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Reach Adaptation and Proprioceptive Recalibration Following Exposure to Misaligned Sensory Input

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Cressman EK, Henriques DY. Reach adaptation and proprioceptive recalibration following exposure to misaligned sensory input. *J Neurophysiol* 103: 1888–1895, 2010. First published February 3, 2010; doi:10.1152/jn.01002.2009. Motor adaptation in response to a visuomotor distortion arises when the usual motor command no longer results in the predicted sensory output. In this study, we examined if exposure to a sensory discrepancy was sufficient on its own to produce changes in reaches and recalibrate the sense of felt hand position in the absence of any voluntary movements. Subjects pushed their hand out along a robot-generated fixed linear path (active exposure group) or were passively moved along the same path (passive exposure group). This fixed path was gradually rotated counterclockwise around the home position with respect to the path of the cursor. On all trials, subjects saw the cursor head directly to the remembered target position while their hand moved outwards. We found that after exposure to the visually distorted hand motion, subjects in both groups adapted their reaches such that they aimed ~6° to the left of the intended target. The magnitude of reach adaptation was similar to the extent that subjects recalibrated their sense of felt hand position. Specifically the position at which subjects perceived their unseen hand to be aligned with a reference marker was the same as that to which they reached when allowed to move freely. Given the similarity in magnitude of these adaptive responses we propose that reach adaptation arose due to changes in subjects' sense of felt hand position. Moreover, results indicate that motor adaptation can arise following exposure to a sensory mismatch in the absence of movement related error signals.

INTRODUCTION

When reaching with altered visual feedback of the hand, the "hand" (i.e., the visual representation of the hand) does not head directly to the target as expected. Thus to compensate for deviations, or errors in reaches, the brain has to resolve the conflict between visual and proprioceptive signals and deduce the appropriate motor command to guide the hand to the target. This process is referred to as visuomotor adaptation and results in the formation of a new visuomotor mapping to guide one's movement (Ghahramani et al. 1996; Krakauer et al. 1999). Visuomotor adaptation has been proposed to arise due to a difference between the desired (predicted) and actual sensory feedback arising from a given motor command. For example, when first reaching with altered visual feedback of the hand, subjects expect to see the visual representation of the hand head to the target. However, because the visual feedback of the hand is misaligned from the actual hand location, the hand is seen to head off on an angle. This gives rise to an error signal, and it is thought that this signal (i.e., the sensory discrepancy between the predicted and actual sensory feedback) is used to amend the motor command and correct the predicted estimate of limb location (Miall and Wolpert 1996; Wolpert 1997; Wolpert et al. 1995).

In the current study, we examined if exposure to a visual-proprioceptive mismatch, in the absence of any voluntary movement, was sufficient on its own to cause one to adapt his or her movements. In other words, we were interested in determining if one needs to experience the sensory consequences of an incorrect voluntary action and see that the hand does not achieve the predicted location before adapting one's reaches in response to conflicting sensory input.

Previous work examining the role of movement and resulting sensory feedback in motor adaptation has created a visual-proprioceptive mismatch by having subjects look through displacing prisms. The results of this work have been contradictory. For example Held and colleagues (Held and Bossom 1961; Held and Freeman 1963; Held and Hein 1958) have demonstrated that subjects adapt their movements in response to a prism-shifted view of the world only if they are allowed to make voluntary movements and receive the contingent sensory feedback (reafference hypothesis). In contrast, others (e.g., Craske 1967; Howard et al. 1965; Mather and Lackner 1975, 1977; Molden 1971; Singer and Day 1966; Wallach et al. 1963) have demonstrated that subjects will show some reach adaptation after passive viewing conditions, depending on the magnitude of the discrepancy between visual and proprioceptive signals and/or the similarity between exposure and testing conditions. Based on these contradictory results, it is evident that the role of movement in motor adaptation has yet to be determined. Moreover, it is important to keep in mind that in these previous studies, the displacing prisms would have shifted not only the seen location of the hand but also the visual representation of the target and the rest of the workspace. Thus some of the changes observed in subsequent goal-directed movements following prism exposure could have arisen because of a spatial realignment of the workspace rather than to changes in the sensorimotor transformations underlying reaches.

In contrast to these previous prism tasks, the present study examined the role of movement in motor adaptation when just the visual feedback of the hand position was shifted. In particular, subjects saw a cursor move directly toward a remembered visual target in a virtual reality setup while they actively pushed their hands out along a robot-generated constrained linear path or had their hands passively moved along the same trajectory. Gradually, over trials, the constrained hand path was

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rotated counterclockwise around the home position with respect to the path of the cursor. Thus because the cursor always moved directly to the target site, there was no visual error indicating that the hand had not achieved its predicted location. And, more importantly, subjects did not execute a voluntary movement or reach to the target in the typical manner.

To examine whether reach or motor adaptation followed from this nonreaching task where subjects merely saw the misaligned cursor move with the hand (i.e., experienced an intersensory based error signal), we had subjects reach freely to the same targets after exposure to the misaligned cursor. Given that we only manipulated feedback of the hand, and not the entire workspace as prisms do, we did not expect a shift in subjects' straight ahead, and any changes in subjects' reaches could not be accounted for by a spatial realignment of the workspace. To discuss our findings in light of previous adaptation protocols and because we are interested in the effect of altered visual feedback of the hand on subsequent motor output, we will refer to these potential adjustments in reaches as visuomotor adaptation.

In addition to assessing visuomotor adaptation, we also examined the degree to which the sense of felt hand position was recalibrated. To examine sensory recalibration, we used a perceptual task that did not allow subjects to employ potentially adapted sensorimotor mappings (Cressman and Henriques 2009). Previous work examining sensory recalibration after exposure to a visual-proprioceptive mismatch in virtual reality environments has typically required subjects to reach to a proprioceptive target (i.e., their left finger) with their adapted (right) hand (Simani et al. 2007; van Beers et al. 2002). While subjects' reaches to the proprioceptive target are altered following visuomotor adaptation, it is not possible to conclude that these changes in reaches arise due to changes in felt hand position of the adapted or opposite (nonadapted) hand. Instead changes in proprioceptive reaches may arise because the motor commands or sensorimotor mappings underlying the reaching movements have been adapted. Moreover, even if subjects were required to reach with their nonadapted hand (i.e., their left hand to a proprioceptive right hand target), there would still be confusion regarding the source of potential reach errors as motor adaptation has been shown to transfer from the trained to the untrained limb (Sainburg and Wang 2002; Wang and Sainburg 2003, 2004, 2006). Thus in our task, we assessed changes in felt hand position following exposure to a visual-proprioceptive conflict in a task in which there was no goal-directed reaching component. In particular, subjects verbally indicated the position of their hand with respect to a visual reference marker. Using this same perceptual task, we previously showed (Cressman and Henriques 2009) that actively reaching with misaligned visual feedback of the hand changes the felt hand position such that the hand is perceived to be shifted in the same direction as visuomotor adaptation. In the current study, we tested whether goal-directed movements are necessary for this sensory recalibration and for reach adaptation.

METHODS

Subjects

In total, 20 healthy, right-handed university students [21.4 ± 6.08 (SD) yr] volunteered to participate in 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. All subjects gave informed consent, and the study was conducted in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee.

General experimental setup

A side-view of the setup is illustrated in Fig. 1*A* and is the same as that used in Cressman and Henriques (2009).

Stimulus display/hand movement

At the start of each trial, the robot manipulandum was positioned below the home position, ~25 cm directly in front of the subject's midline (green circle in Fig. 1*B*). This position was indicated visually by a green filled circle, 1 cm in diameter. Visual stimuli (1 cm diam and represented by the red and black colored circles in Fig. 1*B*) were displayed 10 cm from the home position, 45 and 30° left (counter clockwise, CCW) and right (clockwise, CW) of center and directly above the home position (0°).

MOVEMENT TARGETS. These targets were located 30° left and right of center and directly above the home position (0°; red filled circles in Fig. 1*B*). Subjects actively pushed their hands out along a robot-generated constrained linear path or had their hands passively moved along the same path while viewing a cursor that represented their unseen hand position. The cursor headed directly to one of the three

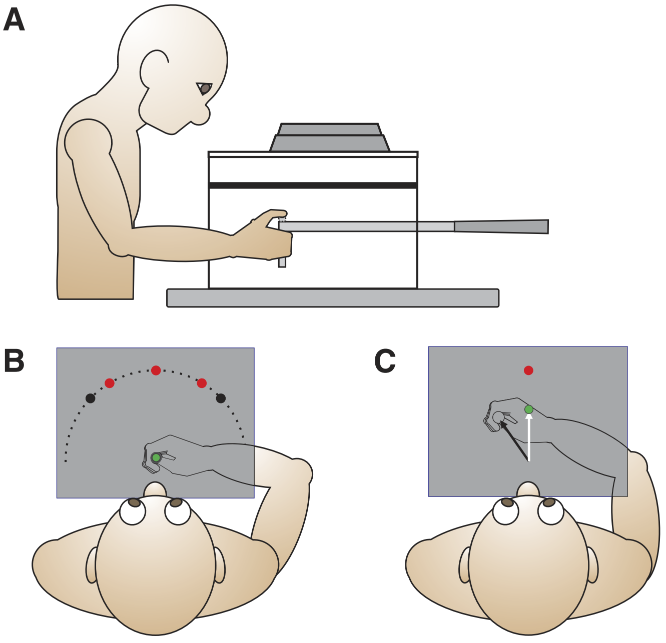

FIG. 1. Experimental setup and design. *A*: side view of the experimental setup. *B*: top view of experimental surface visible to subjects. The center home position was represented by a 1 cm green circle. Movement targets and reference markers for the proprioceptive estimates were located along a circular arc, 10 cm from the home position. They were positioned 30° on either side of center and at center and are shown by the red filled circles. Novel (generalization) reach targets were positioned 45° on either side of center, 10 cm from the home position, and are shown in black. Note that the black dotted line is provided as a reference to indicate the locations of the targets and reference markers and illustrate potential positions that the hand could have been moved to during the proprioceptive estimate trials. *C*: visual-proprioceptive discrepancy introduced in the misaligned cursor hand motion task. The path the hand traveled (black arrow) was rotated 30° CCW with respect to the actual cursor direction (white arrow). On all visually guided hand motion trials the cursor appeared to travel directly to the movement target.

remembered targets. 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 (Cressman and Henriques 2009; Henriques and Soechting 2003; Jones et al. 2010).

REACH TARGETS. To assess reaching errors, we had subjects reach freely to five different target positions without a cursor. The targets included the same three previously described movement targets as well as two additional radial targets located 45° left and right of center (black filled circles in Fig. 1*B*).

REFERENCE MARKERS FOR PROPRIOCEPTIVE ESTIMATES. We assessed changes in subjects felt hand position (i.e., proprioceptive recalibration) by determining the position at which subjects perceived their hands were aligned with three reference markers. The reference marker locations were the same as the three movement targets (red filled circles in Fig. 1*B*). On these trials, subjects actively pushed the robot out from the home position along a constrained path to a location somewhere along the dotted line shown in Fig. 1*B*. Once the hand reached its final position, one of the three reference markers appeared and subjects made a two-alternative forced choice (2-AFC) judgment about the position of their hand (left or right) relative to the reference marker. Subjects were instructed that there were no time constraints during the task.

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 staircases, one starting 20° to the left (CCW) of the reference marker and one starting 20° to the right (CW). The two staircases were adjusted independently and randomly interleaved as outlined in Cressman and Henriques (2009).

Procedure

We had two different groups of subjects. The first group of subjects (11 subjects) actively pushed their hands out along a constrained path while seeing a cursor (active exposure group). The second group of subjects (9 subjects) had their hands passively moved out along the same constrained path (passive exposure experiment). For all subjects, the experiment was completed in one testing session that consisted of two parts. Each part consisted of four tasks as described in the following text and illustrated in Fig. 2. The first part of the testing session (Fig. 2*A*) served as a baseline measure in which we assessed reaching errors and proprioceptive estimates of hand position after subjects were exposed to a veridical cursor during the constrained hand motion task described below. In the second part (Fig. 2*B*), we assessed reaching errors (i.e., visuomotor adaptation) and sense of felt hand position after subjects were exposed to a misaligned cursor during constrained hand motion.

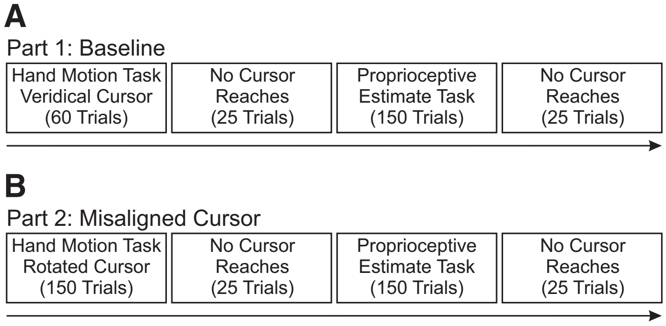

FIG. 2. Schematic showing the order in which the different tasks were completed within a testing session. *A*: tasks run during the 1st half of each testing session, which provided baseline measures of performance. *B*: tasks completed during the 2nd half of each testing session, where the cursor was rotated from the actual hand location during the hand motion task (box 1).

We will begin by describing the tasks used in the first part of the testing session (Fig. 2*A*). The tasks are described in the order in which they were completed.

Baseline hand motion task

In this first task (Fig. 2*A,* 1st box), subjects began each trial with the robot, and hence their hand, positioned directly below the illuminated home position. One of the three movement targets was then displayed. After 500 ms, the target was extinguished, and subjects either pushed the robot handle out along a constrained path (active exposure group) or had their hands passively moved along the same constrained path (passive exposure group) while viewing a cursor that moved with the hand. For the passive exposure group, the hand was moved outward with a constant velocity of 4 cm/s to match the average velocity achieved by subjects in the active exposure group. On movement onset, the home position was turned off. To ensure that subjects' paid attention to the cursor, we had subjects stop their movements when they thought the cursor had reached the remembered target position and, after stopping their movement, indicate via a key press if the cursor had blinked during the movement. The cursor blinked for 30 ms in the middle portion of its trajectory on ~50% of all trials. Subjects in the passive exposure group stopped the robot by pressing a key on a keyboard. After keying in their response regarding the cursor blink (i.e., yes, the cursor blinked, or no, the cursor did not blink), subjects either moved their hands (active exposure group) or had their hands passively moved (passive exposure group) back to the home position via the constrained grooved path. Subjects completed 60 trials, 20 to each of the three movement targets. The trials were pseudo-randomized such that each target was displayed at least once before any target was repeated.

No cursor reaching task: to assess reach errors

This task (2nd box in Fig. 2*A*) was performed immediately after the baseline hand motion task. On these trials, the robot was free moving, such that subjects' movements were no longer constrained to the previously described linear path. A trial would start with the robot handle at the illuminated home position. One of the five reach targets would then appear, and after 500 ms, the home position would disappear. This was the cue for subjects to reach out using the robot handle, without the cursor or any visual feedback of the hand, to the still visible target. Once the reach movement was complete (final position was held for 250 ms), the target would disappear and the home position would reappear, cuing subjects to move back to the home position along a constrained path to begin the next trial. This task consisted of 25 trials (5 reaches to each reach target).

Proprioceptive estimate task: to assess sense of felt hand position

This next task (3rd box in Fig. 2*A*) began with subjects grasping the handle of the robot manipulandum at the visible home position for 500 ms. After 500 ms the home position was removed, and subjects were to actively push the robot handle out along a constrained linear path. The path guided the hand to a location somewhere along the dashed line shown in Fig. 1*B,* which is displayed for reference. Once the hand reached its final position, a reference marker appeared and subjects indicated the position of their hand (left or right) relative to the reference marker. Subjects completed 150 proprioceptive estimates (50 for each reference marker in a randomized order).

No cursor reaching task: to assess reach errors

Immediately after completing the proprioceptive estimates, subjects once again performed a series of reaches without any visual feedback

(4th box in Fig. 2*A*). This was done to ensure that subjects' were still reaching in a similar manner as before the proprioceptive estimate trials.

This ended the first part of the testing session. Subjects were encouraged to take a few minutes break before starting the second half. The tasks in the second half of the testing session (Fig. 2*B)* were the same as just outlined except that the baseline hand motion task was replaced with the misaligned cursor hand motion task described below.

Misaligned cursor hand motion task

The second part of the testing session began with the misaligned cursor hand motion task (Fig. 2*B,* 1st box). This task was very similar to the veridical cursor hand motion task described previously. However, instead of having a cursor accurately represent the position of subjects' hands while they either actively or passively moved along a constrained path, now, the hand path was gradually rotated 30° CCW with respect to the cursor over the first 41 trials in increments of 0.75° (Fig. 1*C*). Subjects completed 150 trials in total, 50 to each movement target with the cursor present. Total testing time was ~2 h/session.

Additional tasks: extra exposure

Three of our 11 subjects in the active exposure group completed a second round of the misaligned cursor hand motion task (box 1 in Fig. 2*B*) to determine if additional exposure to the misaligned cursor would increase visuomotor adaptation and/or proprioceptive recalibration. Specifically, these subjects completed an additional 150 trials of pushing the robot out along a constrained path while observing a cursor that was rotated 30° CW with respect to their hand path. They also completed the no cursor reaching task again. These additional hand motion and reach trials were completed before the subjects performed the proprioceptive estimate task.

Data analyses

The two goals of this study were to determine if exposure to a misaligned cursor when one is not free to make a voluntary reach and/or reaching errors leads to visuomotor adaptation and/or a change in sense of felt hand position. However, before addressing these goals, we first wanted to ensure that subjects were paying attention to the cursor during the baseline and misaligned cursor hand motion tasks and did not notice the visual-proprioceptive mismatch. We found that on average, the robot was stopped 10.2 ± 0.7 (SD) cm after movements were initiated, indicating that the cursor overlapped with the remembered position of the movement targets. In addition, subjects correctly reported whether the cursor had blinked or not on >91% of all trials. *T*-tests revealed no difference in results between the active and passive exposure groups with respect to the distance traveled by the robot ($P > 0.05$) or the percentage of correctly reported cursor blinks ($P > 0.05$). After completing the experiment, all subjects indicated that they were unaware of the sensory mismatch introduced during the misaligned cursor hand motion task. Moreover, no subjects reported being aware of a possible time lag between their movements and the movement of the cursor. Having established that subjects paid attention to the cursor and were unaware of any sensory mismatch, we next examined if subjects adapted their reaches after being exposed to the misaligned cursor. In the statistical analyses discussed in the following text and the following figures, data corresponding to the active exposure group do not include the three subjects who completed an additional round of the misaligned cursor hand motion task.

Reach errors

To examine if subjects adapted their reaches in response to the misaligned cursor, we looked at the reaches completed in the no cursor reach tasks. For each reach trial, we calculated the reaching error by determining the angular difference between a reference vector joining the center home position and the target and the vector joining the center home position and the reach endpoint location. To determine whether subjects' adapted their reaches after exposure to the misaligned cursor and if this adaptation was maintained across the testing session, we analyzed mean reaching errors to the movement targets in a 2 visual feedback during the hand motion task (baseline or misaligned cursor) × 2 time (trials completed before or after the proprioceptive estimate task) repeated measures analyses of variance (RM-ANOVA), for both the active and passive exposure groups. In other words, we compared boxes 2 and 4 in Fig. 2*A* with boxes 2 and 4 in 2*B*.

We also compared reaching errors immediately following the hand motion tasks at the movement targets to reach errors at the novel (45°) reach targets in a one-way RM-ANOVA to measure the extent of reach generalization. In this analysis, reaching errors following exposure to a veridical cursor (2nd box in Fig. 2*A*) were subtracted from those following exposure to a misaligned cursor (2nd box in 2*B*).

As a final analysis, we compared the changes in reaching errors between the active and passive exposure groups using an ANOVA. Like the movement versus novel target analysis just discussed, we subtracted the reaching errors following exposure to a veridical cursor from those produced after exposure to a misaligned cursor for each experiment.

Proprioceptive estimates of hand position

To address our second research question regarding possible changes in proprioceptive estimates of hand position, we determined the locations at which subjects felt their hands were aligned with the reference markers. In particular, we calculated the bias (i.e., accuracy - the point of 50% probability) and the degree of uncertainty (i.e., precision - the difference between the values at which the response probability was 25 and 75%) from the proprioceptive estimates using the binary logistic fit in the Statistical Package for the Social Sciences (Cressman and Henriques 2009; Henriques and Soechting 2003; Wong and Henriques 2009). We excluded six proprioceptive estimates from our analyses as the associated uncertainty was greater than the mean uncertainty across all reference markers +2 SD. To compare the biases and the uncertainty ranges following exposure to a veridical versus misaligned cursor, we used a RM-ANOVA, which included reference marker location (3 locations) as a factor.

Similar to the analysis performed on reaching errors, we also compared changes in biases between the active and passive exposure groups in an ANOVA. In this analysis, changes in bias following exposure to a misaligned cursor during the hand motion task relative to biases completed after exposure to a veridical cursor during the hand motion task were collapsed across reference marker locations. This was done as in both experiments similar changes in bias were observed regardless of reference marker location. Finally, we examined whether the change in bias after exposure to a misaligned cursor was similar to the level of visuomotor adaptation. To perform this analysis, we used a RM-ANOVA to compare mean changes in bias to mean changes in reaching errors for both the active and passive exposure groups.

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

RESULTS

Reach adaptation

We first determined the extent to which subjects' adapted their reaches (i.e., the extent of visuomotor adaptation). Figure 3 displays mean reaching errors for reach trials completed without a cursor to each reach target in both the active (*A*) and

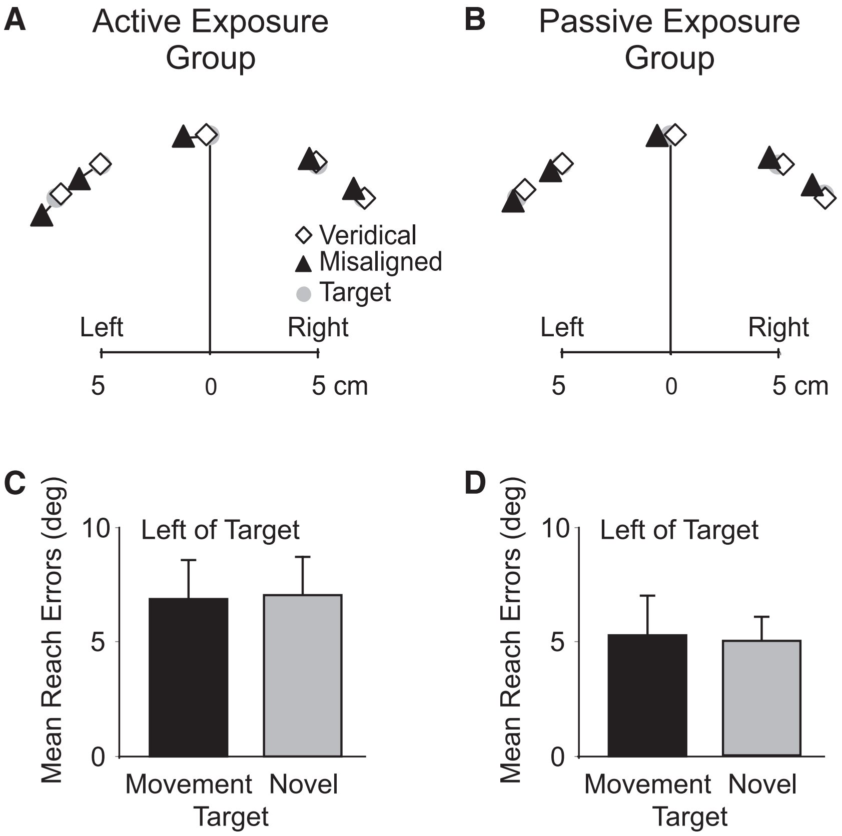

FIG. 3. Mean 2-dimensional (2-D) reaching endpoint errors in the no cursor reaching trials after subjects were exposed to a veridical (◇) or misaligned (▲) cursor during the hand motion tasks for the (*A*) active exposure group and (*B*) passive exposure group. Reach targets are represented as filled grey circles (●) and a line connects each target with the corresponding reach errors. *C* and *D*: mean visuomotor adaptation averaged across subjects and targets following active and passive exposure, respectively, for both trained movement targets (■) and novel targets (▨). Errors are presented taking performance on reaches completed after exposure to a veridical cursor as baseline. In other words, errors achieved on the no cursor reaching trials after exposure to a veridical cursor were subtracted from corresponding errors achieved after exposure to a misaligned cursor. Error bars reflect SE.

passive (*B*) exposure groups. The target positions are represented as filled grey circles and the diamonds and triangles indicate mean reaching errors after subjects were exposed to a veridical and misaligned cursor in the hand motion task, respectively. In comparing reach errors after exposure to the misaligned versus veridical cursor, we find a small leftward shift (on average 6°). In other words, the triangles are shifted to the left of the diamonds. Additional exposure to the misaligned cursor did not increase the level of visuomotor adaptation as we found that the three subjects who completed an additional block of misaligned cursor exposure in the active exposure group had mean reach errors of 6.8° (these data are not shown).

In Fig. 3, *C* (active exposure group) and *D* (passive exposure group), we show the changes in reach errors after subjects were exposed to the misaligned cursor compared with the veridical cursor during the hand motion task for both the movement targets (black bars) and novel targets (grey bars). As suggested in the preceding text and demonstrated by the black bars, subjects reached more to the left of the targets after being exposed to the misaligned cursor compared with the veridical cursor [active exposure, $F(1,7) = 12.902$, $P = 0.009$; passive exposure, $F(1,8) = 10.866$, $P = 0.011$)]. This change in subjects' reaches was maintained throughout the testing session as the magnitude of visuomotor adaptation did not diminish after the proprioceptive estimate task [active exposure, $F(1,7) = 1.381$, $P = 0.278$; passive exposure $F(1,8) = 1.105$, $P = 0.324$]. Furthermore, subjects adapted their reaches to the novel targets such that the reach errors at the novel targets did not differ from those at the trained movement targets [black bars vs. grey bars in Fig. 3, *C* and *D;* active exposure: $F(1,7) < 1$, passive exposure: $F(1,8) < 1$]. Finally, as can be seen by comparing across Fig. 3, *C* and *D,* we found that subjects adapted their movements to a similar extent regardless of whether they actively pushed the robot out while seeing the cursor or were passively moved [$F(1,16) < 1$].

Proprioceptive recalibration

To determine whether exposure to visually deviated hand motion also lead to changes in sense of felt hand position, we now turn to subjects' proprioceptive biases. Figure 4 shows these biases, averaged across subjects after exposure to both a veridical diamonds and misaligned triangles cursor, relative to the corresponding reference markers circles for the active (*A*) and the passive (*B*) exposure groups. In the active exposure group (Fig. 4*A*), we see that subjects' estimates of their unseen hand positions were slightly biased to the left after exposure to a veridical cursor. The mean bias collapsed across all reference markers was 4.6° left of the reference marker. However, more importantly, after exposure to the misaligned cursor, estimates of felt hand position were shifted significantly to the left of the estimates completed after exposure to the veridical cursor [$F(1,7) = 12.294$, $P = 0.010$]. Furthermore, this leftward shift in subjects' biases was observed at all reference marker positions and was of a similar magnitude across the different reference markers [$F(2,14) < 1$]. On average, mean bias after exposure to a misaligned cursor during the hand motion task was 9.5° left of a given reference marker (black bar in Fig. 4*C*), ~4.9° more left than after exposure to a veridical cursor (white bar in Fig. 4*C*). The estimates of the three subjects who completed the additional misaligned cursor hand motion task were shifted ~4° to the left after seeing a misaligned cursor compared with a veridical cursor.

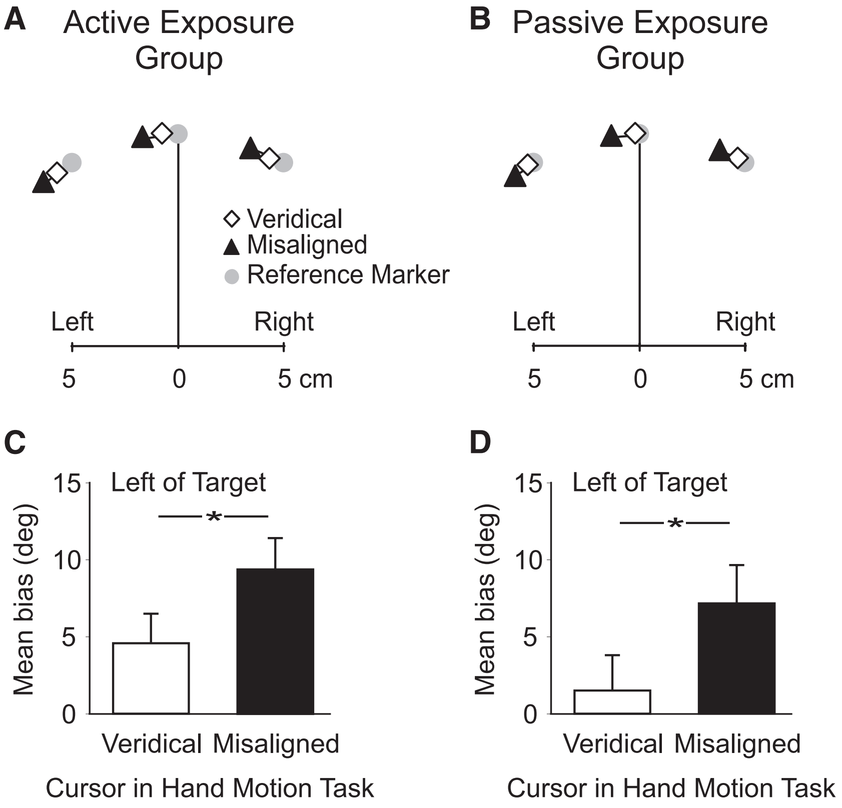

FIG. 4. Mean 2-D biases on the proprioceptive estimate tasks after subjects were exposed to a veridical (◇) or misaligned (▲) cursor during the hand motion task for the active exposure group (*A*) and passive exposure group (*B*). Reference markers are represented as filled grey circles (●) and a line connects each reference marker with its corresponding hand reference marker alignment biases. *C* and *D*: mean biases averaged across subjects and reference marker positions for the active and passive exposure groups, respectively: veridical cursor (□) or misaligned cursor (■). Error bars reflect SE.

A similar pattern of results was observed in the passive exposure group. As shown in Fig. 4*B* (and *D*), the positions at which subjects' estimated their hands were aligned with a reference marker were significantly more to the left, an average of 5.6°, after being exposed to the misaligned cursor compared with a veridical cursor [$F(1,8) = 14.822$, $P = 0.005$]. Like the active exposure conditions, this change in subjects' biases was independent of reference marker location [$F(2,16) < 1$]. Finally, the change in sense of felt hand position was similar across the active and passive exposure groups [$F(1,16) < 1$].

The changes in proprioceptive biases were also similar to the adjustments observed in subjects' reaches (Fig. 5*A*). Specifically, for subjects in both the active and passive exposure groups, there was no difference between the magnitude of visuomotor adaptation and proprioceptive recalibration [active exposure: $F(1,7) = 1.421$, $P = 0.272$, passive exposure: $F(1,8) < 1$]. Moreover, if we plot these changes in proprioceptive estimates as a function of visuomotor adaptation for each subject in both exposure conditions, we see a significant correlation between the magnitude of reach adaptation and changes in felt hand position (Fig. 5*B*, $P = 0.007$).

Finally, subjects in the active exposure group had a similar level of precision in estimating the felt locations of their unseen hands (~10.5°) after seeing a veridical and misaligned cursor [$F(1,7) < 1$], regardless of the reference marker location [$F(2,14) < 1$]. For subjects in the passive exposure group,

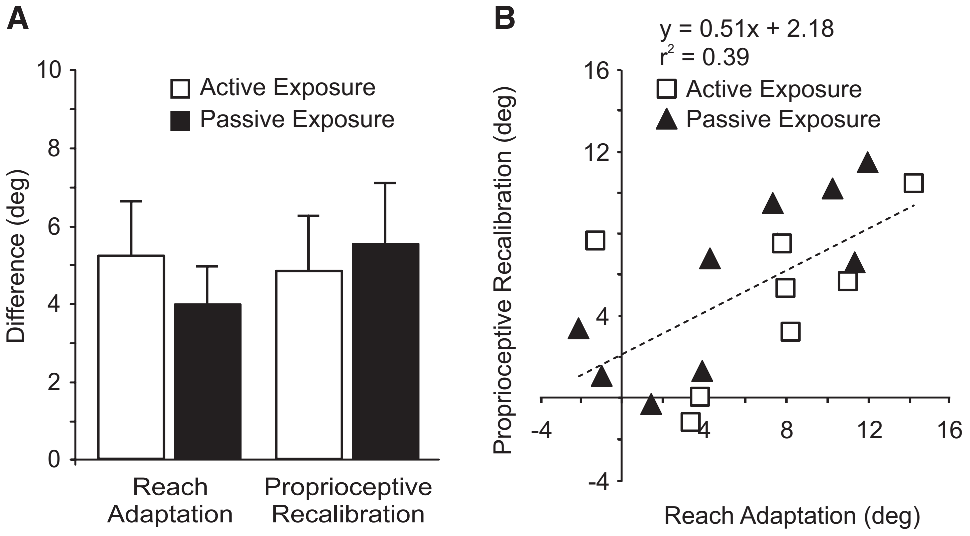

FIG. 5. *A*: the difference in reach errors and proprioceptive biases after exposure to a misaligned cursor compared with a veridical cursor during the hand motion task for the active exposure group (□) and passive exposure group (■). Error bars reflect SE. *B*: the changes in proprioceptive estimates are plotted as a function of reach errors for each subject after exposure to a misaligned cursor compared with a veridical cursor (active exposure group: □, passive exposure group: ▲). - - -, the linear regression line fitted to all subjects' data.

proprioceptive estimates were actually more precise after completing the misaligned cursor hand motion task compared with the baseline hand motion task [$F(1,8) = 8.142$, $P = 0.021$]. As well, proprioceptive estimates were ~5° more precise at the center reference marker position than the left reference marker regardless of the hand motion task completed [$F(2,16) = 9.557$, $P = 0.006$].

DISCUSSION

We found that subjects adapted their reaches and recalibrated sense of hand position after being exposed to a visual-proprioceptive discrepancy. Specifically, after viewing a cursor that misrepresented the location of their hands during nonvoluntary hand motion, subjects misreached in the same direction that their hands were moved and began to feel that their hands were shifted in the direction of the cursor. Both changes in reaches and proprioceptive estimates were shifted by ~5.6° or 19% in the direction of the visual distortion, regardless of whether subjects were exposed to a misaligned cursor when they actively moved their hands along a constrained path or were passively moved along the same path. As well, the change in bias occurred without subjects' decreasing the precision of their proprioceptive estimates. In this way, we were able to show that mere exposure to sensory discrepancies, in the absence of voluntary movement, can lead to sensory recalibration and reach adaptation (i.e., visuomotor adaptation). Thus reach adaptation arises even when one does not have the opportunity to move voluntarily during exposure to the misaligned cursor, contradicting the reafference hypothesis as currently put forth in the prism literature.

Sensorimotor integration: forming a new internal model

According to current models, visuomotor adaptation arises when reaching with altered visual feedback of the hand as a result of a new internal model forming for the new visuomotor mapping (Kawato 1999; Miall and Wolpert 1996; Tong and Flanagan 2003; Wolpert 1997; Wolpert et al. 1995). Specifically, one learns that in order to guide a cursor, that is rotated CW with respect to the hand, to a target, one must actually aim to the left of the target. These error-based changes in reaches arise even when one is unaware of the visuomotor distortion (Klassen et al. 2005). It has been proposed that changes in reaches are driven by sensory errors arising from movement execution (i.e., error-based learning). For example, because the predicted sensory feedback (e.g., attaining the target) does not match the actual sensory feedback (e.g., the cursor indicates the hand is to the right of the target) initially, one adjusts subsequent motor commands to achieve the desired outcome. In addition, the perceived position of the hand is thought to be recalibrated such that proprioceptive signals are remapped to a given visual input (Haith et al. 2008; Simani et al. 2007).

In our study, the cursor always traveled directly to the target, and hence there was no feedback indicating that the path the hand had traveled was incorrect. Moreover, given that the hand moved outward along a constrained fixed path, there was no voluntary movement planning. Subjects could not plan the direction of their movement. As well, subjects in the passive exposure group could not control when their hand motion was initiated or how quickly their hand was moved. While we did not examine muscle activation [e.g., by using electromyography (EMG)] and thus cannot comment on whether subjects in the passive exposure group attempted to actively track the movement of the robot manipulandum by activating their muscles, we can state that for the passive exposure group, any muscle activation would not have produced a corresponding self-generated movement.

However, despite the lack of movement related error signals and voluntary moment, subjects in the current study still adapted their reaches in response to the visual distortion introduced. Specifically, after subjects' hands were moved along a constrained path rotated CCW with respect to a cursor, subjects aimed more to the left (~6° CCW) of an intended target when given the opportunity to reach freely with no cursor present. In addition, we found that proprioception was partially recalibrated in the direction of the visual discrepancy such that subjects perceived their hands were aligned with a visual reference at a more leftward position (~5°) after seeing a misaligned cursor compared with a veridical cursor.

Given that reach adaptation and proprioceptive recalibration occurred after both active and passive misaligned cursor exposure, it appears that the models accounting for visuomotor adaptation discussed above may not be complete. Specifically, we show that one does not need to produce voluntary movement and receive the contingent error information to adapt to altered sensory feedback of the hand. However, it is important to keep in mind that the extent of reach adaptation we find in the current study is much less than what has been shown in previous work in which subjects were introduced to a rotated cursor while performing voluntary movements (Krakauer et al. 1999, 2000; Wang and Sainburg 2005). For example, in our previous study (Cressman and Henriques 2009), we found reaching errors of ~18°, after subjects trained with the same 30° rotated cursor in the same setup. In contrast, the 5° proprioceptive recalibration we find in this current study is comparable to the level of proprioceptive recalibration we previously attained when subjects were allowed to reach freely. Given the similarity in magnitude between the two adaptive responses in the current study and the significant correlation between reach adaptation and proprioceptive recalibration, perhaps the reach adaptation we now observe is due to the change in felt hand position. Subjects feel their hand is more right than it actually is and hence when they go to plan a movement, this misperceived position is taken into account, resulting in leftward reaching errors (Jones et al. 2010; Vindras et al. 1998). Thus perhaps the current models need to account for the role of proprioceptive recalibration in the formation of a new visuomotor mapping.

Motor adaptation following repetition-induced reinforcement

It has recently been proposed that changes in reaches can arise not only due to error-based learning but also after one performs multiple movement repetitions in a particular direction (Diedrichsen et al. 2009). In the task by Diedrichsen and colleagues, a robot passively moved a subject's hand to an elongated box that could be achieved by moving to any position along its horizontal axis. Unbeknownst to the subjects, the robot moved the subject's hand such that it deviated either 8° to the left or 8° to the right of straight ahead. However, the hand always landed in the target box. When subjects were then to aim freely to that target, Diedrichsen found that their movements showed an aftereffect, such that the direction of the movements were biased in the same direction that the robot had moved the hand relative to center. On the basis of these results Diedrichsen has proposed that learning can arise due to a use-dependent process where the brain associates the current goal with the last executed movement.

It is unclear if (or how) use-dependent processes influenced visuomotor adaptation and sensory recalibration in the current study. The results of our no cursor reaching task would suggest that the visuomotor adaptation we observe does not arise due to use-dependent processes directly. Subjects completed the no cursor reaching task twice; once after having their hand moved in a leftward (CCW) direction relative to the target during the hand motion task (biased movement) and then again after completing 150 proprioceptive estimates in which they pushed their hands out along constrained pathways that were, for the most part, symmetrically oriented around center (i.e., the hand moved outwards between 50° CW and CCW of center without a directional bias). Reach errors were similar across the two no cursor reaching tasks. Given this similarity and the fact that the second no cursor reaching task was completed after subjects moved their hands out in a nonbiased direction, it appears that use-dependency processes did not underlie the motor adaptation achieved in the present study. However, use-dependency processes may have given rise to changes in movements indirectly as the ability of use-dependency processes to influence proprioceptive recalibration is currently unknown. Thus future research is required to determine the role of use dependency on proprioceptive recalibration and visuomotor adaptation.

Conclusion

When subjects are exposed to a visual-proprioceptive discrepancy (intersensory based errors), they adapt their reaches and begin to feel their hand is shifted in the direction of the cursor. Based on our present results, we propose that this reach adaptation may be due to changes in visually driven proprioceptive recalibration. Furthermore, in accordance with the reafference hypothesis and error-based learning theories, we suggest that to attain a greater level of reach adaptation (i.e., a level typically attained in visuomotor tasks where subjects are allowed to move freely), one must have the opportunity to make a voluntary movement and experience the sensory consequences of that movement.

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