Effect of visuomotor-map uncertainty on visuomotor adaptation

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Running head:
Visuomotor-map uncertainty affects reaching adaptation.

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Abstract

Vision and proprioception contribute to generating hand movement. If a conflict between the visual and proprioceptive feedback of hand position is given, reaching movement is initially disturbed but recovers after training. Although previous studies have predominantly investigated the adaptive change in the motor output, it is unclear whether the contributions of visual and proprioceptive feedback controls to the reaching movement are modified by visuomotor adaptation. To investigate this, we focused on the change in proprioceptive feedback control associated with visuomotor adaptation. After the adaptation to gradually introduced visuomotor rotation, the hand reached the shifted position of the visual target to move the cursor to the visual target correctly. When the cursor feedback was occasionally eliminated (probe trial), the endpoint of the hand movement was biased in the visual target direction while the movement was initiated in the adapted direction, suggesting the incomplete adaptation of proprioceptive feedback control. Moreover, after the learning of uncertain visuomotor rotation in which the rotation angle was randomly fluctuated on a trial-by-trial basis, the endpoint bias in the probe trial increased but the initial movement direction was not affected, suggesting a reduction in the adaptation level of proprioceptive feedback control. These results suggest that the change in the relative contribution of visual and proprioceptive feedback controls to the reaching movement in response to the visuomotor-map uncertainty is involved in visuomotor adaptation, while feedforward control might adapt in a manner different from that of the feedback control.
Introduction

Vision and proprioception are dominant sensory channels of hand position information. The CNS integrates the redundant sensory information to control hand movement (Smeets et al. 2006; Sober and Sabes 2005; van Beers et al. 1999). When conflict between visual and proprioceptive feedback of hand position is given by a prism goggle (Harris 1963; Martin et al. 1996; Redding and Wallace 1996) or by rotating the movement direction of a visible hand cursor from that of the actual hand (visuomotor rotation) (Cunningham 1989; Imamizu et al. 1995; Krakauer et al. 2000), the reaching movement is initially disturbed but recovers after training. Previous studies have suggested that a new map from sensory input to motor output or new internal model of kinematics is acquired by the successive training (Ghahramani et al. 1996; Imamizu et al. 1995; Kitazawa et al. 1997; Krakauer et al. 2000; Vetter et al. 1999). However, despite the existence of at least two dominant sensory channels (e.g., vision and proprioception) for controlling hand movement, it is still unclear how those redundant sensory inputs are used for visuomotor adaptation.

A recent study has suggested that visuomotor adaptation results in the proprioceptive recalibration of hand position (Cressman and Henriques 2009). The perceived hand position was measured without visual feedback before and after the visuomotor adaptation task and it was found that the ‘felt hand position’ was biased from the actual hand position after the adaptation. Although visuomotor adaptation would result in the bias of felt hand position, it is still unclear whether such perceptual bias significantly contributes to the visuomotor performance.

Other studies, on the other hand, have suggested that multisensory information is not required for movement adaptation under a novel environment; that is, the absence of one
sensory modality is not critical for motor adaptation. For instance, reaching movement can adapt to a novel dynamic force field without visual feedback (Franklin et al. 2007; Scheidt et al. 2005). In addition, deafferented patients who were deprived of limb proprioception due to a severe sensory neuropathy show reaching adaptation to a force field (Sarlegna et al. 2010) or the prism goggle (Bernier et al. 2006; Ingram et al. 2000). However, if both visual and proprioceptive feedbacks of hand position are available for hand movement control, both of them might be used for movement adaptation to a novel environment.

The main objective of this study was therefore to investigate whether visual and proprioceptive feedback control adaptations are progressed equally in a novel visuomotor environment. For this purpose, we focused on the adaptation of proprioceptive feedback control during the learning of visuomotor rotation. We observed the reaching trajectory when the visual cursor feedback was eliminated in some trials (probe trials). If the proprioceptive feedback control completely adapts to the visuomotor rotation, the hand should reach the shifted position of the visual target even in the probe trial; that is, the ‘invisible’ cursor should reach the visual target correctly. We also investigated whether the balance of the adaptation levels of visual and proprioceptive feedback controls are modulated in response to the visuomotor environment. We introduced a random trial-by-trial fluctuation of the visuomotor rotation angle during the training phase. Because subjects were required to adjust their actual hand movement according to the visual feedback to compensate for the random fluctuation of rotation angle, the reliability of proprioceptive feedback would decrease and the adaptation level of proprioceptive feedback control would be reduced. Our results indicate that the adaptation level of proprioceptive feedback control is modulated on the basis of the reliability of the sensory...
inputs. Part of this study has been presented elsewhere in abstract form (Saijo and Gomi 2010b).

Materials and Methods

Subjects and experimental setup

Fourteen naïve subjects (nine males, five females; 20 to 35 years old, average 28.3 ± 3.9) participated in the main experiment. Three of these subjects (one male, two females) and another seven subjects (four males, three females, 21 to 32 years old, average 27.7 ± 3.8) participated in the control experiments. All subjects had normal or corrected-to-normal vision, and all were right-handed. None of the subjects reported any histories of visual or motor deficits. All subjects gave written informed consent to participate in the study, which was approved by the NTT Communication Science Laboratories Research Ethics Committee.

The experimental setup was identical to that of our previous study (Saijo and Gomi 2010a). Briefly, each subject sat in front of the manipulandum (Gomi and Kawato 1996) while strapped securely to the chair back with the head placed on a chin support (Fig. 1A). The right forearm was tightly coupled to the handle with a molded plastic cuff and supported against gravity by a horizontal beam. The manipulandum system was digitally controlled to reduce the dynamical effect of the handle on the subject’s hand. Therefore, subjects were able to move the handle easily in any direction.

Visual stimuli were generated by a computer and projected by a data projector (60-Hz refresh rate; PLUS U2-X2000; PLUS Vision Corp., Tokyo, Japan) on a horizontal screen (1.2 × 1.0 m) placed just above the subject’s forearm. The screen concealed the arm from the
subject's view. The start position (blue circle, 1 cm in diameter) was placed 15 cm leftward and 45 cm forward from the right shoulder position on the screen. The target (green disk, 2 cm in diameter) was shown at one of four positions on the right side from the start position with intervals of 36° and 15 cm from the start position (-36°, 0°, 36° and 72°. Here, the rightward direction was 0° and the counterclockwise (CCW) direction was positive (See Fig. 1A). The cursor (red disk, 1 cm in diameter) was shown just above the hand position, while its position was rotated in the CCW or clockwise (CW) direction around the start position (visuomotor rotation) in the experiments. The computer received the hand position measured by the manipulandum system at 2 kHz in real time and updated the cursor position at 60 Hz (which corresponded to the refresh rate of the data projector).

**Task**

The subject was instructed to move the cursor to the visual target position as soon and as accurately as possible in reaction to the visual target appearance. Figure 1B shows the time sequence of one trial. When the cursor was aligned for 0.5 s to the start position, the cursor and start position were eliminated with a short beep sound. Following a random delay period (0.5 – 1.0 s), the target was shown at one of four positions in pseudo-random order. The actual time of target appearance was precisely measured with a photodiode (Hamamatsu Photonics S1223-1).

There were two types of trials, visual feedback (VF) and probe trials (Fig. 1B). In the VF trial, the cursor appeared immediately after the reaching initiation and was illuminated for 1.0 s. In the probe trials, the cursor did not appear during the movement. For the latter case, the subjects were instructed, in advance, to try to move the invisible cursor to the visual
target if the cursor did not appear.

The short beep sound was given again 2.7 s after the target appearance (which corresponded to the end of the recording time). At the same time, the cursor was again turned on for 1.0 s to indicate the reaching end position in the VF trial, while it was not in the probe trials. Thereafter, the hand was automatically pulled back to around the start position by the manipulandum.

Training sequence

Figure 1C shows the training sequence of the main experiment. The experiment consisted of four training phases: pre-training (10 blocks), training (20 blocks), post-training (10 blocks), and washout (10 blocks) phases. One trial block consisted of eight VF trials (two trials for each target direction, random order) and two probe trials (presented every five trials). To align the ideal hand movement directions between the phases, the probe trials were presented with 0° and 36° targets in the pre-training and washout phases and with 36° and 72° targets in the training and post-training phases.

The visuomotor rotation angle gradually increased in the CCW direction (Kagerer et al. 1997; Saijo and Gomi 2010a). The rotation angle was 0° in the pre-training phase and then was increased 9° every four blocks from the fourth block in the training phase. It reached 36° in the last four blocks of the training phase and was kept at 36° during the post-training phase. In the washout phase, the rotation angle at the first block was 36° and was suddenly changed to 0° from the second block. Post-experiment interviews indicated that all subjects were not aware of the existence of the visuomotor rotation during the experiment. Although in the washout phase they seemed to feel that the condition had changed in some
way, they did not become aware of the disappearance of visuomotor rotation.

There were two training conditions in the main experiment; no-noise and directional-noise. The only difference between them was that the rotation angle was randomly fluctuated in the directional-noise condition. The random angle was chosen from a Gaussian distribution of mean 0° and SD 10° on a trial-by-trial basis and added to the visuomotor rotation angle from the training phase until the first block of the washout phase. All 14 subjects participated in both training conditions. The order of the training conditions was counterbalanced across subjects.

**Control experiments**

We performed two control experiments to confirm whether the observed effect on the reaching movement in the main experiment was actually related to visuomotor adaptation. In one experiment, we investigated whether the changes in the movements in the main experiment were related to the direction of the visuomotor rotation. Five subjects (two males, three females, 29 to 32 years old) learned the CW direction visuomotor rotation. Three of these five subjects (one male, two females) participated in the main experiment and they joined this control experiment after the main experiment. The rotation angle changed -9° in every four blocks from the fourth block in the training phase and it was kept at -36° until the first block of the washout phase. In this condition, the visual target directions were -72°, -36°, 0°, and 36°. To align the ideal hand movement directions along those in the main experiment, the probe trials were presented with 0° and 36° targets in the pre-training and washout phases, and with 0° and -36° targets in the training and post-training phases. In the other experiment, we investigated whether the amount of
training was sufficient to make the movement trajectory stable under the visuomotor rotation in the main experiment. Five subjects (three males, two females, 21 to 31 years old) learned the CCW $36^\circ$ visuomotor rotation as in the main experiment. After the training phase, there were three post-training phases instead of the one post-training phase in the main experiment.

**Data analysis**

The recorded hand position was filtered (fourth-order Butterworth filter; cutoff frequency, 15 Hz) and then the hand velocity and acceleration were computed by numerically differentiating the position data.

The movement initiation was detected when the tangential acceleration exceeded 0.5 m/s$^2$. The movement end was defined as when the tangential velocity fell to 0.05 m/s after the tangential peak velocity. The reaction time (RT) was defined as the time difference between the appearance of the visual target and the reaching onset. Movement time (MT) was obtained from the time difference between the movement initiation and end. Peak velocity (PV) was defined by the tangential peak velocity, and the time to peak velocity ($T_{pv}$) from the movement initiation was obtained.

We quantified two angular errors of reaching trajectory, initial movement direction (ID) and endpoint direction (ED). The ID was obtained by the angular difference between the directions of the visual target and cursor and hand velocity vectors 100 ms after the movement onset. A positive value indicates the CCW direction. The ID is inherently related to the initial feedforward motor command, since it was obtained before the ongoing-movement corrections were induced in response to the visual feedback. The ED
was obtained from the angular difference between the directions of the visual target and the endpoint of the cursor and hand movements.

To analyze the hand movement in the VF and probe trials, the temporal patterns of hand accelerations in the direction orthogonal to the target direction were aligned at the movement onsets and were averaged within the pre- and post-training phases. The mean acceleration pattern across subjects in the probe trial was compared with that in the VF trial to examine the effect of the cursor elimination.

To test the statistical significance of the changes in the above-mentioned indices, the mean of those indices in the pre- and post-training phases were obtained and analyzed in a two-way repeated-measures ANOVA with the factors PHASE (pre/post) and CONDITION (no-noise/directional-noise) or with the factors PHASE and TRIAL TYPE (VF/probe). The significance level was set to 5%.

**Results**

**Effect of visual feedback elimination before and after learning of visuomotor rotation**

Figure 2A shows sample averaged reaching trajectories across subjects in the pre- and post-training phases in the no-noise condition. Note that we show the trajectories for two visual target directions (36°, 0° reach) because the probe trials were presented with those two targets. Black and gray lines indicate the cursor and hand trajectories, respectively. In the pre-training phase (left panels of Fig. 2A), both the cursor and hand reached the visual target. In the post-training phase, on the other hand, the hand reached the 36° CW shifted position from the visual target (right panels in Fig. 2A). Since the cursor movement direction was rotated 36° in the CCW direction from the hand movement direction, the
cursor reached the visual target position. This indicated that the reaching movement
adapted to the visuomotor rotation.

Figure 2B shows the mean initial movement directions (IDs) and endpoint directions
(EDs) of the cursor and hand movements relative to the visual target direction as a function
of trial block. Here, we display the averaged STDs of ID and ED across subjects as the
shaded area in Fig. 2B to show the movement variability across trials. The STDs of IDs and
EDs were obtained in each trial block (e.g., eight trials) for each subject and then averaged
across subjects. Since the visuomotor rotation angle was gradually increased in the training
phase, the ID and ED of hand movements were gradually dissociated from those of the
cursor movements as the training proceeded. The EDs of the cursor and hand movements
were approximately 0° and -36°, respectively, in the post-training phase. On the other hand,
the IDs were slightly biased in the positive direction. This indicated that the reaching
trajectory was slightly curved in the post-training phase. Actually, as shown in the right
panels of Fig. 2A, trajectories were clearly curved in the post-training phase. This may be
caused by the learning of the gradual visuomotor rotation because a similar curved
trajectory was observed in the gradual learning but not in the sudden learning in our
previous study (Saijo and Gomi 2010a).

In the washout phase, a negative aftereffect was observed in both ID and ED. When the
visuomotor rotation angle was suddenly returned to 0° in the second block of the washout
phase, the ID and ED of the cursor movement abruptly changed to negative values since
the cursor and hand movement were aligned. Then they gradually returned to the baseline.
The ED aftereffect was reduced more quickly than the ID aftereffect. This would be caused
by the online adjustment of the movement based on the visual feedback.
The probe trials, in which the cursor was not shown during the movement, were interspaced among the VF trials. Figure 3A shows the averaged trajectories of hand movements in the probe trials (black curves) and in the VF trials (gray curves). In the pre-training phase (left panels), hand trajectories in the probe trials were not largely different from those in the VF trials. However, they were substantially different in the post-training phase (right panels of Fig. 3A). In the middle phase of probe trials, the hand trajectory was curved toward the visual target side, although the hand initially started in approximately the same direction as that in the VF trial.

To examine the statistical difference in the hand movement trajectory between the VF and probe trials, we analyzed the IDs and EDs of the trajectories. Figure 3B shows the averaged IDs (left panels) and EDs (right panels) across subjects in the VF and probe trials. A substantial effect of the probe trial was found in the EDs in the post-training phase. The EDs of probe trials were largely biased in the positive (e.g., CW) direction from those of the VF trials in the post-training phase, although the IDs were not largely different between the two trials.

A two-way repeated-masures ANOVA with the factors PHASE (pre/post) and TRIAL TYPE (VF/probe) in each reaching direction revealed the significant interaction effect on the ED (F(1,13) = 56.02, p < 10^-5 for 0° reaching; F(1,13) = 31.75, p < 10^-4 for 36° reaching). A post hoc test showed that in the post-training phase, the EDs of probe trials in both reaching directions were significantly biased in the positive direction from those of the VF trials (Tukey’s HSD test, p < 10^-7), while in the pre-training phase, a significant ED difference between the probe and VF trials was observed only in the 36° reaching (Tukey’s HSD test, p < 0.05). On the other hand, no consistent effect of the probe trial on the IDs was found. In
the 0° reaching, the interaction effect on the ID was significant ($F_{(1,13)} = 7.80, p < 0.05$). The ID in the probe trial was slightly biased in the negative direction from that in the VF trial in the post-training phase (Tukey’s HSD test, $p < 0.01$). In the 36° reaching, in contrast, no significant interaction effect was observed ($F_{(1,13)} = 2.76, p = 0.12$). Taken together, these results indicate that the curved trajectory in the probe trial after the learning resulted in the endpoint bias in the positive direction.

Figure 3C displays the hand acceleration in the direction orthogonal to the ideal endpoint direction of the hand movement in the pre- and post-training phases. In the pre-training phase (left panels), the acceleration patterns were slightly but not substantially different between the VF and probe trials. In the post-training phase (right panels), in contrast, the significant difference in the pattern was observed. The acceleration in both of the VF and probe trials initially increased and then decreased 100-150 ms after the movement onset. Then, the acceleration in the probe trial increased again in the visual target direction approximately 250 ms after the movement initiation, while it continuously decreased in the VF trial. This indicated that the hand movement in the probe trial was adjusted in the visual target direction after the initiation of the movement in the post-training phase.

Effect of directional noise on reaching trajectory

In the directional-noise condition, a random angle, which was chosen from a Gaussian distribution with of mean 0° and SD 10° on a trial-by-trial basis, was added to the visuomotor rotation angle during the training and post-training phases. Figure 4A shows the averaged cursor and hand movement trajectories. Note that these trajectories are
overlapped in the left panels (Pre). In the post training phase, the endpoint variability of the hand trajectory (gray ellipses) and the variability of the initial phase of cursor movement trajectory (black shaded areas) were larger than those in the no-noise condition (Fig. 2A), while the averaged trajectories were not substantially different from those in the no-noise condition. Note that, the ellipses and shaded areas were obtained from the averaged STDs of trajectories and endpoints across subjects (e.g., averages of within-subject variability), respectively. Figure 4B shows the IDs and EDs of the cursor and hand movements as a function of trial block. In the training and post-training phases, the variability (shaded area) of the cursor movement ID and that of the hand movement ED were larger than those in the no-noise condition (Fig. 2B). The mean IDs and EDs were not substantially different from those in the no-noise condition.

Figures 4C and 4D respectively show the average and STD (e.g., variability) of IDs and EDs of the cursor and hand movements in the pre- and post-training phases. The following statistical test revealed a significant difference in the trial-by-trial variability of IDs and EDs but not in the averages of them between the no-noise and directional-noise conditions across subjects. A two-way repeated measures ANOVA indicated no significant interaction effect of PHASE and CONDITION on the averaged EDs and IDs (All interaction effects of PHASE and CONDITION: p > 0.20; All main effects of PHASE: p < 10^{-3}; All main effects of CONDITION: p > 0.3). On the other hand, the significant interaction effects were observed in the STD of the hand movement ED \( (F_{(1,13)} = 368.22, p < 10^{-10}) \) and in that of the cursor movement ID \( (F_{(1,13)} = 20.72, p < 0.01) \) but not in the STD of the hand movement ID \( (F_{(1,13)} = 0.08, p > 0.5) \) and in that of the cursor movement ED \( (F_{(1,13)} = 4.14, p = 0.063) \). The post hoc test revealed that in the post-training phase, the STD of hand movement ED and that of cursor
movement ID were significantly larger in the directional-noise condition than in the no-noise condition (Tukey’s HSD test, $p < 10^{-6}$). This indicated that the trial-by-trial variability of the hand movement ED and the cursor movement ID significantly increased because of the directional noise. Note that we used a two-way repeated-measures ANOVA for testing the statistical difference not only in the averages but also in the STDs of IDs and EDs, since we considered the STD to be one of the characteristics of trial-by-trial variability of the ID and ED for each subject.

Then, we compared the sizes of the aftereffect between the training conditions (Fig. 4E). The sizes of the aftereffect were assessed by averaging the IDs and EDs in the first trial block when the visuomotor rotation angle was returned to zero in the washout phase. Note that a negative value indicates a large aftereffect. The aftereffect of ED was significantly smaller in the directional-noise condition than in the no-noise one (paired $t$ test, $p < 0.01$), while that of ID was not substantially different between the conditions ($p > 0.6$).

Figure 5A shows the averaged hand trajectories in the probe trials (solid lines). Those in the no-noise condition are superimposed (dotted lines). The late phases of trajectories in the post-training phase were more biased in the visual target direction in the directional-noise condition than in the no-noise one, although the initial phases of trajectories were not markedly different between the conditions. To test the statistical significance of the difference in the probe trial trajectory between the conditions, the mean IDs and EDs of the probe trials in the pre- and post-training phases were analyzed with a two-way repeated-measures ANOVA (Fig. 5B). In both reaching directions, the interaction effect of PHASE and CONDITION was significant for the EDs ($F_{(1,13)} = 5.33$ and $5.07$, $p < 0.05$) but was not for the IDs ($F_{(1,13)} = 3.12$ and $1.67$, $p > 0.1$). A post-hoc test showed that the EDs in the
post-training phase were significantly different between the conditions (Tukey’s HSD test, p < 0.01). These results indicate that the random trial-by-trial fluctuation of visuomotor rotation angle affected the endpoint of hand trajectory in the probe trial but not the initial movement direction. As a result of the trajectory change, the endpoint was closer to the visual target in the directional-noise condition than that in the no-noise one.

Effect of directional noise on reaction time and movement speed

Here we investigated the directional-noise effect on the RT and the movement speed in the VF trials. Figure 6 shows the averaged RTs, MTs, PVs, and T PVs across subjects in the pre- and post-training phases for the no-noise and directional-noise conditions. The RT was not affected by the directional noise but was altered by the training phase. A two-way repeated-measures ANOVA revealed no significant interaction effect on the RT (F(1,13) = 0.76, p > 0.4) and no significant main effect of CONDITION (F(1,13) = 3.80, p = 0.07), but did reveal a significant main effect of PHASE (F(1,13) = 10.92, p < 0.01). On average, the RT slightly increased in the post-training phase (35.7 ± 12.2 ms and 47.2 ± 16.9 ms in the no-noise and directional-noise conditions, respectively). This was relatively small increase compared to that observed when the visuomotor rotation angle was suddenly increased in the training phase in our previous study (133.3 ± 65.6 ms, (Saijo and Gomi 2010a)).

The MT, PV, and T PV were, on the other hand, affected by the directional noise. A significant interaction effect of CONDITION and PHASE on those indices were observed (F(1,13) = 19.08, p < 10^{-3} for MT; F(1,13) = 7.19, p < 0.05 for PV; F(1,13) = 5.26, p < 0.05 for T PV). A post hoc test showed that the MT and T PV were significantly longer and the PV was significantly slower in the directional-noise condition than in the no-noise one in the post-training phase.
(Tukey’s HSD test, p < 0.01 for MT and PV; p < 0.05 for Tpv), indicating that the movement in the VF trial slowed down after the learning in the directional-noise condition.

Control experiment

Here, we further examined whether the trajectory curvature in the probe trial is actually associated with the learning of visuomotor rotation. One could consider that the endpoint of hand trajectory would always be biased in the CCW (or forward) direction in the probe trial because of the mechanical properties of the arm. If so, the learning of the opposite-direction (CW) visuomotor rotation would also lead to the probe trajectory curvature in the CCW direction as in Fig. 3. However, this was not the case. Figure 7A shows the probe trial trajectories after the learning of CW and CCW visuomotor rotations. Clearly, the probe trial trajectories after the CW learning (black solid lines) were biased in the opposite direction of those after the CCW learning (black dotted lines). This suggests that the trajectory curvature in the probe trial was related to the direction of the learned visuomotor rotation.

Next, we examined why the curved trajectories of the VF and probe trials were observed after the training. If the trajectory curvature were caused by an insufficient amount of training, the curvature would be reduced when the training was continued. However, after the additional training, we did not observe any straightening of the movement trajectory. In the second control experiment, we added two post-training phases (for a total of three post-training phases) and examined the change in the trajectories in those additional phases. As shown in Fig. 7B, the curved trajectories in the VF trial and the endpoint bias in the probe trial were still observed when the training was continued (post-2 and 3).
Therefore, we could not simply conclude that the amount of training was insufficient to reduce those trajectory curvatures.

One can consider that the number of probe trials would affect the trajectory curvature in the VF trials. Although we have not examined it directly, that effect would be small. In our previous study (Saijo and Gomi 2010), we used a similar experimental setup but there were fewer catch trials (less than 6% of all trials) than those in the current study (20%). However, the trajectory curvature after the training of gradual visuomotor rotation was observed clearly. Taken together, we currently conclude that the movement with curved trajectory might become relatively stable for this visuomotor environment after several hundreds of trainings.

Discussion

In the current study, we have examined whether both visual and proprioceptive feedback control adaptations are progressed equally in a novel visuomotor environment and whether adaptation levels of visual and proprioceptive feedback controls are modified in response to the visuomotor environment. After the learning of the visuomotor rotation, the late phase of the hand movement was biased in the visual target direction when the online visual feedback was eliminated in the probe trial. This trajectory curvature in the probe trial increased after the learning of the visuomotor rotation with the random trial-by-trial fluctuation of that rotation angle, while the initial phase of the movement was not affected by that fluctuation.

The hand trajectory curvature in the probe trial indicates that the proprioceptive feedback control is incompletely adapted to the visuomotor rotation, whereas both visual
and proprioceptive feedback controls are required for the movement adapted to the visuomotor rotation. The hand movement in the probe trial was accelerated in the visual target direction approximately from 250 - 300 ms after the movement onset (Fig. 3C). Since the visual feedback of hand position was eliminated in the probe trial, this adjustment would be based on the proprioceptive information about the hand position. Although this adjustment direction was in the opposite direction of adapted movement, the movement endpoint was definitely rotated away from the visual target direction (right panels in Fig. 3A), suggesting that the proprioceptive feedback control is partially adapted to the visuomotor rotation.

As we predicted in the introduction, the adaptation level of proprioceptive feedback control certainly appears to be affected by the directional noise. The late phase of the hand movement trajectory was more biased in the visual target direction in the directional-noise condition than in the no-noise condition (Fig. 5). This suggests that the adaptation level of proprioceptive feedback control is reduced by the directional noise. Since the endpoint of hand movement had to be varied on a trial-by-trial basis to move the cursor to the visual target accurately in the directional-noise condition, the reliability of proprioceptive information would be degraded to achieve the task. This decrease in the reliability of the history of proprioceptive feedback would reduce the adaptation level of proprioceptive feedback control.

Furthermore, the reduction of the adaptation level of proprioceptive feedback control in the directional-noise condition implies an increase in the relative weighting of visual feedback control. This idea is supported by the following two observations. First, the aftereffect of the ED was smaller in the directional-noise condition than in the no-noise one
(Fig. 4E). In the washout phase, the negative ID aftereffect was induced by the abrupt change in the cursor movement direction. To reduce the endpoint error, the subjects had to adjust their movement based on the visual feedback. Since the ID aftereffects were not substantially different between the training conditions (Fig. 4E), the small ED aftereffect in the directional-noise condition suggests a more accurate online adjustment by the visual feedback control in that condition.

Second, the movement speed after learning in the directional-noise condition was slower than that in the no-noise condition (Fig. 6). In the directional-noise condition, the endpoint error will become larger if the reaching movement is not adjusted by the visual feedback control. To reduce the endpoint error, the movement would be slowed down by the mechanism of the speed-accuracy trade-off (Fitts 1954), in which the more accurately the subject is required to move, the slower the movement is. Since in the current setup the endpoint error was visually fed back, the larger decrease in the movement speed implies relatively more weighting of visual feedback control.

On the other hand, the early phase of the hand movement trajectory was not affected by the directional noise. This suggests that the initial motor command, which is predictably generated in a feedforward manner, adapts to the averaged visuomotor rotation angle. Previous studies have suggested that movement under a novel visuomotor environment is learned from the prediction error, which is the difference between the predicted sensory consequences of the initial motor command and the observed output (Shadmehr et al. 2010; Tseng et al. 2007). In our results, the prediction error would be predominantly related to the cursor movement ID, since the initial motor command turned on the hand cursor and the rotated cursor movement was fed back. In the directional-noise condition, the trial-by-trial
variation of the cursor movement ID increased compared to that in the no-noise condition (Fig. 4D), indicating that the variability of the prediction error increased. However, the averages and STDs of the hand movement ID not only in the post-training but also in the washout phases were not significantly different between the directional-noise and no-noise conditions. This would be consistent with the hypothesis in previous studies that the directional noise is averaged out from the error history to adapt the feedforward motor command to the mean angle of visuomotor rotation, as frequently modeled by a Kalman filter (Baddeley et al. 2003; Burge et al. 2008) or a Baysian framework (Kording and Wolpert 2004; Korenberg and Ghahramani 2002).

The observations so far suggest that different control processes are involved in the early and late phases of the movement, e.g., feedforward and feedback controllers. Those controllers might adapt to the visuomotor rotation in a different manner: the feedforward controller would adapt to minimize a prediction error, while the feedback controller would adapt to minimize an actual endpoint error using online correction. Previously, Ghez and his colleagues have suggested distinct adaptive mechanisms for planning trajectory and final position (Ghez et al. 2007; Scheidt and Ghez 2007). They focused on the transfer of learning the visuomotor rotation between reaching and movement reversal tasks, both of which had same target locations. They found limited transfer from learning in one task to another and suggested that distinct adaptive mechanisms for trajectory planning and endpoint regulation are involved in the learning of the visuomotor rotation. However, they could not examine the contributions of the online error correction to the visuomotor adaptation. In contrast, our results indicate distinct adaptive behaviors between the early and late phase of trajectory controls in their framework.
In another study, Chen-Harris and her colleagues have suggested distinct adaptive mechanisms for initial and late phases of saccade movement (Chen-Harris et al. 2008). The initial direction of saccade slowly adapted to a novel environment and gradually disappeared. In contrast, the late-phase movement adapted fast and the adaptation was forgotten quickly. Since the saccades are too brief to adjust the trajectory from the visual feedback and since proprioceptive signals from the eyes might not play any significant role in controlling saccade trajectories, they suggested that the control for the late phase of saccade movement is corrected by an internal feedback loop, which is based on fast-adapting forward model of dynamics. Although the adaptive change in the saccade trajectory seems to be similar to that in the reaching trajectory shown in the current study, the contribution of visual and proprioceptive feedback would be different between those two behaviors. In the current experiment, the duration of reaching movement was long enough for the movement correction using the visual and proprioceptive feedback. Previous studies have suggested that, for the reaching movement, the forward model is used to predict sensory consequences of the movement and actual and predicted sensory feedback are compared to correct the ongoing movement (Shadmehr et al. 2010; Wolpert and Ghahramani 2000). Therefore, the adaptive changes in the trajectories of eye and hand movements were similar but would be based on different mechanisms. We need further investigation to elucidate the difference between the two mechanisms.

The effect of the uncertainty of the visuomotor map on the visuomotor adaptation has been investigated in previous studies. Burge et al. (2008) examined its effect on the adaptation rate of the reaching movement and found no significant effect. Wei and Kording (2010) also examined its effect and found that the uncertainty of visuomotor map made
adaptation faster. Because we changed the visuomotor rotation angle gradually in the
current experiment, it is difficult to evaluate the adaptation rate from our results. However,
our results do not conflict with their findings. Since the movement trajectories in the VF
trials were not substantially different between the no-noise and directional-noise conditions
(Fig. 4C), the adaptation rate might not have been affected or might have been made faster
by the directional noise. In contrast, the difference in the probe trial trajectories between
those conditions (Fig. 5) suggests that the uncertainty of the visuomotor map influences the
adaptation level of proprioceptive feedback control.

Previous studies on the multisensory integration for reaching generation have examined
the movement difference among pointing movements to a visual target, to a proprioceptive
target (indicated by the other hand), and to visuo-proprioceptive targets (McGuire and
Sabes 2009; Simani et al. 2007; Sober and Sabes 2005; van Beers et al. 1999; van Beers et al.
2002). However, it might be difficult to use this method to investigate the effect of
visuomotor adaptation on the multisensory integration. Although van Beers et al (van
Beers et al. 1999; van Beers et al. 2002) examined the effect of a prismatic shift of the visual
field on the reaching to those three targets and have found the movement direction
dependent precision of visual and proprioceptive inputs, they have found no effect of
prism adaptation on the weightings of visual and proprioceptive inputs. In addition, a
recent study has shown that the adaptation of reaching movement to a visual target is not
transferred to the reaching movement to a proprioceptive target (Bernier et al. 2007).

We, in contrast, interspersed the probe trials, in which the visual feedback was turned off,
among the VF trials. This method would be suitable for investigating the adaptation of
proprioceptive feedback control. Recently, Smeets et al (2006) have designed a paradigm in
which they turned off the visual feedback of the reaching movement during several trials and observed a continuous change in the movement trajectory. They have suggested that removal of visual feedback reveals an important information about the mechanism of proprioceptive recalibration (Smeets 2006). Although they showed that the sensory recalibration is not affected by the multisensory integration, the effect of visuomotor adaptation on the sensory recalibration could not be examined because they did not introduce sensory conflict.

Another study, which analyzed subjective reports of felt hand position before and after the learning of the visuomotor rotation, has suggested that visuomotor adaptation leads to a partial proprioceptive recalibration (Cressman and Henriques 2009). Since we did not measure hand position perception in the current experiment, we could not argue the relationship between such a perceptual bias of hand position and the bias in the probe trial, which would be related to the adaptation of proprioceptive feedback control. However it might be worth investigating that relationship from the view point of the contributions of the cognitive and control processes to the visuomotor adaptation.

In the present study, we showed that, to achieve the reaching movement under the condition with sensory conflict between the visual and proprioceptive feedback, both visual and proprioceptive feedback controls are adapted. Those feedback controls would adapt to the novel visuomotor environment in a manner different from that of the feedforward control associated with the movement initiation. Visuomotor adaptation might involve those multiple adaptive processes and its strategy would be flexibly modulated in response to the novel environment.
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References


Martin TA, Keating JG, Goodkin HP, Bastian AJ, and Thach WT. Throwing while looking


Figure captions

Figure 1. A: Experimental setup. The cursor and visual target were projected on the horizontal screen, which hid the subject’s arm from his/her view. The visual target was presented at one of four positions 15 cm from the start position. B: Time sequence of one trial. The cursor was shown immediately after the hand movement initiation in the visual feedback (VF) trial, while it was not in the probe trial. C: Training sequence. The hand and cursor were moved in the same direction in the pre-training phase. The cursor movement direction was shifted 9° every four trial blocks in the training phase and was kept at 36° during the post-training phase. It was abruptly changed to 0° in the second block of the washout phase. In the directional-noise condition, a random angle was added on a trial-by-trial basis from the training phase to the first block of the washout phase. D: Schematic of hand and cursor movement trajectories. The initial movement direction (ID) and endpoint direction (ED) are defined as the initial velocity vector and endpoint directions relative to the visual target direction, respectively. The IDs and EDs of both hand and cursor movements were obtained.

Figure 2. A: Hand (gray) and cursor (black) trajectories averaged across subjects. The white and gray disks indicate the start position and the visual target, respectively. The dotted circle indicates the ideal end position of the hand movement after the training. The movement direction was defined as the ideal ED of hand movement. The shaded area and ellipse show the trial-to-trial variability of trajectory and endpoint averaged across subjects, which were obtained from the averaged STDs of trajectories and endpoints across subjects.
B: Mean IDs and EDs of the hand and cursor movements across subjects as a function of trial block. 0° indicates the visual target direction. The CCW direction was positive. Shaded areas around the solid lines indicate the averaged trial-to-trial variability across subjects. Thin stairstep-like black lines indicate the visuomotor rotation angle. If the hand movement ID and ED are on these lines, the corresponding cursor movement ID and ED should be zero.

Figure 3. A: Hand trajectories in the VF (gray) and probe (black) trials averaged across subjects. The format is the same as Fig. 2A. B: Mean IDs and EDs in the pre- and post-training phases. The error bars indicate the SE across subjects. C: Hand movement accelerations in the direction orthogonal (see panel A) to the hand target direction in the pre- and post-training phases. Shaded areas indicate the SE across subjects. Time zero corresponds to the movement onset.

Figure 4. Reaching trajectories (A) and mean IDs and EDs (B) in the directional-noise condition shown in the same format as Fig. 2. C: Mean ID and ED in the pre- and post-training phases of VF trials. Left and right panels show those of the hand and cursor movement, respectively. The white and gray bars correspond to the no-noise and directional-noise conditions, respectively. The error bars indicate the SE across subjects. D: Averaged STD of ID and ED in the pre- and post-training phases across subjects. The format is the same as C. E: Aftereffect assessed by the averaged ID and ED in the first block when the visuomotor rotation angle was returned to zero in the washout phase. The error bars indicate the SE across subjects.
**Figure 5.** A: Hand trajectories of the probe trials in the no-noise (dotted lines) and directional-noise (solid lines) conditions averaged across subjects. The format is the same as Fig. 2A. Note that the dotted lines are exactly the same data as the black lines in Fig. 3A. B: Mean IDs and EDs of the hand movement in the probe trials of the pre- and post-training phases. The error bars indicate the SE across subjects.

**Figure 6.** Reaction time (RT) and movement speed in VF trials. White and gray bars indicate the no-noise and directional-noise conditions, respectively. The error bars represent the SE across subjects. Top left: reaction time. Top right: movement time. Bottom left: peak velocity. Bottom right: time to peak velocity from the movement initiation.

**Figure 7.** Results of control experiments. A: Hand trajectories in the VF and probe trials after the leaning of CW visuomotor rotation. The solid and dotted lines indicate the averaged trajectories after the leaning of CW and CCW visuomotor rotation, respectively. Note that the dotted lines are the same data as in Fig. 3A. The format is the same as Fig. 2A. B: Hand trajectories in the extended training phases. Post-1, 2, and 3 indicate the first, second, and third post-training phases, respectively. The format is the same as Fig. 2A.
The images show bar charts comparing reaction times (RT), movement times (MT), peak velocity (PV), and trapezoidal velocity (TV) before (Pre) and after (Post) exposure to no-noise and directional noise conditions. The significance levels are indicated by * (p < .05), ** (p < 10^-2), *** (p < 10^-3), and n.s. (not significant). The charts illustrate statistically significant differences in performance metrics under the noise conditions compared to the no-noise conditions.