. On trials in which the 0 cm central reference marker was visual, subjects were not made aware that the reference marker was located directly in front of their midline.

Hand positioning. The position of the hand with respect to each reference marker was adjusted over trials using an adaptive staircase algorithm (Kesten 1958; Treutwein 1995). For each reference marker there were two corresponding staircases, a left and a right, that were adjusted independently and randomly interleaved. Each staircase began such that the hand was 3 cm to the left or right of the reference marker. The position of the hand was then adjusted over trials depending on subjects' pattern of responses, such that the differences between hand locations in subsequent trials (step size) decreased each time subjects reversed their response pattern from left to right or from right to left within a particular staircase. This ensured that subjects were tested more frequently at positions closer to their sensitivity threshold. If subjects responded consistently, the two staircases converged toward a certain position at which subjects had an equal probability of reporting left or right. This position represented the location at which subjects perceived their hand was aligned with the reference marker.

REACH AFTEREFFECTS. Immediately after completing the proprioceptive estimate + reach task, subjects completed 18 final reach aftereffect trials without the cursor (sixth box in Fig. 2*A*). These were carried out in a manner similar to that of the previous 12 reach aftereffect trials (second box) but now all 9 reach target and reference marker positions were presented visually and subjects had to reach to each target twice. Each experimental session was approximately 1.5 h in length.

Sessions 3 and 4: reach training with misaligned cursor

In these testing sessions, the cursor was translated 4 cm rightward with respect to the actual hand location in the reach training task. In all other aspects, sessions 3 and 4 (Fig. 2*B*) were the same as testing sessions 1 and 2 (Fig. 2*A*), respectively. To ensure that subjects were unaware of the visuomotor distortion, the visuomotor distortion was gradually introduced over the first 41 reach training trials. This was done by shifting the start position of the hand 1.0 mm leftward every trial, as shown in Fig. 1*C*. In other words, after each reaching trial, the groove that guided the subject's hand back to the start position was gradually altered so that the hand was returned to a location more left of body midline and the start location of the cursor. Shifting the start position of the hand, as opposed to the cursor, ensured that visual feedback during the reach trials appeared to come from a constant center location.

Experiment 2: passive rotation

STIMULUS DISPLAY. *Reach targets.* The reach targets were located radially, 10 cm from the home position at 5, 30, and 60° counterclockwise (CCW) and CW of center (red open circles in Fig. 1*D*).

Proprioceptive reference markers. The alignment reference markers were also located radially, along an arc 10 cm from the home position (yellow circles in Fig. 1*D*). The 0° center reference marker was in the exact same position as the 0 cm reference marker from *experiment* 1 and represented visually or proprioceptively. Additional visual reference markers were located 60, 45, and 30° CCW and CW of the 0° reference marker. The markers located 30° from the 0° reference marker were at the same positions as those of the 5 cm reference markers in *experiment* 1.

TESTING SESSIONS. The testing sessions were carried out in a manner similar to that of *experiment* 1 (Fig. 2 and Table 1). Differences between the two experiments included target and reference-marker location, the starting position of the hand with respect to the reference markers in the proprioceptive estimate trials (20°), and the visuomotor distortion introduced during the misaligned reach training trials. In this experiment, the cursor representing hand position in the misaligned reach training trials was gradually rotated 30° CW with respect to the hand over the first 41 trials, in increments of 0.75° (Fig. 1*E*). The distortions introduced in the two experiments were chosen in particular because the 4-cm shift in the translated-reach training task corresponds to the average horizontal shift achieved across our workspace when the cursor was rotated 30°.

Experiment 3: active translation

In this experiment and *experiment* 4 (described in the following text), we wanted to examine whether proprioceptive recalibration would occur when subjects actively positioned their hand in the proprioceptive estimate trials. In contrast to the first two experiments, subjects were instructed to push their hand out after the green home position was removed in the proprioceptive estimate trials. When subjects initiated their movements, they were immediately forced into a robot-generated path as described earlier. This path guided the hand to somewhere along the dashed lines shown in Fig. 1*B*.

Another minor change from *experiment* 1 included decreasing the number of testing sessions to two, one involving training with the veridical cursor (Fig. 2*A*) and one with a translated cursor (Fig. 2*B*). This was accomplished by having both the visual and proprioceptive center reference markers included within the same testing session and decreasing the number of visual reference markers at which we assessed proprioceptive recalibration. Specifically, in the first half of the proprioceptive estimate + reach task the 0 cm proprioceptive central reference marker was presented, whereas in the second half the 0 cm visual central reference marker was displayed. Proprioceptive recalibration was not assessed at the most peripheral reference markers (10 cm left and right of center). Thus 12 proprioceptive estimate trials were interspersed with the 5 reach trials in the proprioceptive estimate + reach task. In all other aspects, this experiment was the same as *experiment* 1.

Experiment 4: active rotation

In this experiment, we modified *experiment* 2 such that subjects actively positioned their hand during the proprioceptive estimate trials, subjects completed only two testing sessions, and proprioceptive recalibration was not assessed at the most peripheral reference markers (60° CCW and CW from center).

Data analyses

REACH ERRORS. We analyzed reaching errors (i.e., aftereffects) made in the reach aftereffect trials to determine whether *1*) subjects adapted their reaches to the reach targets after aiming with a misaligned cursor, *2*) reach adaptation was maintained across the proprioceptive estimate + reach tasks, and *3*) reach adaptation generalized across the workspace to novel targets. Reach errors were defined as the lateral (*experiments* 1 and 3) or angular differences (*experiments* 2 and 4) between a movement vector (from the home position to reach endpoint) and a reference vector (joining the center home position and the target). To determine whether subjects had indeed adapted their reaches following exposure to a misaligned cursor and whether this adaptation was maintained, we analyzed mean aftereffects in a two visual feedback during training (i.e., after training with a veridical cursor vs. a misaligned cursor) × 2 time (where the trials were completed after the reach training task vs. the proprioceptive estimate + reach task) repeated-measures (RM) ANOVA, for each experiment. In other words, we compared boxes 2 and 6 in Fig. 2*A* with boxes 2 and 6 in Fig. 2*B*.

After establishing that subjects had adapted their reaches to the reach targets after training with a misaligned cursor, we then examined whether this adaptation generalized across the workspace. To do this, we compared aftereffects to the trained reach targets with those made to the novel targets in a one-way RM-ANOVA. In this analysis, reach errors after training with a veridical cursor (box 6 in Fig. 2*A*) were subtracted from reach errors after exposure to a misaligned cursor (box 6 in Fig. 2*B*).

PROPRIOCEPTIVE ESTIMATES OF HAND POSITION. To determine the locations at which subjects felt their hand was aligned with the reference markers, we fitted a logistic function to each subject's responses for each reference marker in each testing session (the fourth boxes in Fig. 2). An example of this is shown for a representative subject in Fig. 3. Based on each logistic function, we then calculated the bias (the point of 50% probability, represented as circles in Fig. 3) and uncertainty (the difference between the values at which the response probability was 25 and 75%; shaded region in Fig. 3). Bias is a measure of the accuracy of hand-reference marker alignment and the magnitude of the uncertainty range defines its precision. 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 within an experiment + 2SDs. Based on this analysis, $<4\%$ of all hand-reference marker estimates were excluded.

To determine whether proprioceptive estimates of hand position were altered after reaching with misaligned visual feedback of the hand, we compared biases and the uncertainty ranges across the veridical and misaligned testing sessions using a RM-ANOVA. Additional factors in the ANOVA included *1*) reference-marker location and *2*) the modality of the center reference marker. In *experiments* 1 and 2, we also included the between-subjects factor of testing order (i.e., visual vs. proprioceptive reference marker displayed in testing sessions 1 and 3).

Finally, we examined changes in proprioceptive biases across the four experiments. To do this, we first found the mean difference in bias after subjects reached with a misaligned cursor compared with a veridical cursor during reach training for each subject in each experiment. Only biases related to the six common reference-marker positions were included (i.e., the reference markers from *experiment* 3 or *experiment* 4). For the passive *experiments* 1 and 2, in which subjects completed the proprioceptive estimate task twice for each reach training condition, we used the biases for the peripheral reference markers from the proprioceptive estimate task when the center reference marker was proprioceptive. We then performed an ANOVA on these mean differences in bias.

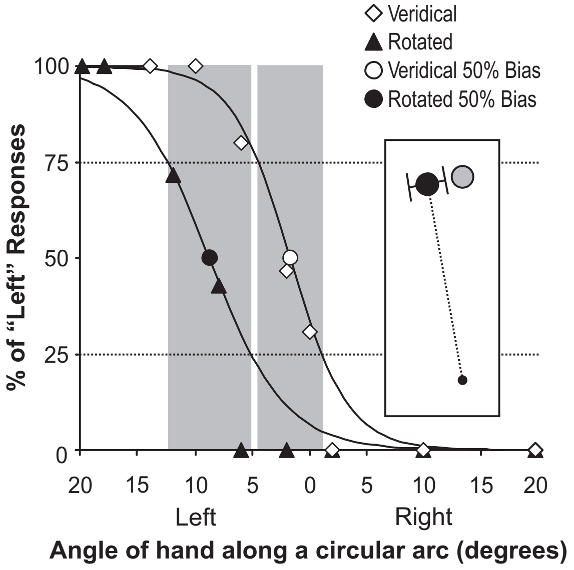

FIG. 3. Percentage of left responses for a single subject when the 0° visual reference marker was displayed in the proprioceptive estimate + reach tasks after the subject trained with a veridical cursor (diamonds) and rotated cursor (filled triangles). Symbols represent the mean percentage of responses by which the subject reported the hand was left of the visual reference marker across various hand angle positions (left or right of the 0° visual reference marker). To determine the angle at which subjects perceived their hand was aligned with the reference marker, we used an adaptive staircase procedure. Subjects reported if they were left or right of the reference marker and then based on their pattern of responses the position of their hands was adjusted over trials. We then fit a logistic function to the responses to define bias and uncertainty, where bias is the probability of reporting left or right equally often (50%, indicated by the 2 filled circles) and uncertainty is the difference between the values at which the response probability was 25 and 75% (region indicated by the shaded rectangles). From this figure we see that the position at which the subject perceived the hand was aligned with the reference marker was shifted leftward after reaching with a rotated cursor. This is also illustrated in the *inset*, which displays the reference marker position at 0° (gray circle) and the bias (black circle) after reaching with the rotated cursor.

All ANOVA results are reported with Greenhouse–Geisser corrected P values. Differences with a probability of <0.05 were considered to be significant. Tukey's honestly significant difference post hoc tests were administered to determine the locus of these differences (alpha = 0.05).

RESULTS

Visuomotor adaptation

Mean reaching endpoint errors (i.e., aftereffects) for trials completed to trained and novel targets without a cursor are displayed in Fig. 4 for each of the four experiments. In Fig. 4*A* we see that mean endpoint errors for the trained targets in *experiment* 1 (filled black bars) and *experiment* 3 (white bars) after training with translated visual feedback of the hand were on average 3.4 cm more to the left of the target than that after training with a veridical cursor. Thus subjects adapted their reaches in response to training with the translated cursor [*experiment* 1: $F(1,10) = 313.225$, $P < 0.001$; *experiment* 3: $F(1,9) = 212.82$, $P < 0.001$]. Furthermore, the size of reach aftereffects did not diminish between reaches completed after the reach training task (Fig. 4*A*, *left bars*) compared with reaches completed after the proprioceptive estimate + reach

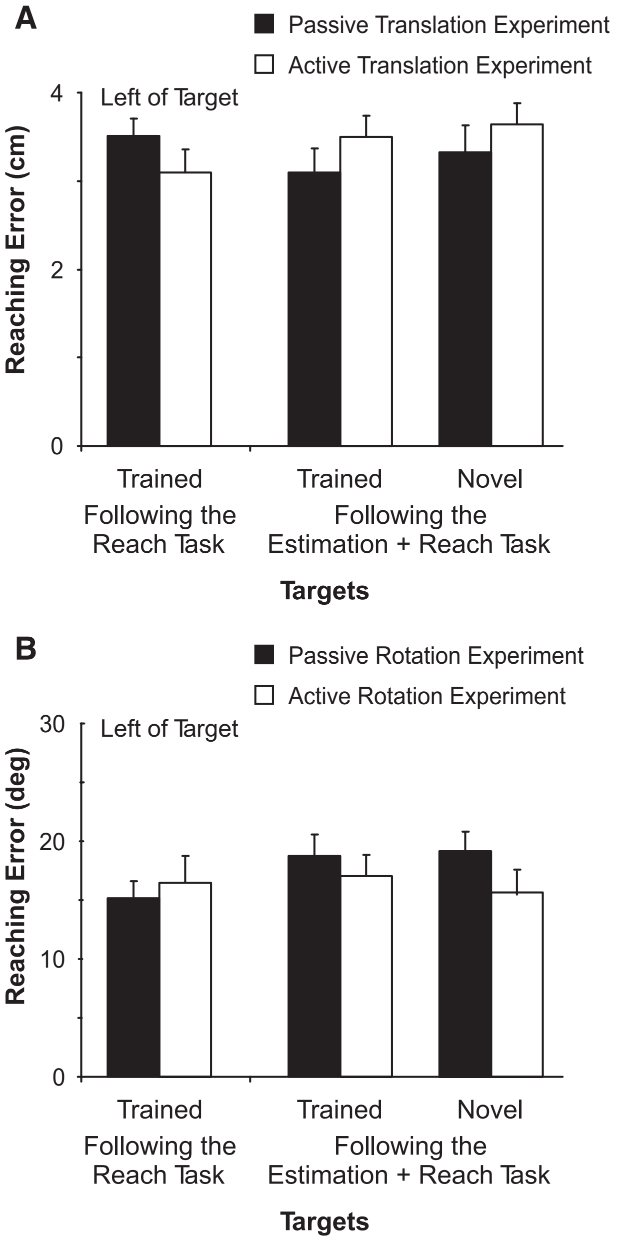

FIG. 4. Reach aftereffects after training with a translated (*A*) or rotated (*B*) cursor. Mean reaching errors are provided in cm (*experiments* 1 and 3) or degrees (*experiments* 2 and 4) at movement endpoint for the reach aftereffect trials in which subjects aimed with no cursor are plotted for the trained and novel targets. Subjects reached to the trained targets following the reach training task and the proprioceptive estimate + reach task, whereas the novel targets were only reached to following the proprioceptive estimate + reach task. Errors are presented taking performance on reaches completed after the veridical–visual reach task as baseline (i.e., the errors achieved on reach aftereffect trials after training with a veridical cursor are subtracted from corresponding errors achieved after reaching with a misaligned cursor). Performance in the passive experiments (*experiment* 1 and 2) are shown by the filled black bars and performance in the active experiments (*experiment* 3 and 4) are indicated by the white bars. Error bars reflect SE.

task (*middle bars*) [*experiment* 1: $F(1,10) < 1$; *experiment* 3: $F(1,9) < 1$]. This suggests that the level of adaptation was maintained across the tasks. Finally, as illustrated by the final set of bars in Fig. 4, reach errors generalized across the workspace and the aftereffects observed at the novel targets were similar in magnitude to the aftereffects at the trained targets [*experiment* 1: $F(1,10) = 3.483$, $P = 0.092$; *experiment* 3: $F(1,9) < 1$]. Taken together these results indicate that subjects adapted their reaches to all targets after aiming with a translated cursor, even those for which they had not trained.

The aftereffects plotted in Fig. 4*B* show that subjects also adapted their reaches in *experiments* 2 and 4, after aiming with a rotated cursor. In both *experiment* 2 and *experiment* 4, subjects' reaches without a cursor deviated on average by 18° CCW for the trained targets, indicating that their reaches had been adapted [*experiment* 2: $F(1,15) = 147.877$, $P < 0.001$; *experiment* 4: $F(1,9) = 119.796$, $P < 0.001$]. These aftereffects were maintained across tasks and in fact in *experiment* 2, the aftereffects were about 4.5° greater following the proprioceptive estimate + reach task than those after the reach training task [$F(1,15) = 9.291$, $P = 0.008$]. In *experiment* 4, there was no difference in aftereffects across these two tasks [$F(1,9) = 1.752$, $P = 0.218$]. Finally, visuomotor adaptation generalized across the workspace to novel, nontrained targets [*experiment* 2: $F(1,15) < 1$; *experiment* 4: $F(1,9) = 4.044$, $P = 0.075$].

Proprioceptive recalibration

BIAS. In Fig. 5 we display the positions at which subjects perceived their hand was aligned with the reference markers (gray circles) after training with both a veridical (diamonds) and misaligned (filled triangles) cursor. On average, subjects shifted the position at which they felt their hand was aligned with a reference marker leftward after training with a misaligned cursor. Specifically we see that in the passive translation experiment (Fig. 5*A*; see also Fig. 6*A*), subjects' estimates of their unseen hand positions were fairly accurate after training with a veridical cursor, especially for reference markers located to the right of center. On average, the mean bias across all reference markers was 0.95 cm left of the reference marker. However, after visuomotor adaptation, proprioceptive estimates of hand position relative to the reference markers were shifted significantly to the left of the veridical estimates [$F(1,9) = 53.172$, $P < 0.001$]. Mean bias after reach training to reach with a translated cursor was 2.93 cm left of a given reference marker (black bar in Fig. 6*A*). This estimate was about 2 cm more left than that after training with a veridical cursor (white vs. black bar in Fig. 6*A*) and was in the direction of visuomotor adaptation. Furthermore, changes in hand-reference marker alignment estimates were observed at all reference markers [$F(6,54) = 1.005$, $P = 0.373$], regardless of whether the center reference marker was proprioceptive or visual [$F(1,9) = 2.338$, $P = 0.161$].

Similar shifts in proprioceptive estimates of hand location were also found after subjects adapted their reaches to a rotated cursor. For example, we see in Fig. 5*B* (see also Fig. 6*B*) that adapting one's reaches to a rotated cursor shifted the position at which subjects perceived the hand was aligned with the reference markers more CCW compared with training with a veridical cursor [$F(1,14) = 18.74$, $P = 0.001$]. On average subjects' biases were shifted 6.6° in the CCW direction after reaching with a misaligned cursor. Subjects' shifted their hand-reference marker alignment estimates at all reference marker positions [$F(6,84) < 1$], regardless of the modality of the center reference marker [$F(1,14) = 3.133$, $P = 0.099$].

Proprioceptive sense of the hand was also recalibrated when the hand was actively positioned. Specifically, in the active

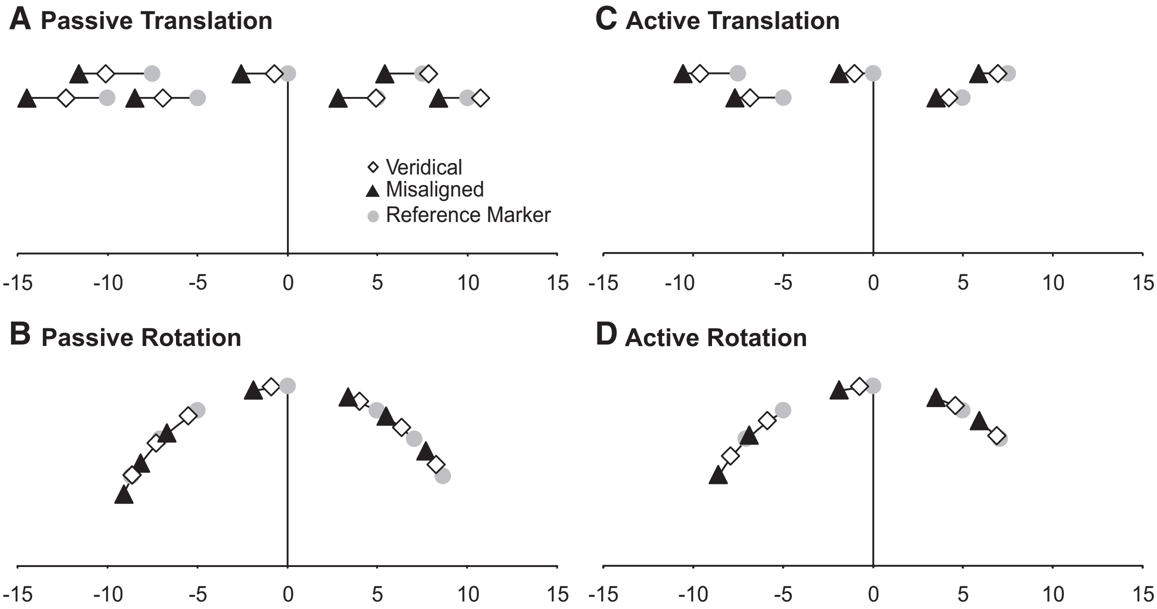

FIG. 5. Mean 2-dimensional (2-D) biases in the proprioceptive estimate tasks after subjects trained with a veridical (diamonds) or misaligned (filled triangles) cursor for (*A*) *experiment* 1: passive translation, (*B*) *experiment* 2: passive rotation, (*C*) *experiment* 3: active translation, and (*D*) *experiment* 4: active rotation. The actual reference-marker positions are represented as filled gray circles and a line connects each reference marker with its corresponding hand-reference marker alignment estimates. Since the influence of visuomotor adaptation on hand-reference marker alignment was the same, irrespective of whether the center reference marker was visual or proprioceptive in *experiments* 1 and 2, results are collapsed across testing sessions with similar visual feedback during reach training (i.e., veridical cursor or misaligned cursor). For all experiments, the mean bias represented at the 0° and 0 cm reference markers represents the average bias achieved when the center reference marker was both visual and proprioceptive.

translation experiment (see Figs. 5*C* and 6*C*), we once again observed a more leftward bias in the positions at which subjects perceived their unseen hand was aligned with the reference markers after training with a translated cursor compared with a veridical cursor [$F(1,9) = 8.958, P < 0.015$]. This shift in sense of hand position was similar across all reference-marker positions [$F(5,45) < 1$]. The mean bias after training with a translated cursor was 2.1 cm left of the marker compared with a mean bias of 1.2 cm after aiming with a veridical cursor.

Figures 5*D* and 6*D* show the results obtained in the active rotation experiment. Similar to the previous experiments, we observe that estimates of hand-reference marker alignment were once again shifted to CCW (or leftward) after subjects adapted their reaches to a rotated cursor [$F(1,9) = 29.418, P < 0.001$]. The mean bias, relative to the reference marker, after adaptation was 11.2° CCW of the reference marker compared with a mean bias of 4.4° CCW of the reference marker after aiming with a veridical cursor. This change in hand-reference marker alignment was of a similar magnitude at all reference-marker positions [$F(5,45) < 1$].

UNCERTAINTY RANGE. Figure 7 displays the magnitude of the uncertainty ranges averaged across all reference markers for the various testing sessions within each experiment. In the passive translation experiment (Fig. 7*A*), subjects' levels of precision in estimating the location of their unseen hand were similar after reach training with a veridical (white bar) and misaligned cursor (black bar) [$F(1,9) < 1$], regardless of the modality of the center reference marker [$F(1,9) < 1$] or reference-marker location [$F(6,54) = 2.055, P = 0.117$]. Likewise, in the passive rotation experiment (Fig. 7*B*), uncertainty was similar regardless of whether subjects performed the proprioceptive estimation trials after reaching to targets with a veridical or rotated cursor [$F(1,14) = 2.151, P = 0.165$]. Although uncertainty did vary with reference-marker position [$F(6,84) = 2.435, P = 0.049$], post hoc analyses failed to determine the locus of this effect. Furthermore, and importantly, this difference in uncertainty was the same whether these proprioceptive estimates of hand position were made after training with a veridical or rotated cursor [$F(6,84) = 1.094, P = 0.367$]. We found that levels of precision were also maintained or even improved following visuomotor adaptation in the active hand-placement experiments. Specifically, subjects' levels of precision were similar after training with a veridical and misaligned cursor [$F(1,9) < 1$], at all reference-marker positions [$F(5,45) = 1.979, P = 0.134$] in the active translation experiment (Fig. 7*C*). Finally, we found that subjects were slightly more precise (1.3° more precise) after training with a rotated cursor compared with the veridical cursor [$F(1,9) = 7.124, P = 0.026$] in the active rotation experiment (Fig. 7*D*).

Proprioceptive calibration

PASSIVE VERSUS ACTIVE HAND-PLACEMENT TASKS. In addition to addressing our question of interest, our results speak to how well one is able to localize the hand. For example, if we examine subjects' proprioceptive estimates after training with a veridical cursor (white bars in Fig. 6), we find some interesting results. In three of the four experiments, subjects had a slight leftward (or CCW) bias in estimating the location of the hand relative to the reference markers after training with a veridical cursor (passive translation experiment: $P = 0.006$; active translation experiment: $P = 0.014$; active rotation experiment: $P = 0.045$). Subjects' estimates did not differ from the reference-marker location in the passive rotation experiment ($P = 0.12$). The magnitudes of these leftward biases were

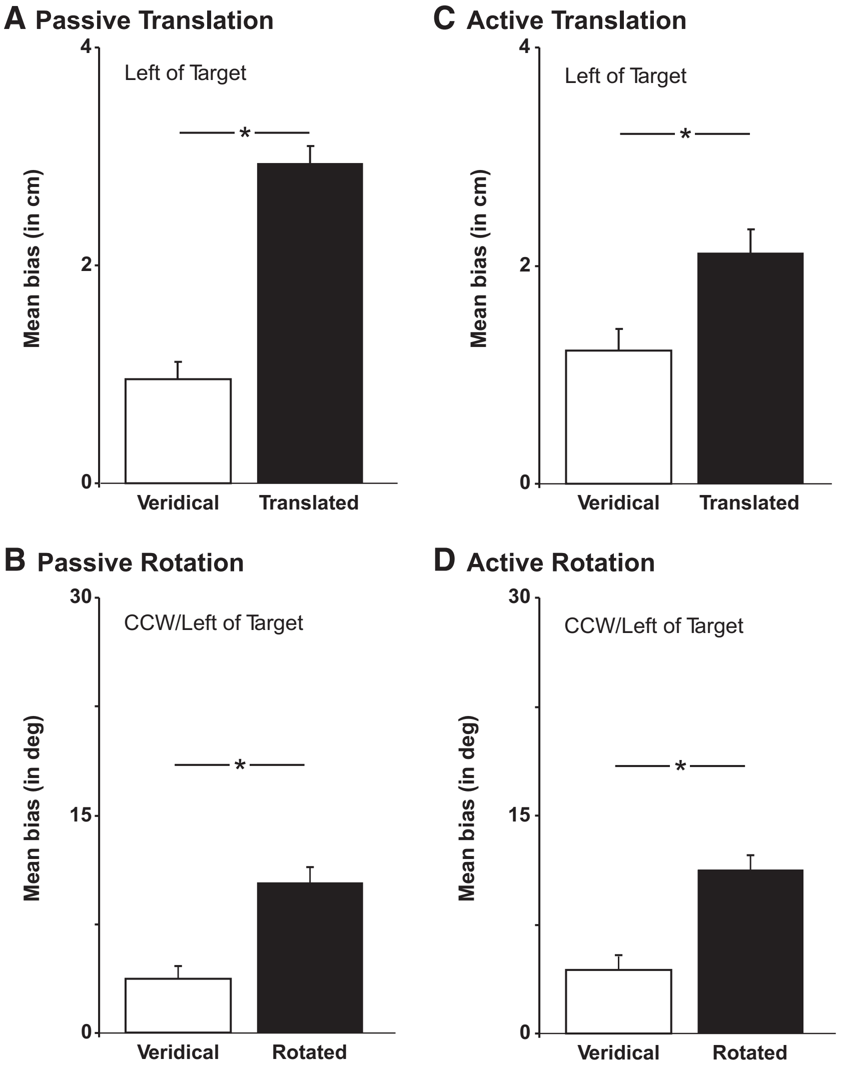

FIG. 6. Biases in the proprioceptive estimate tasks averaged across subjects and reference marker positions following reach training with a veridical cursor (white bars) or with a misaligned cursor (blacks bars) for (*A*) *experiment* 1: passive translation, (*B*) *experiment* 2: passive rotation, (*C*) *experiment* 3: active translation, and (*D*) *experiment* 4: active rotation. Error bars reflect SE and the asterisks indicate values showing significant differences ($P < 0.05$).

similar, regardless of whether the robot passively positioned the hand or subjects actively moved the hand into position. Specifically, there was no difference between the biases achieved in *experiment* 1, when the robot passively moved the hand into position, compared with *experiment* 3, when subjects actively moved the hand ($P = 0.57$). This similarity for active versus passive biases was also found when comparing the proprioceptive biases in *experiments* 2 and 4 ($P = 0.84$). Finally, there was no difference in precision after subjects passively positioned their hand after training with a veridical cursor compared with when they actively positioned their hand when the reference markers were arranged along an arc (*experiments* 2 and 4: white bars in Fig. 7, *B* and *D*, $P = 0.24$). Subjects were slightly more precise after actively positioning their hand compared with passively positioning their hand when the reference markers were arranged linearly (*experiments* 1 and 3: white bars in Fig. 7, *A* and *C*, $P = 0.04$).

Visuomotor adaptation versus proprioceptive recalibration

In Fig. 8 we show the changes in proprioceptive estimates after training with a misaligned cursor compared with a veridical cursor in relation to the level of visuomotor adaptation achieved. Both the changes in proprioceptive bias and visuomotor adaptation are expressed as a percentage of the distortion introduced during the reach training trials (e.g., 4-cm translation or 30° rotation). In Fig. 8*A* we show the mean changes in proprioceptive estimates averaged across subjects in each of the four experiments. The left bars show changes in proprioceptive biases after subjects trained with a translated cursor during the reach training task, whereas the right bars show changes in bias after subjects aimed with a rotated cursor during the reach training task. The black bars represent changes in bias when the hand was passively positioned and the white bars reflect changes when the hand was actively positioned. In general, subjects shifted the position at which they perceived their hand was aligned with the reference markers leftwards after adapting to misaligned visual feedback of the hand by roughly 25% of the visual distortion introduced. The magnitude of proprioceptive recalibration was similar across the four experiments [$F(3,43) = 2.014$, $P = 0.126$], despite the different visuomotor distortions introduced during reach training and the differences in how the hand was positioned.

On average, subjects recalibrated proprioception by 25% and adapted their reaches by 69% of the visual distortion

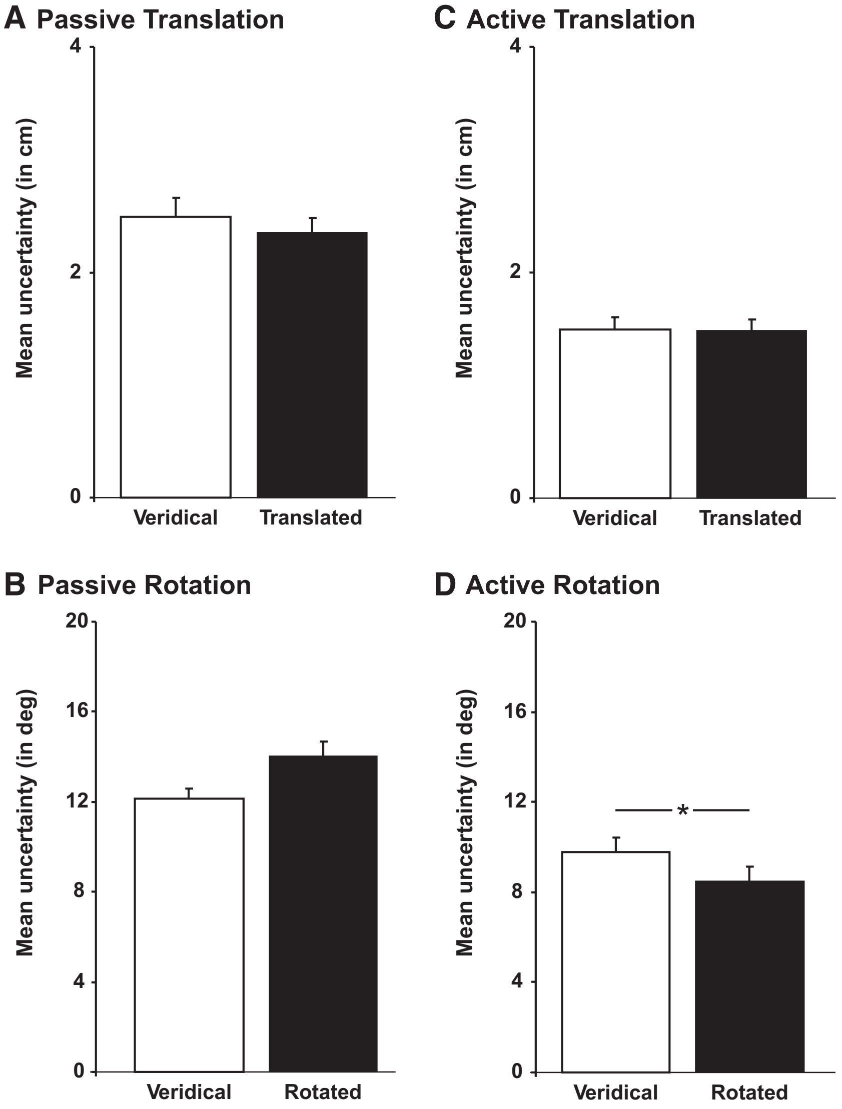

FIG. 7. Magnitude of the uncertainty ranges in the proprioceptive estimate tasks averaged across reference-marker positions and subjects following reach training with a veridical cursor (white bars) or with a misaligned cursor (black bars) for (*A*) *experiment* 1: passive translation, (*B*) *experiment* 2: passive rotation, (*C*) *experiment* 3: active translation, and (*D*) *experiment* 4: active rotation. Error bars reflect SE and the asterisks indicate values showing significant differences ($P < 0.05$).

introduced. In Fig. 8*B* we plot these changes in proprioceptive estimates as a function of visuomotor adaptation (i.e., changes in the mean reach aftereffects) for each subject in each experiment. From this figure we see that *1*) almost all subjects recalibrated proprioception to some extent; *2*) in all but one instance proprioceptive recalibration was less than visuomotor adaptation; and *3*) the magnitude of proprioceptive recalibration was similar regardless of the level of visuomotor adaptation obtained. In accordance with this last observation, analysis did not reveal any significant correlations between the magnitude of proprioceptive recalibration and the level of visuomotor adaptation achieved in the four experiments ($P > 0.05$).

DISCUSSION

The goal of the present study was to determine whether learning to reach with misaligned visual feedback of the hand leads to sensory recalibration. In other words, do subjects begin to feel their hand is at the same position at which they see a cursor representing their hand during visuomotor adaptation paradigms? To address this question, we determined the position at which subjects perceived their hands were aligned with a reference marker after adapting their reaches in response to a translated or rotated cursor. Our alignment tasks involved subjects indicating the position of their hand after the hand was either passively moved by a robot manipulandum or subjects actively pushed the robot out along a constrained path. Thus in contrast to previous studies, we examined sensory recalibration under conditions in which subjects could not evoke the newly formed sensorimotor transformations to produce an adapted movement. Specifically, in both the passive and active experiments, subjects could not plan or execute a self-generated movement in a particular direction. We found that regardless of experimental manipulation, subjects shifted the position at which they felt their hands were aligned with a reference marker leftward after training with a misaligned cursor relative to their estimates after training with a veridical cursor. This change in hand-reference marker alignment bias was in the same direction as subjects adapted their reaches during the reach training and was a quarter of the magnitude of the visuomotor distortion introduced (or, approximately one third of the magnitude of the reach aftereffects observed). This suggests that subjects partially recalibrated proprioception with the visual information provided during the

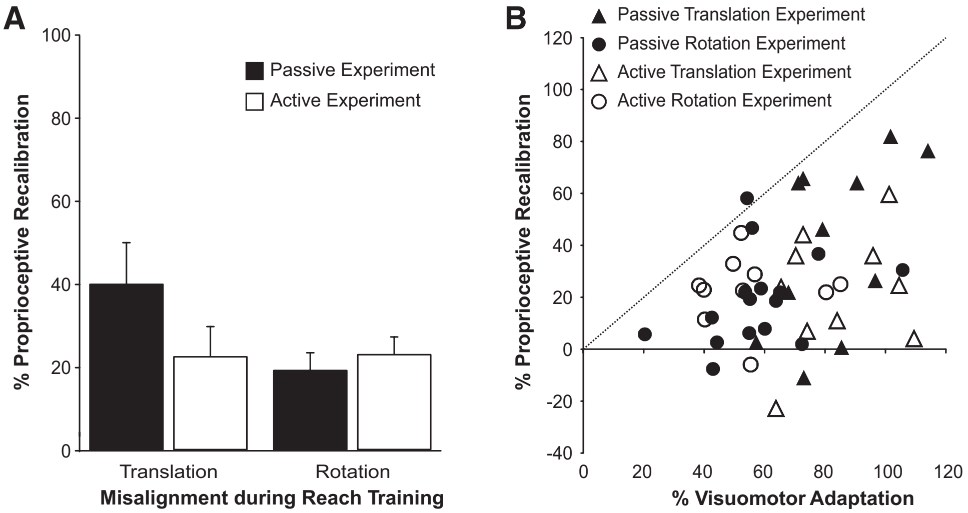

FIG. 8. The changes in proprioceptive estimates after reaching with a misaligned cursor compared with a veridical cursor for each of the 4 experiments. Differences are expressed as a percentage of the visual distortion introduced during the misaligned reaching training task. *A*: the percentage of proprioceptive recalibration averaged over subjects for each experiment. The *left bars* represent results achieved in *experiments* 1 and 3, in which the cursor was translated with respect to the hand during the misaligned reach training sessions; the *right bars* represent results from *experiments* 2 and 4, in which the cursor was rotated with respect to the hand during the misaligned reach training sessions. The results of the passive *experiments* 1 and 2 are shown by the black bars and the results of the active *experiments* 3 and 4 are shown by the white bars. Error bars reflect SE. *B*: the change in sense of hand position is shown for each subject in each experiment as a function of the changes in reach aftereffects resulting from visuomotor adaptation (*experiment* 1: passive translation = filled triangles; *experiment* 2: passive rotation = filled circles; *experiment* 3: active translation = unfilled triangles; *experiment* 4: active rotation = unfilled circles). The dotted line is a unit slope and so indicates equivalent levels of proprioceptive recalibration and visuomotor adaptation.

reach training such that they began to feel their hand was shifted in the direction at which they saw it.

Proprioceptive recalibration

There is currently some debate in the literature regarding how visual and proprioceptive signals are integrated and/or calibrated. For example, Smeets and colleagues (2006) recently proposed that visual and proprioceptive signals are not aligned (i.e., not mutually calibrated). Instead, the unaligned sensory signals are integrated in an optimal manner when one has to reach to a target (van Beers et al. 1996, 1998). In their task (Smeets et al. 2006), subjects reached to visual targets in blocks of trials that alternated in terms of whether visual feedback of the hand was available. Reaching endpoints indicated that whenever vision was removed, reach errors drifted in a predictable manner to the same position as that of the previous block of no vision trials. Because seeing one's hand during reaching trials did not lead to changes in reaching movements in the no vision trials, Smeets et al. (2006) put forth that visual and proprioceptive signals are not calibrated.

At first glance our results appear to contradict Smeets and colleagues' proposal. However, it is important to note that, unlike our experiments, Smeets et al. (2006) did not introduce a distortion between the visual and proprioceptive signals during their visually guided reach training trials. According to Redding and Wallace (1996, 1997), for recalibration between vision and proprioception to occur, the two signals must be misaligned. In agreement with this proposal and similar to the suggestions of Smeets and colleagues, we find no difference when we compare our proprioceptive biases produced after subjects trained with veridical visual feedback of the hand to biases achieved in a related study from our lab in which subjects did not perform any reach training. In our previous study (Jones et al. 2009), subjects completed only the proprioceptive estimate trials. Their biases were similar to those of our subjects who had the opportunity to first perform a reach training task while a cursor accurately represented the location of their hand ($P > 0.05$). Thus our assertion of proprioceptive recalibration following misaligned reach training does not contradict Smeets and colleagues (2006). Instead, as put forth by Redding and Wallace (1996, 1997), our results suggest that if there is no discrepancy between visual and proprioceptive signals, there is no recalibration of proprioception. On the other hand, when there is a discrepancy between sensory signals, one recalibrates proprioception such that the felt position of the hand is shifted in the direction of the visual feedback.

Influence of visuomotor distortion and hand placement on proprioceptive recalibration

Previous work using perceptual tasks to assess proprioceptive recalibration has given rise to contradictory results. For example, a study by Malfait et al. (2008) reported that proprioception was recalibrated following visuomotor adaptation. Subjects in that study tracked a moving target around a square using a robot manipulandum. Visual feedback of hand position was provided at the two left corners of the square and was *translated* 5 cm left relative to the actual hand location. Thus to guide the visual representation around the square object, subjects would have had to trace a rectangular path. After adapting their reaching movements, subjects performed a perceptual task in which they were asked to compare the path drawn by a cursor to the path of *passive* hand displacement. Subjects reported that passive hand paths that followed the edges of a narrow rectangle matched the visual square, suggesting that in addition to recalibrating their reaches, proprioception was also recalibrated to the visual feedback. In contrast to the findings reported by Malfait and colleagues (2008), Wong and Henriques (2009) found no evidence of proprioception recalibration when subjects had to make judgments regarding the geometry of their unseen hand path. In their study, subjects were exposed to a *rotated* cursor and *actively* pushed the robot into position during the proprioceptive estimation trials. Specifically, subjects learned to reach *1*) 30° CW or CCW of a target to guide a cursor to the target (similar to our *experiments* 2 and 4) or *2*) with a curved hand path to make a cursor move in a straight line. After adapting to the visuomotor distortion, subjects were asked to indicate the directional tilt of the constrained path that the actively moved hand had just traversed or the curvature of the path.

In the current study, we manipulated the visuomotor distortion introduced and how the hand was positioned, to determine which, if any of these two factors, could account for the differences discussed earlier. As shown in Fig. 8, we found that proprioception was recalibrated in all four experiments. Furthermore, the level of proprioceptive recalibration was similar, regardless of whether subjects were exposed to a translated versus rotated cursor or had the robot passively move their hand or actively positioned it themselves. These results imply that the experimental manipulations of visuomotor displacement and hand positioning cannot account for the differences found between Malfait et al. (2008) and Wong and Henriques (2009). Furthermore, given that proprioceptive recalibration was independent of hand placement, it calls into question the proposal by Wong and Henriques (2009) that the additional signals recruited during active hand positioning lead to a more robust global estimate of hand proprioception and thus less visually induced recalibration.

In our tasks, and the study by Malfait and colleagues (2008), subjects could have based their responses on endpoint positional signals. In other words, subjects did not need to pay attention to the path taken by the hand during the proprioceptive estimation trials and, instead, waited until the hand was stationary before making an estimate of where the hand was relative to the reference. It was not possible for the subject to use this same strategy of comparing final endpoint positions in the study by Wong and Henriques (2009) because the goal of the task was to indicate hand-path geometry. Endpoint position would not have provided any information regarding the path that the hand had just traversed and, in fact, the endpoint positions after adapting their hand to produce a curved path would have been the same as the positions achieved before adaptation. Thus perhaps the differences between the experiments are explained by the ability of subjects to use endpoint positional information. At this point this is merely a suggestion; future work is required to determine the exact nature of proprioceptive recalibration in movement-related signals.

Given previous research that suggests people are better at localizing their limb after it has been actively moved than when it has been passively positioned (Coslett et al. 2008; Laufer et al. 2001; Paillard and Brouchon 1968), we thought that the sense of hand position would be less susceptible to proprioceptive recalibration in the active hand placement experiments. The improved ability to localize a limb after an active movement has been attributed to changes in the firing of sensory receptors (Al-Falahe et al. 1990; Burke et al. 1978a,b; Gandevia et al. 1992; Hullinger and Vallbo 1979; Rymar and D'Almedia 1980) and central representations (Prud'homme and Kalaska 1994), including centrally generated neuronal events (i.e., an efference; Gandevia 1987; McCloskey 1980). Contrary to our hypothesis, we found similar levels of proprioceptive recalibration regardless of how the hand was positioned. Thus it is unclear whether additional sensory and efferent signals present during active movements were or were not recalibrated by vision. Moreover, we found no difference in accuracy when comparing subjects' proprioceptive estimates after training with a veridical cursor across the active and passive hand-positioning tasks. Instead we found a consistent, slightly leftward bias in hand-position estimates. This "overlap effect," previously reported by Crowe et al. (1987), refers to the hand overestimating the location of a target. Finally, we found only a slight increase in precision after active hand positioning. Given the lack of differences between the paradigms after reach training with a veridical cursor, perhaps it is not that surprising that we found no differences in the magnitude of proprioceptive recalibration between the different experiments.

One potential reason why our results differ from previous work demonstrating an advantage for movement reproduction following active movements, is the same point that we keep highlighting: our technique for measuring proprioceptive estimates of hand position occurred in the absence of free-reaching movements. In contrast to our task, most studies examining limb localization following active versus passive movements have subjects respond by making a free reaching movement (often with the other limb). In our active positioning experiments, the robot-generated constrained paths forced subjects to move their hand to the testing position via a direct linear route. Once at the testing position, subjects estimated the position of the hand relative to a reference marker. Thus subjects were not able to make on-line corrections in response to tactile cues while the hand was moving outward and they were not trying to get the hand to the reference marker position. It remains to be determined whether there is a difference in proprioceptive estimates depending on the ability of one to make corrective submovements during the hand's trajectory and the task goal (i.e., attempting to match a desired position vs. making a judgment about a current position).

Proprioceptive recalibration: an overall shift in hand position?

For our final experimental manipulation we manipulated the modality of the center reference marker such that both proprioceptive and visual reference markers were presented in our proprioceptive estimate task. The proprioceptive reference marker was based on an internal reference and subjects estimated the position of their hand relative to body midline. The proprioceptive reference marker was included because *1*) it provided us with the opportunity to discuss our findings in light of previous adaptation experiments in which subjects reached to a proprioceptive target; and *2*) by comparing results across conditions in which the center reference marker was visual and proprioceptive, we were able to determine whether there was a general shift in the felt hand position. In other words, did their hand feel more to the right than it actually was due to the visually guided reach training?

Previous work examining the sensory components associated with visuomotor adaptation following exposure to displacing prisms typically has subjects perform two alignment tasks. In the first task, subjects reach to a position in space which they perceive to be straight ahead of body midline (proprioceptive recalibration). In the second task, visual recalibration, subjects indicate when a visual target is aligned with body midline. In most instances, results indicate a shift in straight-ahead reaches and visual alignment estimates following prism exposure in the direction to which subjects would have adapted their reaches (Harris 1963; Hay and Pick 1966; Redding and Wallace 1996). van Beers et al. (1999) found similar adjustments when subjects reached to visual and proprioceptive targets with the left hand during exposure to left and right displacing prisms. Yet given that displacing prisms shift the whole visual field, it is unclear whether these results are due to shifted view of the hand or to a shifted view of the workspace. In our study we manipulated only the location of the seen hand. This was done by representing the location of the hand with a cursor. We found shifts in the position at which subjects perceived the hand was aligned with our proprioceptive reference marker, which were in the same direction that they adapted their reaches. Moreover, this change in hand-reference marker alignment bias at body midline was of the same magnitude as that when a visual reference marker was displayed at the same location ($P > 0.05$). Given that we found that hand-reference marker alignment biases were shifted regardless of reference-marker modality, our results suggest that subjects began to feel their hand near the location at which the cursor was presented. In other words, proprioception was recalibrated and our results do not reflect a specific visual–proprioceptive realignment.

Link between proprioceptive recalibration and visuomotor adaptation

What do our results signify in terms of visuomotor adaptation? Typically models accounting for visuomotor learning include a role for sensory feedback, both the predicted and actual sensory feedback arising from a motor command. The difference between these sources of feedback is then used to update the forward model by correcting the predicted estimate of limb location and amending the motor command in subsequent movements (Miall and Wolpert 1996; Wolpert 1997; Wolpert et al. 1995). Our findings indicate that learning a new visuomotor mapping may lead not only to changes in the predicted location of the hand for guiding movements, but also to changes in the predicted estimates of hand position across different sensory modalities. However, it is important to keep in mind that these changes in the estimate of felt hand position were only a fraction of the changes observed in the movements of the unseen hand. Thus it is unlikely that sensory recalibration is the sole source driving changes in reaching movements.

Moreover, it is also possible that sensory recalibration occurs concomitantly but separately from visuomotor adaptation and thus would not contribute to the changes in reaching movements. In accordance with this proposal, visuomotor adaptation has been demonstrated in the absence and modulation of proprioceptive input. For example, deafferented individuals have been shown to adapt their reaches in response to altered visual feedback of the hand (see Bernier et al. 2006; Ingram et al. 2000; Miall and Cole 2007). As well, Bernier and colleagues (2009) recently demonstrated that in healthy subjects proprioceptive input (as measured by median nerve somatosensory-evoked potentials) is attenuated in primary somatosensory cortex on exposure to misaligned visual feedback of the hand. These findings imply that it is not necessary for proprioceptive recalibration to underlie visuomotor adaptation and that part of the adaptive process may be to reduce conflicting proprioceptive input.

Furthermore, in our experiment proprioceptive recalibration was assessed in a perceptual task. According to Goodale and Milner [1992; Milner and Goodale (1995)] there is a dissociation between processing sensory information (specifically, visual information) for perception and action. It is conceivable that the proprioceptive recalibration we found does not underlie visuomotor adaptation. Instead, visuomotor adaptation (or sensorimotor recalibration) and proprioceptive recalibration may be two independent adjustments arising from learning to reach with misaligned visual feedback of the hand. A proposal that does not seem that far-fetched, given that the proprioceptive recalibration we found was only about one third of the size of reach aftereffects.

We will conduct further experiments to determine the relationship between proprioceptive recalibration and visuomotor adaptation. Specifically, we will look to manipulate the visuomotor distortion introduced during the reach training tasks and attempt to determine whether proprioceptive recalibration can occur in the absence of changes to reaches. In the present experiments we wanted subjects to adapt their reaches to the visuomotor distortion and attempted to create a similar visuomotor distortion across the different paradigms. In other words, we choose a 4-cm shift in the translated-reach training task and a 30° rotation in the rotated-reach training task because the 4-cm shift corresponded to the average horizontal shift achieved across our workspace when the cursor was rotated 30°. With these similar levels of distortion, we were able to determine that proprioception was recalibrated regardless of the visuomotor distortion introduced (translated vs. rotated) and how subjects positioned their hands (active vs. passive). Under these conditions, we also found that proprioception was recalibrated to a similar extent, regardless of experimental manipulation. It is unclear what would have happened if we had manipulated the extent of the visuomotor distortion introduced. For example, if we had introduced a cursor that was rotated 60° CW with respect to the hand, we would expect to see greater deviations in subjects' reaches than what we observed when the cursor was rotated only 30°. Would this lead to an increase in proprioceptive recalibration? If so, this would indicate a systematic change in proprioceptive recalibration and visuomotor adaptation, providing support for the proposal that proprioceptive recalibration contributes to visuomotor adaptation. For now, it is evident that proprioceptive recalibration does arise after learning to reach with misaligned visual feedback of the hand.

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