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# Visuomotor Adaptation Does Not Recalibrate Kinesthetic Sense of Felt Hand Path

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**Wong T, Henriques DYP.** Visuomotor adaptation does not recalibrate kinesthetic sense of felt hand path. *J Neurophysiol* 101: 614–623, 2009. First published November 19, 2008; doi:10.1152/jn.90544.2008. Motor control relies on multiple sources of information. To estimate the position and motion of the hand, the brain uses both vision and body-position (proprioception and kinesthesia) senses from sensors in the muscles, tendons, joints, and skin. Although performance is better when more than one sensory modality is present, visuomotor adaptation suggests that people tend to rely much more on visual information of the hand to guide their arm movements to targets, even when the visual information and kinesthetic information about the hand motion are in conflict. The aim of this study is to test whether adapting hand movements in response to false visual feedback of the hand will result in the change or recalibration of the kinesthetic sense of hand motion. The advantage of this cross-sensory recalibration would ensure on-line consistency between the senses. To test this, we mapped participants' sensitivity to tilted and curved hand paths and then examined whether adapting their hand movements in response to false visual feedback affected their felt sense of hand path. We found that participants could accurately estimate hand path directions and curvature after adapting to false visual feedback of their hand when reaching to targets. Our results suggest that although vision can override kinesthesia to recalibrate arm motor commands, it does not recalibrate the kinesthetic sense of hand path geometry.

## INTRODUCTION

Humans rely on multiple sources of sensory information, such as vision and haptic sensation, when deducing the shape or contour of an object or guiding their hand to a target. Haptic sensation is based on both tactile and proprioceptive inputs from sensors in the muscles, tendons, joints, and skin. Although the two sensory modalities process and organize their inputs differently, humans still perform better when they have information from more than one modality (Desmurget et al. 1995; van Beers et al. 1996). For instance, participants reach more accurately to targets when they can see and feel their hand (Rossetti et al. 1995; van Beers et al. 1996). This enhanced performance is likely due to the participants optimally combining these sensory signals, giving more weight to the more reliable modality in a given task and movement direction (Jacobs 1999; van Beers et al. 1999, 2002). Although studies have found that vision is less precise than proprioception when used to localize hand position in depth direction (van Beers et al. 1999, 2002), in many cases, vision proves to be a more reliable source of information for inferring shapes, positions, sizes (Proteau and Isabelle 2002), and movement direc-

tions along the azimuth direction (van Beers et al. 1999, 2002). When proprioception and vision provide contradictory information, the brain will rely more on vision than on other cues (Mon-Williams et al. 1997; Rock and Victor 1964). Therefore the final perception of an object's characteristics tends to more closely resemble the visual estimate than the haptic one. However, what is the impact of this visual dominance on haptic perception?

The dominant influence of vision has been demonstrated by studies in which participants reach to a target while their hand location is visually misrepresented. In these studies, the participants' hand was hidden and they were shown a cursor that was, unknown to them, programmed to move along a certain direction or curvature that was misaligned with the actual (and felt) hand path. In an attempt to produce a straight-looking path when moving the hand cursor between two targets, participants responded to what looked like their hand curving rightward by learning to curve their hand path leftward (Flanagan and Rao 1995; Wolpert et al. 1995). They made these curved paths even in darkness when visual feedback was removed. Likewise, in many visuomotor-adaptation studies, where the cursor motion was shifted or rotated relative to the actual direction of the hand, participants learned to adjust their reaching movements to accommodate for false visual feedback of their hand path (Ghahramani et al. 1996; Krakauer et al. 1999; Vetter et al. 1999). This visually driven adaptation of hand movements (i.e., visuomotor adaptation) occurs regardless of whether visual feedback of the hand is provided continuously (Krakauer et al. 1999) or only at the end of the reaching movement (Bernier et al. 2005). It also occurs regardless of the magnitude (Bock et al. 2003) or the abruptness of the visuomotor task (Kagerer et al. 1997). The persistent deviation in hand path following the removal of the cursor after the adaptation is known as an *aftereffect*. The presence of aftereffects demonstrates that participants' motor commands have been altered in response to the imposed perturbation (Redding and Wallace 1996). This new visuomotor mapping is the result of the feedforward control of the new internal model. It has been proposed that adaptation and the aftereffects that follow may also be the result of cross-sensory recalibration or realignment (Redding et al. 2005; Simani et al. 2007), although kinesthetic sensitivity following visuomotor adaptation has not been directly measured in these studies.

Previous work on haptic sensing has shown that arm kinesthesia can be remarkably sensitive to absolute curvature and direction of a hand path. When participants were asked to

move along various curved contours, either by using their fingers or gripping and moving the handle of a robot manipulandum, their estimates of an arm movement were remarkably straight, deviating from a straight edge by only about 0.4– 0.7% of its length (Gordon and Morison 1982; Henriques and Soechting 2003; Miall and Haggard 1995). In terms of detecting direction of hand motion, participants' haptic estimate of hand motion along the cardinal direction deviated by only 2–5° (Fasse et al. 2000; Henriques and Soechting 2003). Similarly, when participants were asked to explore pairs of two-dimensional angles by scanning their index fingers along the edges, they could differentiate angle differences of 4.7° (Voisin et al. 2002a,b).

Given that kinesthesia is sensitive enough to detect the curvature or direction of a hand path, the aim of the present study was to investigate whether the recalibration of motor commands, after adapting to false visual feedback of the hand during reaching, would lead to a recalibration of participants' kinesthetic sense of hand path. If vision does recalibrate kinesthesia, participants should misestimate the felt angle or curvature of their hand path in the direction of the visual distortion. For example, in the first experiment (the tilt experiment), adapting to a visual cursor with its motion rotated 30° counterclockwise (CCW) with respect to the hand should lead to participants estimating their felt hand path as being more CCW than it was before. Likewise, in the second curvature experiment, adapting to a cursor programmed to curve outward should lead to a hand path that feels more outward when they move along a straight path. Nevertheless, if vision does not recalibrate the kinesthetic sense of hand path curvature (or angle) participants' estimate of tilt or curvature of the unseen hand path should not change following adaptation to the false visual feedback of the hand.

## METHODS

### Participants

A total of 96 participants gave informed consent to participate in this study in exchange for course credit. Participants were randomly assigned to one of the two experiments. All participants were right-handed and reported normal or corrected-to-normal vision. All procedures involved in the experiment were approved by the York Human Participants Review Subcommittee.

### Apparatus

To measure sensitivity of hand motion, participants were seated securely with their trunks fit snugly against the edge of the table, while grasping the vertical handle of a two-jointed arm robot manipulandum (Interactive Motion Technologies) with their right hand (Fig. 1A). The chair was locked onto a floor track to prevent any forward movement.

A black cover was placed on top of the robot manipulandum so that participants were not able to view their arm. The robot was programmed to keep the hand inside a horizontal planar region just above waist level. At a specified boundary, participants felt resistance on the manipulandum as if they were hitting a wall or moving within a groove. A resistance force was generated perpendicular to the wall and proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s) (Henriques and Soechting 2003). This "haptic" wall or groove assumed one of two contours that were tested in separate experiments. In the tilt-detection experiment, participants moved along a straight 15-cm-long groove (i.e., two adjacent walls between which the handle moved smoothly).
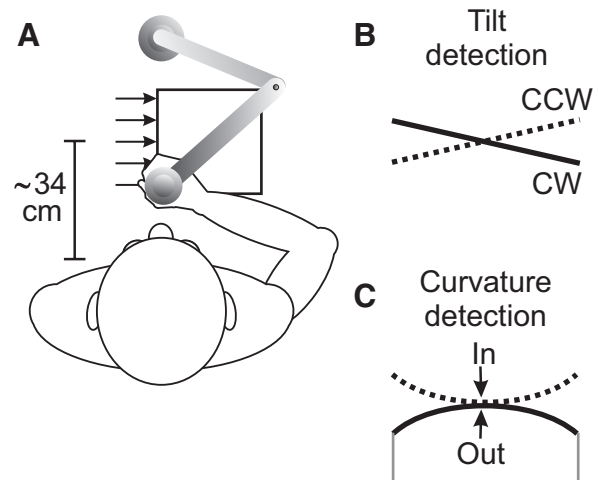


FIG. 1. *A*: above view of the experimental setup and the boundaries generated by the robot manipulandum. Participants gripped the handle of the robot arm that constrained the hand to move in a horizontal plane just above waist level. The robot exerted a force field (shown here by arrows) so that participants felt a boundary creating a resistance, as if they were hitting a wall. *B*: the contours of the boundaries, generated by the manipulandum, along which participants moved their hands when detecting the directional tilt (above) or curvature (below) of their resulting hand path, for paths tested along the left–right cardinal direction. Participants were also tested along the sagittal direction (not shown). Boundaries were 15 cm in length. For tilt detection, participants judged whether their hand path had tilted clockwise (CW, solid line) or counterclockwise (CCW, dashed line) as illustrated by a diagram they could see and refer to before judging (similar to the one shown here). *C*: for curvature-detection, participants judged whether their hand path curved outward (solid line) or inward (dashed line), again referring to a diagram similar to the one shown here.

This groove tilted on either side of the cardinal directions (Fig. 1B, dotted line for counterclockwise [CCW] tilt and solid line for the clockwise [CW] tilt). In the curvature-detection experiment, the curved contour, 15 cm in base length, fell on one side of a square boundary (15 × 15 cm, as shown in Fig. 1A) and no force was exerted within this square boundary. Participants were asked to move along the curved side, which curved either inward (dotted line, Fig. 1C) or outward (solid line) relative to the center of the square boundary. The "haptic" wall or groove that participants moved along was always aligned with the body's midline and centered in depth on a "center spot" (located on average 33.8 ± 4.8 cm in front of the participant) and the hand always started near this position. In the visuomotor tasks, the start hand position was also at this "center" location.

Participants felt the contour for as long as they wanted and no restrictions were imposed on the participants' strategy for decision making (Henriques and Soechting 2003; Soechting et al. 2006). Typically, participants moved along the boundary a few times, usually taking 1 s from one end to the other before responding. The experimenter keyed in the response for each trial.

In the visuomotor tasks, participants had to reach to visual targets by moving a cursor with the unseen robot handle. The visual stimuli were displayed on an LCD screen located (2.8 cm) above the handle of the robot manipulandum (Fig. 2A), so it laid on the same platform that blocked the view of the arm. This way, the cursor was located 1 cm above the hand. Participants moved the cursor by moving the robot handle with their unseen hand back and forth between targets. All reaching occurred in the dark.

### Procedure

MEASURING KINESTHETIC SENSITIVITY OF HAND PATH. In the tilt experiment, 57 participants (mean age = 21 ± 2.6 yr) were asked to report whether the felt hand trajectory tilted CW or CCW from the
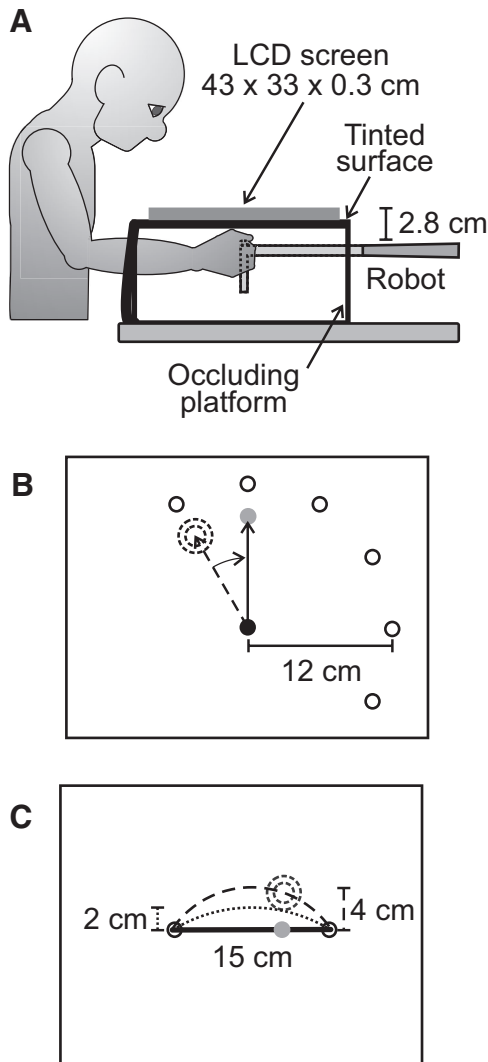
FIG. 2. The experimental setup and the visuomotor-adaptation tasks. *A*: side view of the experimental setup. The view of the participant's arm and the robot arm was covered with a tinted, occluding platform and a curtain that draped at the entrance of the platform when the participants inserted their arm to grip the handle. The visual display for the visuomotor-adaptation tasks was presented on a flat liquid crystal display (LCD) monitor, placed on the platform that hid the arm so that the screen was only 2.8 cm above the top of the gripped robot handle. *B*: display of the visuomotor-adaptation task for tilt experiment on the LCD screen. The cursor (gray circle) represented the location of participants' hidden hand and moved to scale with the motion of the hand. The cursor was programmed to gradually deviate, eventually deviating 30° CW (as shown) or 30° CCW relative to the hand. In this example of the 30° CW, participants had to learn to move their hidden hand up and left (dashed line, dashed handle) to produce a path that looked like it was moving directly forward to one of the 6 targets (open circles). The 6 targets were displaced 12 cm radially from the start target (black circle): with one on the midline and the other 5 located 30° CCW and 30, 60, 90, and 120° CW from the midline. *C*: display of the visuomotor-adaptation task for curvature experiment. The cursor was gradually curved either inward (as shown) or outward relative to the participants so that participants learned to move their hidden hand so that it curved outward (dotted/dashed line). This adaptation resulted in a straight-looking path moving laterally (as indicated by the cursor that represented the participants' hand movement). One group of participants was tested on a final peak of an outward curve of 2 cm or a radius of 6.6 m$^{-1}$ (dotted line); another group was tested on a final peak of 4 cm or a radius of 11.1 m$^{-1}$ (dashed line). Two targets (open circles, 15 cm apart) located at the end of the highlight path (shown by the black line). In this illustration, the straight path is along the left–right cardinal direction. In the other display for the curvature adaptation task, a straight path ran sagittally between targets along the midline (not shown) and the cursor was deviated either to the left (outward) or right (inward).

lateral or the sagittal direction with respect to the body (Fig. 1*B*). Twenty-seven participants were tested in both the lateral and sagittal directions (Groups 1 and 2 in Table 1), whereas 18 participants were tested in only one direction, either lateral or sagittal (due to time constraints or mechanical problems, they were not tested in the other cardinal direction) (Group 3). The remaining 12 formed a subgroup, tested only in the lateral direction, on multiple days (discussed in more detail in the next section) (Group 4). In the curvature experiment, 39 participants (mean age = 21 ± 4.9 yr) were asked to report whether the hand, moving along the haptic wall, curved inward or outward (Fig. 1*C*). Fifteen of the 39 participants were tested on only one direction of the contour due to time constraints.

Participants were tested on a set of 50 trials relative to the lateral direction and another set of 50 trials relative to the sagittal direction prior to the visuomotor-adaptation task (i.e., pre adaptation); the order in which participants did each set was counterbalanced. About half of the participants were first tested for hand paths in the lateral direction followed by the sagittal direction and the other half of the participants completed the conditions in the reverse order. Their kinesthetic sense of hand path was retested in the same order following the visuomotor-adaptation task (i.e., postadaptation), after reaching to visual targets with false visual feedback of their hand (see following text).

The angle of the tilted boundary or the curvature of the boundary was adjusted over trials using a two-alternative forced-choice (2-AFC) adaptive-staircase algorithm (Kesten 1958; Treutwein 1995). For the two staircases of the tilt experiment, one staircase started at 20° CW, whereas the other started at 20° CCW relative to the cardinal axes. The two staircases for the curvature experiment started with a radius of 0.33 m (curvature of 3.0 m$^{-1}$) directed outward or inward. The bias (the point of 50% probability) and the degree of uncertainty (the difference between the values at which the response probability was 25 and 75%) were calculated using the binary logistic fit in the Statistical Package for the Social Sciences (SPSS).

After assessing each participant's haptic sensitivity for hand path geometry (each set took about 30–40 min to complete), participants proceeded to the next session of the experiment: adapting their hand movements to false visual feedback of the hand.

ADAPTING MOVEMENTS TO FALSE VISUAL FEEDBACK OF THE HAND. For the visuomotor task in the tilt experiment, the cursor was rotated CW for 28 participants and CCW for another 17 (Groups 1–3 in Table 1). Participants moved the cursor (gray circle, 1-cm diameter) back and forth between a fixed central start target (black circle, 1-cm diameter) and one of six radially displaced visual targets (open circles, 1-cm diameter) on a black background (Fig. 2*B*). All targets were positioned 12 cm from the start position, radially placed at 30° increments, ranging from 30° CCW from the body midline to 120° CW. The start circle was located close to 33.8 cm in front of the participant, along the body's midline (the "center" spot described earlier). Once the cursor was on the start circle, one of the six radial targets would randomly appear. Participants made out-and-back movements to the target for a total of 90 trials with visual feedback (cursor). For the first 10 trials, the hand movement and cursor were aligned (no visual distortion). The cursor motion was then gradually rotated in either the CW or the CCW direction relative to hand motion, starting from the 11th trial by increments of 0.75°, and reached the final magnitude of 30° by the 50th trial where it remained throughout the rest of the trials. Participants had to learn to direct their hand 30° in the opposite direction for the cursor to move directly to the target. Because the distortion was gradually introduced, participants were unaware that they were adjusting their hand movements accordingly. Immediately afterward, they again moved to the targets for an additional 10 trials in an absence of visual feedback of the hand. In these trials, the cursor disappeared after moving 2 cm away from the start circle and reappeared at the same location when participants made a hand movement back to the center. The cursor disappeared before any cursor–hand discrepancy would be noticeable; this small window of

TABLE 1. *Tilt direction experimental design*

| Group | Preadaptation | Visual Distortion | | Postadaptation |
|---|---|---|---|---|
| 1 (*n* = 7) | Sagittal and Lateral | Gradual (100 trials) | | Sagittal and Lateral |
| 2 (*n* = 20) | Sagittal and Lateral | Gradual (100 trials) + Additional Full (40 trials) between sets | | Sagittal and Lateral |
| 3 (*n* = 18) | Sagittal (or Lateral) | Gradual (100 trials) | | Sagittal (or Lateral) |
| | | *Extended training with visuomotor adaptation task* | | |
| 4 (*n* = 12) | Lateral | Day 1 | Gradual (260 trials) | Lateral |
| | | Days 2–4 | Full (200 trials each day) | |
| | | Day 5 | Full (260 trials) | |

view helped participants return their hand to center where the next trial began. Twenty participants (of the 27 who were tested in both lateral and sagittal directions) also performed an additional 40 reaches with rotated visual feedback of the hand (with a distortion of 30°) in between sets of tilt-detection trials for the different cardinal axes (Group 3 in Table 1).

For the extended training visuomotor condition (*n* = 12) of the tilt experiment, another group of participants performed a total of 1,120 trials of visuomotor-adaptation training (Group 4 in Table 1). On day 1, these participants were first exposed to gradually rotated visual feedback of the hand (across 50 trials as in the single-day condition described earlier; white and gray circles in Fig. 3*A*) and then 200 trials with the cursor motion fully rotated 30° relative to the hand in the CW direction (black circles in Fig. 3*A*). After these 250 reaches made with a cursor, participants then reached for another 10 trials without a cursor after the first 2 cm of the movement (like the no-cursor trials in the single-day condition described earlier) to measure aftereffects (white squares in Fig. 3*A*). Participants continued for the next 3 days with an additional 190 trials with this 30° cursor rotation (followed by another 10 reaches without the cursor, for a total of 200 trials each of

these 3 days) and another 250 trials on the fifth and final days (also followed by 10 trials without a cursor, for a total of 260 trials). Over the 5 days, there were a total of 1,020 trials where the cursor and the hand movements were misaligned by 30° (black circles in Fig. 3*A*). Participants were then asked to judge the tilt of their hand paths after the visuomotor adaptation on day 1 and day 5. These participants, however, were tested only along the lateral direction. Table 1 shows the sequence of the experimental design for each group.

For the visuomotor-adaptation condition in the curvature experiment, a separate group of participants moved the cursor with their unseen hand between two targets (open circles, 1-cm diameter). In the lateral direction, the targets were 7.5 cm left and 7.5 cm right of the participant's midline, whereas for the sagittal direction, the targets were 7.5 cm further and 7.5 cm closer from the center spot along the midline. To initiate a trial, participants moved the cursor (gray circle, 1-cm diameter) to the first target. Once the cursor overlapped with the target, the target disappeared and a second target was displayed. In this way only one target was visible at any given time. To encourage participants to move the cursor along a straight path, a line was connected between the two targets at all times (Fig. 2*C*).
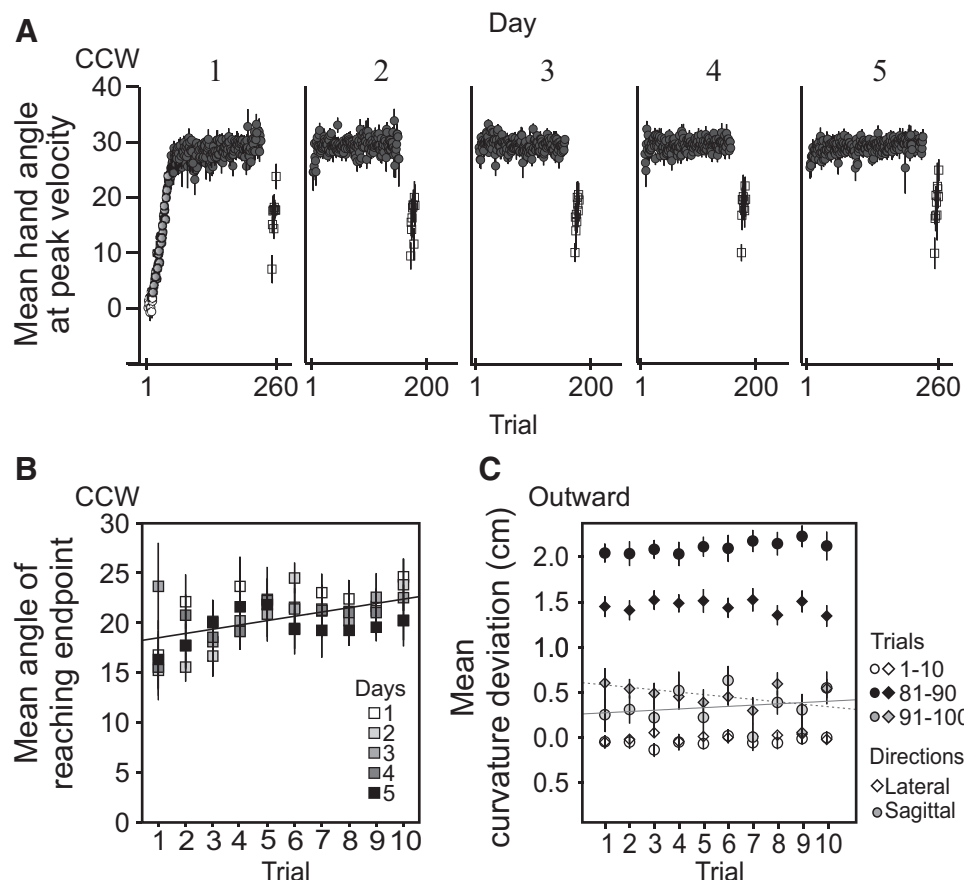


FIG. 3. Visuomotor adaptation for the tilt and curvature experiments. *A*: mean angular deviation of the hand motion at peak velocity averaged across all participants. Abscissa indicates the number of trials. White circles represent angular deviations produced with no visuomotor rotation in which hand motion and cursor were aligned (trials 1–10); gray circles represent gradual visuomotor rotation (trials 11–50); black circles represent 30° visuomotor rotation (trials 51–250 on day 1, trials 1–190 on days 2 to 4, trials 1–250 on day 5); and open squares represent rotation in the absence of cursor feedback (trials 251–260 on days 1 and 5, trials 191–200 on days 2 to 4). *B*: reaching endpoint (in degrees) of the aftereffects of the 10 trials for all 5 days, averaged across subjects. A linear regression was fitted to the aftereffects for all 5 days (black line). *C*: curvature deviation (in cm) for both perturbations in lateral (diamonds) and sagittal (circles) directions, averaged across all subjects. For both movement directions, the mean curvature deviation when there was no distortion of the cursor motion (trials 1–10, open symbols), along with movements made at the end of adaptation (trials 81–90, black symbols) and with movements made in an absence of visual feedback (trials 91–100, gray symbols) for movements along the lateral (diamonds) and sagittal (circles) directions. Linear regression was fitted into trials 91–100 for both lateral (dash gray line) and sagittal (solid gray line). Error bars represent SE of all participants.

In this curvature visuomotor task, the cursor was programmed so that straight-line motion on the visual display eventually required a curved motion of the unseen hand. This visual distortion was gradually introduced similar to the tilt visuomotor task. Specifically, the cursor and hand motion were aligned for the first 10 trials and then misaligned gradually by either 0.05 or 0.1 cm, starting with the 11th trial, and reaching the final distortion magnitude by the 50th trial. The final distortion for the curved path was bent in either an outward or an inward direction so that the midpoint of the arc measured from a straight line was either 2 cm ($6.7 \text{ m}^{-1}$) for 25 participants (Fig. 2C, dotted line) or 4 cm ($11.1 \text{ m}^{-1}$) for 14 participants (Fig. 2C, dashed line). The purpose of the differing final peaks was to determine whether the magnitude of the visual distortion influenced participants' sense of hand path curvature. Participants performed 90 trials with visual feedback (cursor) and an additional 10 trials without visual feedback of the hand. In contrast to the visuomotor tilt task, participants were shown a crosshair as they moved along the line to indicate how far their hand was between the two targets in these 10 trials. This crosshair did not provide information about how much their hand deviated from the straight path. Participants found it easier to reach to the targets if they had the crosshair to indicate whether their hand had traveled far enough to the target, in the absence of the cursor. On completing the visuomotor distortion task, participants performed the kinesthetic curvature-detection task, in which they judged the curvature of their hand paths based on kinesthesia alone.

## Data analysis

For the haptic task, we measured the bias of the tilt and curvature before and after participants adapted their hand movements in response to false visual feedback of the hand. Biases and uncertainty ranges were calculated using binary logistic function in SPSS fitted to the 2-AFC responses. One-sample *t*-test was used to assess the acuity of the haptic sense in both geometries before visuomotor adaptation. Differences in biases and uncertainty ranges before and after the visuomotor adaptation were analyzed using paired *t*-test. To assess learning during the visuomotor task, we compared differences for the last 10 trials of movement performed without visual feedback (i.e., aftereffects) with those trials when cursor and hand motion were aligned (trials 1–10) using either paired *t*-test (single day) and repeated-measures ANOVA (5 days) for the tilt experiment.

For the curvature experiment, we measured the midpoint deviation of the curvature—the perpendicular distance of the hand movement at the midpoint of the movement from the straight line. To calculate the percentage of the adaption in the curvature experiment, first we measured the curved hand path deviation: *1*) made with the visible cursor at the end of adaptation of each session (e.g., trials 81–90) from a straight hand path when the cursor and hand were aligned (trials 1–10) and *2*) made in the absence of visual feedback from the first 10 trials. We then calculated the gain between these two differences in deviations by dividing the latter by the former. To assess learning, we compared difference between aftereffects and the first 10 trials using paired *t*-test. The level of significance was fixed at $P < 0.05$ for all analyses. Additional analyses are detailed in RESULTS.

## RESULTS

### Visuomotor adaptation

Figure 3A shows the mean angular deviation of the hand motion at peak velocity relative to targets for all participants who learned a 30° CW visuomotor rotation, across the 5 days. Participants began to reach to the targets with a veridical cursor for the first 10 trials on day 1 (white circles). As the cursor motion gradually changed across the next 40 trials (trials 11–50, gray circles) the direction of the hand path was also slowly deviated so that participants moved their hand 30° CCW relative to the target (and cursor motion). When the cursor motion was fully rotated by 30° CW (after trial 50 and onward, black circles), the hand reaching direction was consistently rotated by the same amount as the cursor rotation but in an opposite direction. After the 250 reaching movements with the cursor, participants reached for an additional 10 trials (trials 251–260) without the cursor to assess the degree of adaptation (open squares). On average, participants' hand movement in these open-loop trials continued to be deviated by 72% (21.8 ± 7.2°) of the total distortion for day 1. If participants' hand movement had not adapted, reaching direction would have been the same as that for the first 10 trials of day 1 (white circles).

When participants performed the task at the following days (days 2–5), and started reaching with a fully rotated (visible) cursor motion, the angular movement at peak velocity relative to targets (black circles) continued to be deviated by the same amount to the hand movement performed at the end of adaptation with the visible cursor of the previous day. These deviations remained constant across days [$F_{(8,48)} = 1.1$, $P = 0.4$, repeated-measures ANOVA], suggesting that participants were able to retain the learned visuomotor rotation after 24-h breaks. We compared the reaching endpoint locations of the last 10 trials (reaching without cursor as aftereffects) on each day and the first 10 trials in day 1 (reaching with veridical cursor as control) and found there were significant differences between aftereffects and control [$F_{(5,45)} = 24.1$, $P < 0.0001$, repeated-measures ANOVA]. This suggests that movement angle at peak velocity without the cursor was significantly different from when the cursor was aligned with the hand. Thus hand movements remained deviated even after the cursor had been removed, indicating that adaptation had taken place. However, no significant difference was observed between the aftereffects measured across days [$F_{(4,36)} = 0.56$, $P = 0.69$, repeated-measures ANOVA], suggesting that despite extended visuomotor rotation training, the magnitude of adaptation did not increase. Overall, participants' hand paths on average were deviated by 20.3 ± 0.9° (68% of the imposed rotation) relative to the targets as shown by the aftereffects.

To assess whether the aftereffects decayed with repeated reaches, in Fig. 3B, we fit a regression line to the reaching endpoints of the aftereffects across the 10 trials (e.g., trials represented by the square in Fig. 3A) for all 5 days. If deadaptation occurred, the slope would be negative (i.e., aftereffects would have been smaller across multiple reaches). We found a small significantly positive slope between the reaching endpoints across the 10 trials [ß = 0.42, $t_{(471)} = -3.78$, $P < 0.001$], indicating that aftereffects even increased slightly with additional reaches across days. Our results suggest that adaptation did not decay with repeated reaches.

Performing the kinesthetic task following adaptation did not lead to deadaptation. In the experiment in which participants were exposed to a single day of the visuomotor tilt adaptation task, performance in the second set of 40 visuomotor rotation trials (with full distortion) was not decreased from the previous set of reaches prior to the kinesthetic task [$t_{(19)} = -0.58$, $P > 0.05$, paired *t*-test]. Instead, significant differences were observed between aftereffects and the control [$F_{(2,38)} = 138.2$, $P < 0.0001$, repeated-measures ANOVA], indicating that adaptation had taken place. Furthermore, no significant difference

was observed between aftereffects following the first set of adaptation (after the first 90 trials) and those after the second set of adaptation (the next 30 trials) [$t_{(19)} = 2.2$, $P > 0.05$, paired $t$-test]. Overall, participants' hand paths continued to deviate on average by 66% of the imposed rotation when reaching without the cursor. These results indicate that brief exposure to a visuomotor rotation was sufficient to help consolidate learning.

In the curvature visuomotor-adaptation task, the overall magnitude of the hand movements produced in the aftereffects was smaller than that produced when the cursor was visible and distorted. This is illustrated in Fig. 3C, where the deviations during the 10 trials of training with the cursor visible and fully distorted (trials 80–90; solid symbols) deviated by 1.5–2.5 cm in the midpoint of the path, with smaller deviations for movements made in the sagittal direction (diamonds). For the aftereffects, the last 10 trials made when the cursor was removed (trials 91–100, gray symbols), the deviations were on average <0.5 cm. Nonetheless, paired $t$-test revealed significant differences between aftereffects and controls (trials 1–10, open symbols) in both lateral [$t_{(32)} = -6.92$, $P < 0.0001$] and sagittal [$t_{(27)} = -4.9$, $P < 0.0001$] hand movement directions for both distortions, indicating adaptation had taken place. When compared with the magnitude of the movement deviation produced under full distortion, participants' hand motion curved 33% in the lateral direction and 20% in the sagittal direction in the absence of the cursor. The extent of adaptation is similar to that found by Wolpert et al. (1995) for a similar paradigm. Deadaptation did not occur in the curvature experiment as shown by the relatively flat slopes (not significantly different from zero, $P > 0.05$) found in both directions, and for both magnitudes of distortions, across the last 10 trials performed without visual feedback (solid and dashed lines).

Adaptation to a falsely curved hand path was smaller than an adaptation to misaligned hand direction, as illustrated by the smaller aftereffects following curvature adaptation. This is probably because humans are accustomed to making straight hand movements (i.e., moving their hand along straight or flat surfaces) and have less experience in making movements in one specific direction over another. The greater familiarity with straight hand motion may lead to greater resistance to visually drive adaptation of curved hand motion. Nonetheless, participants' hand movement continued to deviate in the direction of visual distortion, even when visual feedback of the hand (cursor) was removed. Thus we conclude that in all circumstances hand path adapted to altered visual feedback.

*Tilt experiment*

Participants' haptic sensitivity was mapped in the tilt experiment based on their response to the tilt direction of the hand path along the lateral and sagittal cardinal directions. The biases for all participants are drawn in Fig. 4A and their mean in Fig. 4B. Dashed lines shown in Fig. 4, A–C represent tilt biases measured prior to the visuomotor-adaptation task. The tilt bias represents the hand path direction that participants would perceive to be equally likely to be tilted CW or CCW away from the lateral and sagittal directions. One-sample $t$-test revealed that the angles of hand paths that participants felt in the lateral direction prior to the visuomotor adaption (dash lines) were not significantly different from a perfect horizontal line ($P > 0.05$). However, participants were less accurate for the sagittal direction; they regarded haptic boundaries tilted about 3–5° CCW as feeling "collinear" with the sagittal direction (i.e., biases were significantly different from zero, $P < 0.01$).

Next, we measured how accurate participants were at estimating the cardinal angle of their unseen hand path after they adapted their arm movements in response to false visual feedback of their hand. These postadaptation biases (after reaching to visual targets with false visual feedback of their hand) are shown as solid black lines in Fig. 4, A and B. If visually recalibrated movements led to an altered kinesthetic perception of the hand path, then these biases should be more CCW than the preadaptation biases (dashed lines) following CCW adaptation, and more CW following CW adaptation. However, this is not what we found. Postadaptation biases overlapped with those biases measured prior to the visuomotor adaptation, for both hand path movement directions and following both directions of visuomotor rotation. As can be seen, the bars in Fig. 4D for biases prior to adaptation (open bars) do not differ significantly from those following adaptation (solid bars) for the different cardinal directions and distortion groups (CCW cursor rotation in the lateral [$t_{(16)} = -1.13$, $P = 0.28$] and sagittal directions [$t_{(14)} = -1.58$, $P = 0.14$]; CW rotation in the lateral [$t_{(18)} = 0.25$, $P = 0.819$] and sagittal directions [$t_{(20)} = 0.28$, $P = 0.78$]). These results suggest that participants' kinesthetically based estimates of hand path were not affected by the visuomotor adaptation.

We also examined whether visuomotor adaptation affected the precision of hand path judgment by introducing noise to the estimate of hand proprioception. To address this, we compared the uncertainty range (the difference between the values at which the response probability was 25 and 75%) to the felt estimates made before and after the visuomotor adaptation. If visuomotor adaptation had reduced the precision of participants' hand path judgment, we would expect the uncertainty range to become larger. We did not find a significant difference between the precision of hand path judgment for both felt hand path movement directions and both visuomotor rotations [$t_{(18)} = -0.53$, $P = 0.60$ in the lateral direction and $t_{(20)} = -0.73$, $P = 0.47$ in the sagittal direction for CW visuomotor rotation; $t_{(16)} = -0.77$, $P = 0.45$ in the lateral direction and $t_{(14)} = -0.87$, $P = 0.40$ in the sagittal direction for CCW visuomotor rotation]. Thus precision of hand kinesthesia was also not affected by the visuomotor adaptation.

To ensure that the consistent kinesthetic estimates of the hand path following visuomotor adaptation were not due to insufficient adaptation or experience, we ran another group of participants ($n = 12$, Group 4 in Table 1). Participants performed extended (5 days) visuomotor training sessions with a 30° CW visual distortion (1,120 trials). In Fig. 4C, participants' tilt biases following this further training (solid lines) again overlapped with those prior to adaptation (dashed lines) and were not significantly different [$t_{(11)} = 0.15$, $P = 0.71$]. These values are also shown in Fig. 4D, *right*, which shows the mean tilt biases for all participants after the extended visuomotor training (solid bar) along with their corresponding preadaptation biases (open bar). We also found no significant difference in the uncertainty range after extended training with false visual feedback of the hand [$t_{(11)} = 0.29$, $P = 0.78$]. This suggests that the haptic sensitivity continued to be robust even

**A** 100 trials of CW rotation    100 trials of CCW rotation

**B**    2 cm

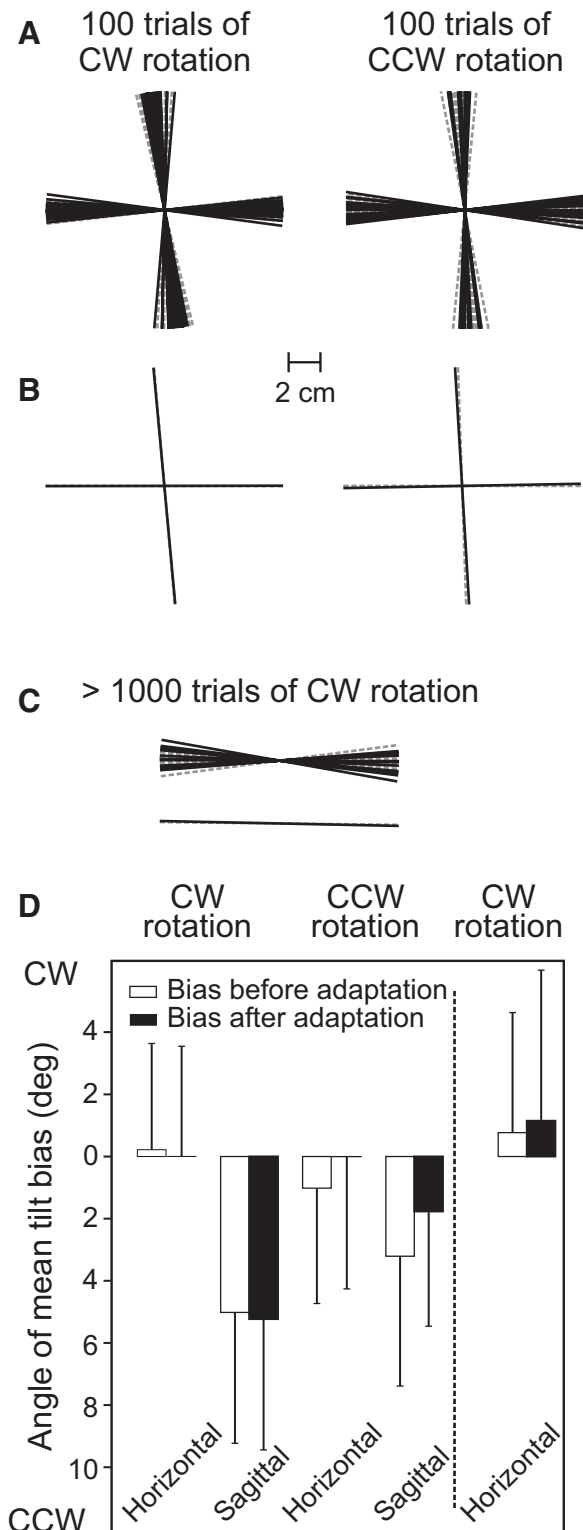**C** > 1000 trials of CW rotation

**D**

FIG. 4.   Results for the tilt-detection experiment. *A* and *B*: tilt biases measured prior to learning to reach with a rotated cursor (dashed lines) and immediately afterward (solid lines) for all participants (*A*) and averaged across participants (*B*) for the lateral and sagittal directions. *Left panels* are biases for participants who were in the CW rotation group and *right panels* are biases for those who were in the CCW group. *C*: tilt biases before and after reaching for 1,120 trials with false feedback of the hand for another group of participants. *D*: bar graph showing the angle of mean tilt bias (in degrees) and SD (error bars) before (white bars) and after (solid bars) around 100 reaches with CW or CCW rotated cursor motion (*left*), and after more than 1,000 reaches with CW rotated cursor motion (*right*).

following an extended period of training and the lack of differences was not due to insufficient exposure to adaptation.

*Curvature experiment*

For the curvature-detection experiment, we assessed participants' haptic sensitivity to hand path curvature and compared curvature biases measured before and after visuomotor adaptation. Figure 5*A* shows the 1SD range of curvature biases across participants in the outward distortion task (*left*) and the inward distortion task (*right*). The ranges of biases were drawn because the mean curvature biases were too small to be detectible from a straight line. These estimates of hand path, prior to visuomotor adaptation (dashed lines), did not significantly deviate from a straight line ($P > 0.05$, one-sample *t*-test) in both cardinal directions. The biases following adaptation to two different distortion magnitudes of curvature (peaked at 2 or 4 cm) did not significantly differ from each other for either movement direction or inward–outward distortions ($P > 0.05$), so we collapsed the data for the plots and for further analysis. The solid arcs in Fig. 5*A*, representing the range of curvature bias measured after visuomotor adaption, overlapped with dashed arcs, representing those measured prior to adaptation. The bars representing curvature biases, averaged across subjects, in Fig. 5*B* are of similar size both for preadaptation (open bars) and postadaptation (solid bars). There was no significant difference between the biases measured before and after participants learned to curve their hand motion to produce visually straight paths [$t_{(19)} = -0.95$, $P = 0.36$ in the lateral direction and $t_{(15)} = -0.03$, $P = 0.98$ in the sagittal direction for inward distortion; $t_{(12)} = -5.5$, $P = 0.59$ in the lateral direction; and $t_{(11)} = -0.03$, $P = 0.98$ in the sagittal direction for outward distortion]. Biases, averaged across participants, are given both in units of curvature (inverse meters) and as displacement of the hand at the peak as shown in Fig. 5*B*.

When we tested whether participants' precision in detecting whether the curvature of the hand path changed after visuomotor adaptation, we found no significant difference in the uncertainty ranges of curvature prior to and after adaptation [$t_{(19)} = 0.63$, $P = 0.54$ in the lateral direction and $t_{(15)} = -0.11$, $P = 0.91$ in the sagittal direction for inward distortion; $t_{(12)} = -0.8$, $P = 0.54$ in the lateral direction and $t_{(11)} = 0.93$, $P = 0.37$ in the sagittal direction for outward distortion]. This suggests that participants' precision on curvature detection was not affected by visuomotor adaptation.

DISCUSSION

In this study, we measured participants' haptic sensitivity before and after they were trained to reach to visual targets with false visual feedback of their hand. Participants moved their unseen hand along two different contours—tilted or curved—produced by a robot manipulandum in both lateral and sagittal directions. Participants estimated whether their hand path was tilted CW or CCW or whether their hand path curved outward or inward. In the visuomotor-adaptation task of the tilt experiment, participants learned to deviate their hand movement in an opposite direction of their adapted reaches with respect to the targets to compensate for the visuomotor rotation. Moreover, in the curvature experiment, participants learned to curve their hand movements to produce movements
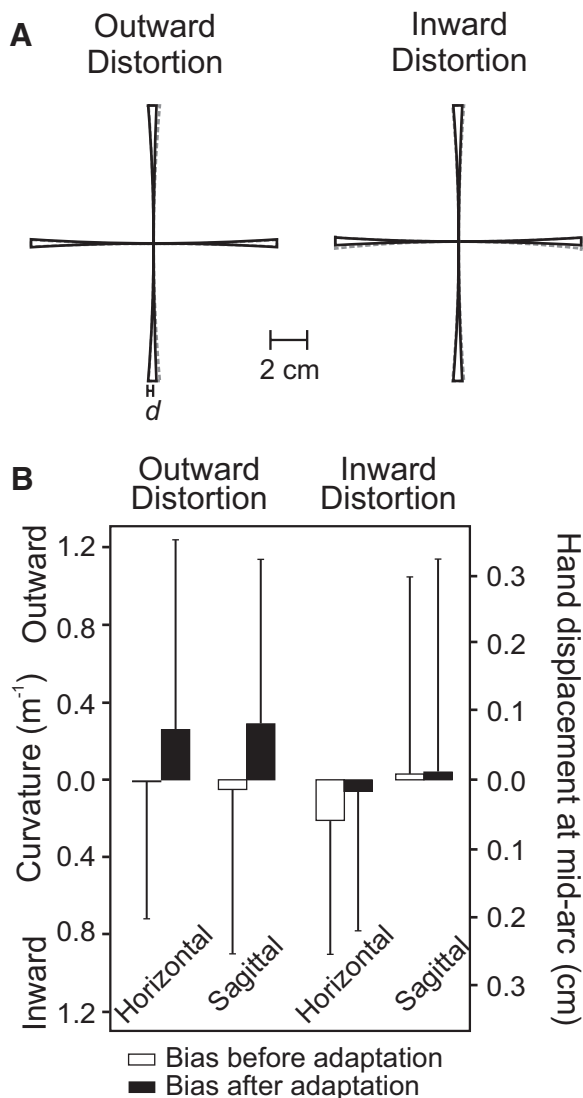
FIG. 5. Results for the curvature-detection experiment. Curvature biases and corresponding hand displacement for all participants measured prior to and after adaptation to an inwardly curved (*right*) and outwardly curved (*left*) distortion in visual feedback of the hand. *A*: the arcs represent the 1SD range of curvature biases across the participants. The dashed arcs are those measured prior to adaptation to the curved visual feedback, whereas solid arcs are those measured afterward. Displacement (*d* in *A*) for the curvature bias corresponds to half of the width of the arcs. *B*: bar graph shows the average biases and SD (error bars), reported as either units of curvature ($m^{-1}$) on the left or hand displacement (cm) of the right ordinate before adaptation (white bars) and after adaptation (black bars) for both curved directions of the cursor.

that were visually straight. We assessed their adaptation by measuring the deviations of their hand movements made to the same target without a cursor: the resulting aftereffects suggested that their motor commands were recalibrated by this false visual feedback of the hand. Despite recalibration of the motor command, participants were very good at detecting the direction or curvature of the felt hand path even after this adaptation. That is, even after participants unknowingly recalibrated their limb movements in response to false visual feedback of hand motion, biases in what participants felt as strictly cardinal or a straight hand path did not change. Furthermore, participants' uncertainty ranges were unaffected by this visual recalibration of the arm motor system. Our results

suggest that despite learning a new visuomotor mapping, the resulting recalibration of the arm motor command did not affect or recalibrate participants' kinesthetic sense of arm movement.

The brain can adapt to a variety of distortions of visual feedback of the hand when reaching to or tracking targets, including rotations and lateral shifts by adjusting their hand movements (Baraduc and Wolpert 2002; Ghahramani et al. 1996; Krakauer et al. 2005; Vetter et al. 1999; Yamamoto et al. 2006). This adjusted hand movement can be retained (~60–70%) after 24 h (Klassen et al. 2005; Krakauer et al. 2005; Miall et al. 2004) or even a year later (Yamamoto et al. 2006). In line with the previous studies, our participants did show retention after the performance of the kinesthetic task and following a 24-h break (Fig. 3*A*). Moreover, participants continued to make deviated hand paths toward the target even in an absence of visual feedback. These aftereffects likely result from recalibrating the movement in response to new or conflicting sensory information, suggesting that the internal model has been updated (Bernier et al. 2005; Kagerer et al. 1997; Yamamoto et al. 2006). Although Redding et al. (2005) and Simani et al. (2007) suggested that aftereffects may be due to vision realigning or recalibrating proprioception, estimates of proprioception following adaptation in their studies involve participants making self-generated movements (in the absence of visual feedback). Thus it is not clear whether the results of these open-loop reaches are due to sensory recalibration, rather than just motor recalibration. The goal of our study was to test whether motor recalibration also leads to the recalibration of haptic sensitivity of hand movement.

We found that participants' haptic sensitivity remained the same after visuomotor adaptation in both experiments. Moreover, the uncertainty range did not become larger as would be expected if visuomotor adaptation affected the precision of hand path judgment with the introduction of noise to the proprioceptive estimates. The lack of sensory recalibration is not due to loss of adaptation or motor recalibration. The small deviations in reaching when participants performed the visuomotor-adaptation task on subsequent days following the initial day of training demonstrated that this new visuomotor mapping or internal model persisted. Plus, the aftereffects following adaptation did not significantly decay (Fig. 3, *B* and *C*). Although the small adaptation produced when the cursor moved along a curved path does not strongly rule out the possibility that vision does recalibrate kinesthesia, the substantial and persistent adaptation produced when the hand cursor was rotated does suggest that visuomotor recalibration does not lead to recalibration of participants' kinesthetic sense of hand path.

It has been postulated that adaptation is driven by a mismatch between the senses. Yet, several studies have shown that deafferented patients can adapt their arm movements to altered visual feedback of their hand as quickly as or even more quickly than people with intact afferents (Bernier et al. 2006; Miall and Cole 2007), suggesting that adaptation does not require a conflict between the senses. Others have also shown that deafferented and healthy participants exhibit similar aftereffects when the cursor representing their hand becomes veridical (aligned with the hand movement) (Bernier et al. 2006) or when visual feedback was removed (Ingram et al. 2000). These aftereffects produced by deafferented patients suggest that the

motor command was indeed being recalibrated to match with the false visual feedback of their hand location, but not their proprioception, since deafferented patients lack proprioception input. This suggests that intact proprioception is not necessary for visuomotor adaptation (Bernier et al. 2006, 2007; Ingram et al. 2000) and further indicates that a mismatch between visual and proprioceptive feedback is also not necessary for driving adaptation. This suggests that the goal of adaptation is not to match these senses by recalibrating one or the other or both.

What likely drives adaptation or the formation of an internal model is the discrepancy between the actual movement and the desired movement (Cunningham 1989). In the case where vision is provided and the task involves moving a visual cursor (representing the hand) to a visual target, vision tends to dominate. Here, the feedback about the arm movement relies almost exclusively on visual information even when it is false. The visual error signal is used to adjust the motor commands during movements to develop a forward model. This feedforward model for anticipating or predicting the visually driven motor command together with an inverse (kinematics) model for calculating a new set of joint motion are necessary for the end effectors to move to its preferred path. Thus deviations in reaches during adaptation or the aftereffects could be due only to the motor commands being recalibrated, rather than to any misalignment or change in kinesthetic estimates of hand path. However, even if the existing mismatch between the motor command and the (distorted) visual feedback serves as an essential signal for the CNS to update or develop the internal model, does this also result in the recalibration of the sensory estimates of hand position as well?

A recent study by Smeets et al. (2006) suggests that reaching with veridical feedback of the hand does not recalibrate proprioception. In their study, participants reached to visual targets with their unseen hand after they have learned to reach with veridical feedback of the hand. When participants reached to visual targets without visual feedback of their hand, they produced a consistent bias in their reaching endpoints. When they were given veridical visual feedback of the hand, it was not surprising that the bias disappeared as the cursor hit the target at every reach. When these participants then returned to reaching without visual feedback, however, their reaching endpoints slowly drifted back toward the initial bias. If proprioception was calibrated by vision, then reaching errors produced without visual feedback after learning to reach should be smaller than those produced prior to the visually guided reaching. Since there is an eventual return of the bias in the endpoint when reaching without the visual feedback, perhaps hand proprioception was not calibrated by vision when it was available during the visually guided reaching. Nevertheless this study does not address whether visuomotor recalibration or forming a new internal model of motor output may result in changes to sensory estimates of hand motion since the visual feedback of the hand was not altered. It is possible that in this study the same internal model is used for both closed- and open-loop reaches, with a higher weighing on vision than proprioception when vision is available.

Could this drift in participants' estimate of hand motion in the dark affect their sense of hand geometry? A study by Brown et al. (2003), like that of Smeets et al. (2006), showed that hand location tends to drift over time in the absence of

visual feedback. When participants were asked to reach to a target without visual feedback, their hand movement trajectory was systematically displaced in one direction. The hand movement trajectories were consistently shifted in parallel with those made with visual feedback. If drift resulted from proprioceptive decay, then the movement distance and direction should vary as the hand drifted away from the start location. The preservation of the movement trajectories over time suggests that proprioception serves as a reliable source for maintaining the correct hand path geometry, after long periods of time without vision.

It is possible that the reason why we did not find that vision recalibrated kinesthesia was that the kinesthetic-detection task differed from the visuomotor-adaptation task, so that any transfer of cross-sensory recalibration would have been diminished. It has been shown by Cothros et al. (2006) that adapting reach movements made in a curled forced field when gripping the handle of the robot only moderately transferred to reach movements made without gripping the handle. These authors attributed their results as suggesting that haptic information associated with gripping the handle may have served as a contextual cue that aids in recalling a previously learned force field. Yet this is not a problem in our study, since both our kinesthetic-detection and visuomotor-adaptation tasks require participants to generate their hand movement while holding the robot handle, and any cues associated with the handle would have persisted throughout the experiment. Moreover, while adapting to a force field may involve developing an internal model of the object/handle as well as of the arm dynamics, this may not be the case when adapting to altered visual feedback. Working with and manipulating objects may impose loads on the hand in everyday life, but they rarely change the seen location of the hand. Finally, subsequent studies using the robot manipulandum in both Gribble's lab (Malfait et al. 2008) and our lab (Cressman and Henriques 2008) suggest that vision does recalibrate the proprioceptive estimate of hand position when the hand is passively moved by the robot. Passive hand movements are more difficult to estimate than active movements that involve inputs from additional muscles spindle fibers and efferent signals to estimate hand motion. For this reason, proprioceptive signals generated from passive movements are likely more susceptible to recalibration from vision.

Other direct or indirect measures of kinesthesia or proprioception tend to involve tasks that require movements of the adapted arm (Simani et al. 2007; Smeets et al. 2006; van Beers et al. 1999). However, because recalibration of the motor commands can also lead to generalization of adaptation to *1*) novel target vectors (Ghahramani et al. 1996; Simani et al. 2007; Vetter et al. 1999), *2*) opposite untrained hand (Sainburg and Wang 2002), and *3*) nonvisual targets as well (Simani et al. 2007), it is difficult to distinguish whether the results are due to calibration of other senses or of the motor commands. In our study, by contrast, we constrained participants' hand motion along a defined contour to make sure that our measure of kinesthesia was not confounded by planning or programming the direction of their arm movement, in other words, using the newly formed internal model to produce the motor output. That is, our participants did not have to plan and execute a movement in a particular direction. Instead they had to follow a contour or kinesthetic wall in direction that is neither known nor self-generated. Therefore we can be confident that partic-

ipants were merely estimating hand path direction rather than producing adapted hand paths.

*Conclusion*

We found that humans' kinesthetic sense of felt hand path was robust. That is, even after participants unknowingly recalibrated their limb movements with false visual feedback of their hand motion, their biases or kinesthetic estimate of hand path geometry remained unchanged. Moreover, participants' uncertainty ranges were also unaffected by this visuomotor-adaptation task. Our results suggest that despite learning a new visuomotor mapping through the reaching adaptation task, the recalibrated arm motor command does not lead to a recalibration of participants' kinesthetic sense of hand path geometry.

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