Interpreting ambiguous visual information in motor learning

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Previous studies have shown that learning to reach accurately with an imposed visuomotor rotation requires a remapping of the relationship between vision and motor output. In this preliminary study, we examine how the brain works out the appropriate motor adjustments, in this case for both arms, based on visual images. Specifically, we investigate how visual errors seen while adapting reaches to visual targets affect the movements of both the trained and untrained hand. In our task subjects learned to make accurate reaches to targets in four visual feedback conditions: rotated 45°, rotated 105°, reversed left to right and rotated 45° plus reversed. In all conditions the rotation was applied to the subject's feedback of their hand and not the targets. In the reversed and rotated-reversed condition, when the subject used their right hand, the feedback looked like their left hand (and vice versa). After a training period with one hand (e.g., right) subjects were tested with the opposite hand (e.g., left) on the same task. We predicted that after reaching with the right hand with reversed visual feedback the control of the left arm would also be altered—more so than after learning an equal-sized adjustment to right-arm reaching with a rotated, but non-reversed, view of their hand movements. Our results showed that people were able to learn the visuomotor adaptation with reversed visual feedback, but more interestingly, that learning occurred for the untrained hand as well for the reversed conditions alone. Here, vision alone—when it resembles the image of the opposite hand—led to improved initial performance for this opposite, untrained arm when reaching in a similar task. The brain seems to take advantage of reversed visual feedback of the arm to adjust the motor commands to the untrained arm in a way that facilitates transfer of the adaptation from one arm to the other.

Keywords: learning, visuomotor adaptation, visually guided reaching

Introduction

An important aspect of visually guided movement is making sense of incoming visual information to produce a series of motor commands that is appropriate to the context. This process of interpreting visual information is complex because it involves a number of other processes, including multisensory integration, which requires the brain to assess the accuracy of the information provided by each modality. Sometimes sensory information from other modalities is congruent with visual information, but sometimes it is not and this means the brain needs to combine and interpret these inputs in a reliable way in order to produce the correct motor output. This process is further complicated when sensory feedback is ambiguous, i.e., when the same sensory signals can be interpreted in a number of ways and elicit different responses. In this situation, what response we make is determined by context, prior experience, and learning.

This preliminary study examines how the brain interprets and resolves visual error signals during a motor learning task. Subjects learned to make reaching movements with one arm (e.g., right arm) while viewing mirror-reversed visual feedback of this hand, so that based on the incoming visual information it looked like they were reaching with their other arm (in this example, their left). Based on a lifetime of experience, the usual adaptive response to that visual information is to adjust the commands to the left arm but in this situation that response is unhelpful. This mirror-reversed view of their hand is ambiguous because it is not only used for adapting the reaching (right) hand but may also be used to adapt the opposite (left) but stationary hand as well, given that it resembles this hand. Thus, the same visual error signifies to each arm controller that motor commands for that arm need to be adjusted. While a handful of studies have shown that people can adapt to a reversed view of the world after prolonged exposure (Harris, [1965](#); Melvill Jones, Guitton, & Berthoz, [1988](#); Welch, [1978](#)), in our study we were less interested in demonstrating that people could adapt their reaches when seeing a mirror-reversed view of their hand, and more so in showing that there are additional implications for the motor circuitry of the

opposite hand given the ambiguous visual feedback of the hand. Of course, when subjects learn to reach with the reversed view of their right hand, they are not fooled into thinking they are actually reaching with their left arm, but the point is that vision, which has a powerful influence on motor learning, is conveying an image of the opposite arm, and this may affect how well that arm performs the same task. If so, then after subjects adapt to a reversed view of their right arm reaching, their control of the left arm should be altered more than it is after learning an equal adjustment to reaching with the right arm while viewing the arm rotated, but not reversed. We predict greater transfer to the untrained arm (manifested as better initial performance) following adaptation to reversed visual feedback than following rotated feedback when performing the same task. If this is true, then we can infer that the brain not only interprets the visual error signals as requiring adjustments to the motor commands for the reaching hand (i.e., right arm), but also to the opposite (left) hand even though the left arm is not actually moving.

Varying degrees of transfer to the untrained arm have been demonstrated in different tasks (Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Dizio & Lackner, 1995; Kitazawa, Kimura, & Uka, 1997; Malfait & Ostry, 2004; Morton, Lang, & Bastian, 2001; Parlow & Dewey, 1991; Sainburg & Wang, 2002; Schulze, Lüders, & Jäncke, 2002; Stoddard & Vaid, 1996; Teixeira, 2000), but these studies provide subjects with a cursor for visual feedback of their hand. It is possible that bimanual transfer in these cases is the result of the brain developing a new internal model of the cursor or object mechanics (Clower & Boussoaud, 2000; Liang et al., 2007; Morton et al., 2001) which either hand can exploit. If this is the case, then our subjects should show no bimanual transfer when they see a rotated (but non-reversed) view of their actual hand, rather than a cursor, and so should develop an internal model specific to the reaching hand. But in the mirror-reversed viewing condition where the view of the hand is ambiguous, the visual errors signals are not only used to develop the appropriate internal model for the reaching hand but may be interpreted in such a way as to also recalibrate the neural circuitry of the opposite hand given that the view of the reaching hand resembles the opposite hand. In this way, we can test how the brain deals with ambiguous visual feedback during motor learning.

Methods

Subjects and apparatus

Forty-seven right-handed subjects (mean age = 22 ± 2, 28 females, 19 males) were recruited from the University
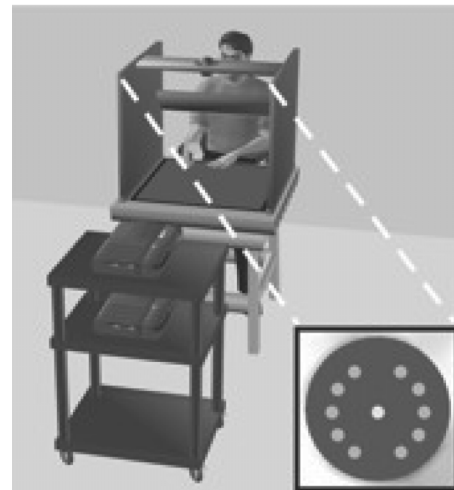
Overview

Figure 1. Experimental apparatus and target display. Subjects made reaching movements on a digitizing tablet in the horizontal plane while viewing a superimposed image of the targets and visual feedback of their hand on a vertical screen. Inset shows configuration of targets. The image of the subject's hand was captured by a camera mounted above the digitizing tablet. Subjects could not see their actual hand during the experiment due to an occluding screen placed in front of the subject.

community to participate in this study. Twenty-four subjects participated in both the 45° rotated and the rotated-reversed conditions, 8 in the 105° rotated condition, and another 15 in a strictly mirror-reversed condition. Subjects gave written informed consent before participating in the experiment and were given course credit in return for their participation.

Subjects were seated at a horizontal surface just below elbow height, facing a vertical screen positioned 65 cm from the subject. Figure 1 depicts the experimental apparatus, but for clarity the vertical screen is not visible in this figure. A camera (Logitech QuickCam Pro 4000, video resolution of 640 × 480 pixels, frame rate of 30 fps) positioned 60 cm above the horizontal surface was connected to a laptop computer equipped with software (Video Capturix 2005, capture rate of 30 fps) to capture the image of the subject's hand in real time. This image was back-projected onto the vertical screen such that the subject was able to view the image of their hand in real time throughout the experiment (field of view of 28 cm in diameter). Subjects were not able to see their hand directly in the horizontal plane because of an occluding screen positioned at an angle of approximately 45° in front of the subject. A second projector was used to back-project the experimental targets and the two images were superimposed such that the targets and the image of the subject's hand were in the same vertical plane, as illustrated in Figure 2, which shows the subject's point of view during the experiment. Hand position and

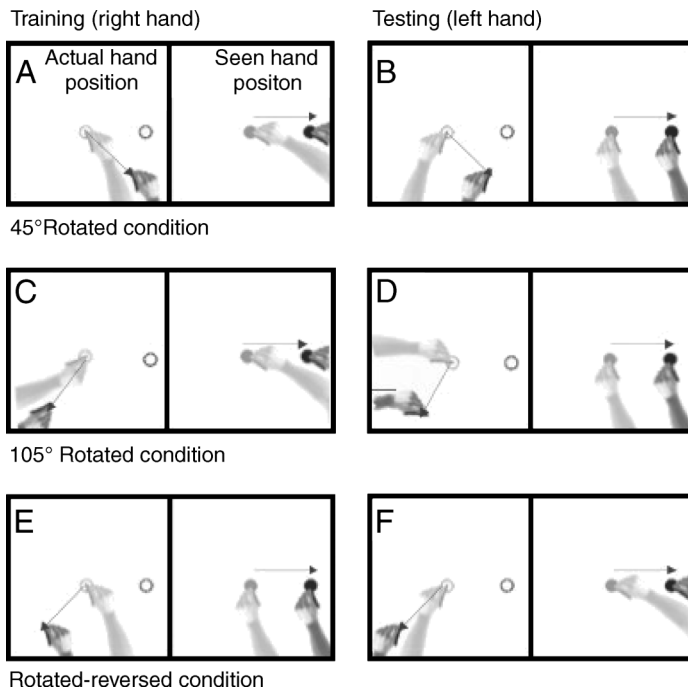Training (right hand)   Testing (left hand)

Figure 2. Visual feedback conditions. The example provided here is for a subject who trained with their right arm and tested with their left. A and B illustrate actual and seen arm positions for the rotated condition (note that the image of the hand is rotated 45° relative to the actual position of the hand), C and D illustrate the rotated 105° condition where the seen position of the hand is rotated 105° relative to the actual hand position, and E and F show the mirror-reversed and rotated condition (note that the image of the hand is rotated and mirror-reversed relative to the actual hand position). A, C, and E illustrate the training period and B, D, and F show the subsequent testing period when subjects switched to performing the task with their untrained arm. The left side of each panel illustrates the actual position of the subject's arm at the start and at the end of the reach. The right side of each panel shows the visual feedback viewed by the subject. Light gray arms indicate initial position at the beginning of a trial, and the darker arms show final position when the reach is complete. Light circles show central target, dark circles indicate reach target.

trajectory data were collected continuously as subjects moved a stylus across a digitizing tablet (Wacom Intuos3, 12 in. × 12 in. digitizing surface, resolution of 5080 lines per inch, sampled every 20 ± 7 milliseconds) to perform the reaches. Scaling between the digitizing tablet and the projected targets was 1:1 such that a movement of 10 cm on the tablet produced a movement of the same magnitude of the hand image on the projection screen.

Procedure

The task required subjects to view a central target on the vertical screen and move their hand in the horizontal plane, from a starting position at the midline of their body at the base of the tablet. After subjects moved their hand to the center target, one of ten random peripheral targets would appear briefly for one second and subjects were then required to move the stylus along the tablet to the remembered location of the target as quickly and as accurately as possible while making one smooth movement, and while simultaneously seeing the image of the hand making this movement. Each trial consisted of subjects moving their hand from the center target to a peripheral target and then returning to the center target. The targets consisted of ten radially arranged circles (1.5 cm in diameter), placed 10 cm from the central starting point, with two to the left and right, and the other 8 were located 22.5° and 45° above them relative to center (inset in Figure 1 shows display viewed by subjects). Throughout the experimental sessions, subjects were not given any explicit instructions about where they should fixate their eyes, other than to watch the vertical screen to see the targets and their hand.

Visual feedback of the hand was altered in order to produce four different feedback conditions: the image of the hand was rotated 45° counterclockwise (CCW) as illustrated in Figures 2A and 2B (45° rotated condition) and 105° CCW as illustrated in Figures 2C and 2D by rotating the position of the camera (105° rotated condition). In the other two conditions, visual feedback was reversed horizontally using the video capture software, such that the image of the right hand looked like the left hand and vice versa. For one of the feedback conditions, the hand was merely mirrored reversed and in another condition the image of the arm was both rotated 45° and reversed as illustrated in the right panels of Figures 2E and 2F. In either case, only the image of the hand was affected and not the location of the targets.

Subjects performed three epochs of trials: baseline, training, and testing. The baseline epoch consisted of 30 trials (3 to each target in random order) with each hand under unaltered visual feedback conditions. For these trials the peripheral target remained visible throughout the trial. The training epoch involved 200 trials (20 to each target, also in random order) using one hand with the image of the hand in one of the four feedback conditions. The purpose of the training period was for subjects to learn to reach accurately with the altered visual feedback, so the peripheral target was on for 1 second and subjects began moving their hand when it disappeared. The target then reappeared for 1 second after the subject completed their reach in order to provide feedback to the subject about the accuracy of their performance. A reach was considered completed when the subject's hand remained stationary for a total of 2 seconds. The testing epoch involved 30 trials with the opposite hand (the one not used for training) under the same feedback condition in order to look at how learning to adapt to the altered feedback transferred to the untrained hand. The only difference between the training and testing conditions (besides the

switching of arms) was the absence of feedback about the target at the end of the reach (the target did not reappear when the reach was complete). In this experiment we were particularly interested in initial performance in the testing condition rather than learning across trials, since initial performance would be most indicative of how well the adaptation transferred. For each feedback condition, subjects were split into two groups in order to examine a possible effect for direction of transfer: half of the subjects trained with their left hand and tested with their right hand (LR group) and the other half trained with their right hand and tested with their left hand (RL group). The same 24 subjects performed the 45° rotated and the rotated-reversed conditions, but the order of conditions was counterbalanced and experimental conditions were separated by at least 2 weeks (mean number of days between conditions = 29 ± 9) to ensure no carry over of learning from one condition to the other. We also tested for and found no order effect for these two conditions ($F_{1,22}$ = 1.590, p = .220). Separate groups of subjects participated in the reversed-only and 105° rotated condition. Each condition took about an hour to complete.

Data analysis

To quantify the amount of deviation in hand paths, we calculated and analyzed three measures of deviation: absolute angle at peak velocity, mean hand path deviation, and maximum hand path deviation. Angle at peak velocity was calculated by determining the point at which the subject's hand reached maximum velocity and then calculating the angle between a straight line connecting the center target to the peripheral target and a line starting at the center target that intersects the point of peak velocity. Mean hand path deviation was calculated by determining the distance from each point on the trajectory to a straight, hand path between the center target and the peripheral target and averaging these deviations to arrive at an overall measure of mean hand path deviation in hand path for the whole trajectory. These three measures of hand path deviation were used to assess performance based on the assumption that initial trajectory errors would be manifested as larger deviations in hand path and as subjects adapted to the task they would produce straighter trajectories with less deviation. Maximum hand path deviation was determined by identifying the single position where the hand deviated most from a straight path to the target. These three variables showed nearly identical patterns throughout the analysis, so for brevity we only report deviations in absolute angle at peak velocity. Hand-path deviations for reaches made under normal visual feedback (the baseline) did not differ significantly across the two hands for any of the conditions (p < 0.05).

Results

Figure 3 illustrates hand trajectories for example subjects while reaching under the four feedback conditions (dark traces) for the first trials to each of the 10 targets (top row) and the last of the training trials to the same target (middle row) with the right hand and the first trials for the same visual feedback condition with the opposite left hand (bottom row). Baseline hand trajectories (when there was no altered visual feedback of the hand) are shown in gray. The start and end points of each trajectory were determined by the point at which velocity reached/slowed to 10% of peak velocity.

Figure 4 shows the absolute angle at peak velocity, averaged across subjects, for all four feedback conditions. In Figure 4A, these angular deviations are averaged again, plotted across blocks of 10 trials during the training session (left side) and testing session with the opposite hand (right side). Figures 4B and 4C show a subset of the results of Figure 4A in order to compare the magnitude of learning (B) between first 10 trials (block 1 of training) and last 10 trials of training (block 20) and to compare the magnitude of bimanual transfer (B) between the reaches during the first 10 trials of the trained hand (block 1 of training) with those of the first 10 trials of the untrained hand (block 1 of testing) for different feedback conditions. We compared deviations in hand path across these blocks for the different feedback conditions (Figure 4A left side, and Figure 4B) and found that in all cases deviations in hand path (across the three measures of hand path deviation, Table 1) became significantly smaller during the 200 trials of training, although performance did not always achieve baseline levels (dashed line) as consistent with other visuomotor adaptation studies, (Abeele & Bock, 2003; Ghilardi, Gordon, & Ghez, 1995; Klassen, Tong, & Flanagan, 2005). Angular deviations at peak velocity decreased by 55% for the 45° rotated condition ($F_{1,23}$ = 120.99, p = .001) and by 51% for the 105° rotated condition ($F_{1,7}$ = 39.38, p = .001) (Figure 4B, black and gray solid lines). The angular deviations were reduced by 66% for the reversed condition ($F_{1,26}$ = 29.10, p = .001) and by 62% for the rotated-reversal condition ($F_{1,23}$ = 111.16, p = .001), as shown by the dotted and dashed lines in Figure 4B. The amount of reduction in hand path deviation for the four feedback conditions was similar for measurements of average hand path deviation and maximum hand path deviation as shown in Table 1. And while the initial deviations for 45° rotation condition were smaller than the other three visual feedback conditions, angular deviations of 17° versus 32° (block 1), this disparity is larger than the disparity following training (block 3), 7° versus 15°, the dots representing the last 10 trials in Figure 4B cluster close to each other.

After demonstrating that adaptation occurs in all feedback conditions, we next tested whether this improved
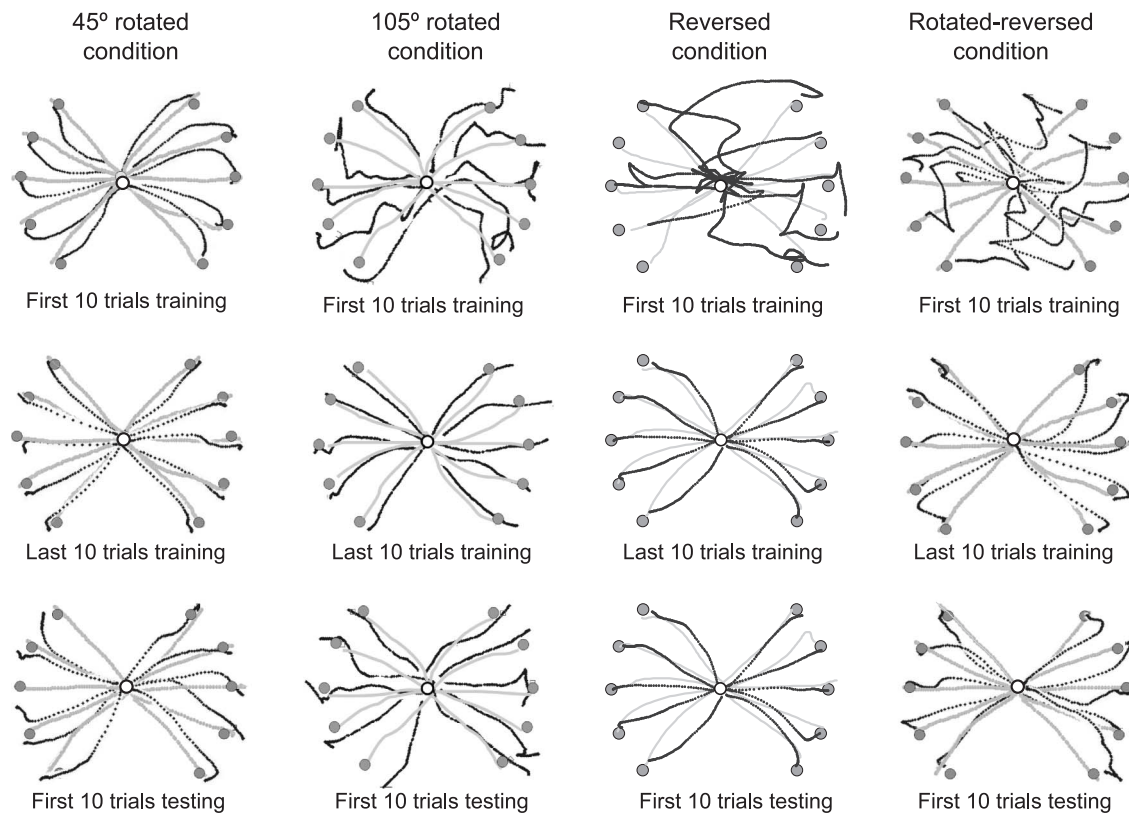
Figure 3. Hand paths for typical subjects. From left to right columns show trajectories for the rotated 45°, rotated 105°, reversed, and rotated-reversed conditions. Gray lines show baseline hand paths, dark lines show experimental hand paths. Each plot shows 10 consecutive trials, one to each target. First row illustrates the first 10 trials of the training epoch (right hand in this case), second row shows the last 10 trials of the training epoch (right hand), and the third row depicts the first 10 trials of the testing epoch (left hand).

performance during training results in an initial improvement in performance for the opposite untrained hand by comparing errors in block 1 (first 10 trials trained hand) to those in block 4 (first 10 trials untrained hand), as illustrated by the lines in Figure 4C. If the amount of deviation in block 4 is less than that in block 1 (the lines slope downward), we can interpret this to mean that the adaptation has generalized across hands resulting in improved initial performance with the untrained hand compared to the initial performance of the trained hand. We found that the amount of generalization or bimanual transfer differed across the visual feedback conditions. For both the 45° rotated and 105° rotated conditions, the amount of initial deviations for the untrained hand (block 4) was not significantly smaller than those produced for the trained hand (block 1), with an average difference of only 0.2° ($F_{1,23} = 0.001$, $p = .979$) and 2.4° or a drop of 8% ($F_{1,7} = 0.616$, $p = .434$), respectively. This lack of change in performance is also illustrated by the flat black line for the 45° rotated condition and the slightly tilted gray line for the 105° condition in Figure 4C connecting average performance in block 1 and block 4. Even for measures of maximum hand path deviation and average hand path deviation, we found no significance difference between

initial reaches with the trained hand and those with the untrained hand (Table 1).

However, we did see significant bimanual transfer after subjects learned to reach with a reversed view of their hand. In the mirror-reversed condition, initial angular deviations at peak velocity for the untrained hand showed an almost significant decrease of 8.1° (a 29% reduction) compared to the initial deviations for the trained hand ($F_{1,26} = 3.94$, $p = 0.058$), as illustrated by the downward-sloped dotted line in Figure 4C. In the rotated-reversed condition, the decrease was similar, with an average drop of 9.2° (a 29% reduction), and significant ($F_{1,23} = 24.054$, $p = .001$). Likewise, we found a similar significant decrease in maximum hand path deviations and average hand path deviations for the untrained arm compared to the trained hand.

Effect of hand order and task difficulty on adaptation and transfer

We found no significant differences between subjects who were trained with their left hand and were tested with their right (LR group) and those who were trained with
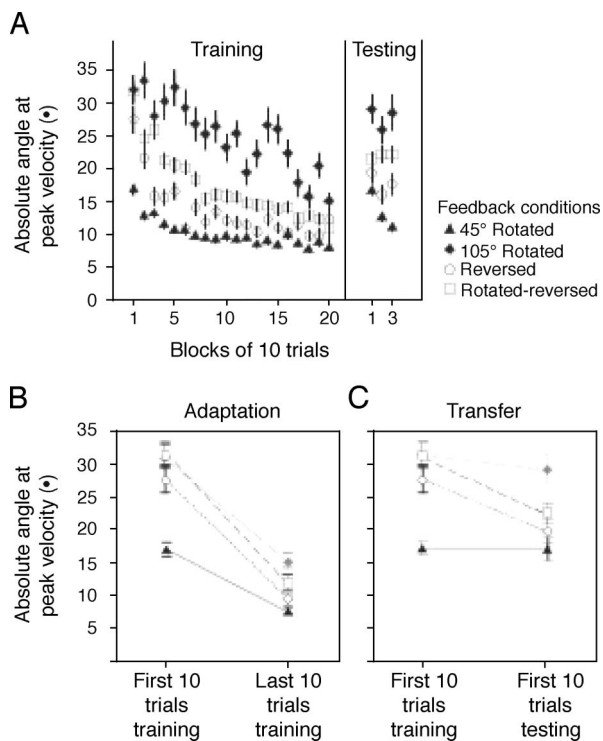
Figure 4. Mean performance of all subjects binned into relevant blocks. Panel A shows means for all feedback conditions across blocks of 10 trials for training and testing epochs. Panels B and C highlight mean performance in the most relevant blocks to illustrate adaptation (B) and transfer (C). Black solid lines represent group means for the rotated 45° condition; gray solid lines represent the rotated 105° condition; dotted lines show reversed condition; and black dashed lines indicate the means for the rotated-reversed condition. Bars represent standard error of the mean.

Discussion

This study demonstrates that visual feedback during unimanual motor learning affects the motor performance of both hands. Only in the mirror-reversed condition and the rotated-reversed feedback condition, where subjects viewed a reversed image of their arm, did we see improvement in initial reaching for the untrained, opposite hand. That is, when subjects learned to reach with their right hand while seeing what *looked* like their left hand, they then made smaller initial deviations in reaching when they switched to reaching with their left (untrained) hand compared to when they learned to reach under only a rotated viewing condition. We confirmed this disparity in the amount of generalization was not related to the magnitude of initial errors in the training epoch or the difficulty of the task since we also found no transfer following adaptation to a 105° rotated view of the hand.

Since we did not see any improvement for this opposite untrained hand when the visual feedback was rotated but not reversed during training, this suggests that cross manual improvement in the reversed condition is not merely the result of the more common bimanual transfer (learning with one hand generalizing to the other). Instead, our findings suggest that the brain is using or interpreting this ambiguous view of the hand in the reversed condition as requiring adjustments to the motor commands of both hands—the hand that is doing the actual reaching and the hand that the visual feedback resembles. Thus, the reversed image of the hand provides online information about the position of the reaching hand in order to steer it to the target, and because the image also resembles that of the opposite hand, it also provides error signals which the opposite arm controller can use to recalibrate the motor commands for this arm offline. This was equally true whether it was the right or the left hand that was initially trained. The reversed image of the hand during training means different things for each of the arm control systems, in a way that the rotated and unreversed image does not.

Role of visual feedback in motor adaptation and transfer

Previous studies have shown that people can adapt to reversed visual feedback while wearing reversing prisms, which invert the entire visual field left to right. Adapting to a drastic change in feedback takes place slowly and generally requires extensive training before adaptation is complete and subjects can perform tasks accurately (Sekiyama, Miyauchi, Imaruoka, Egusa, & Tashiro, 2000; Sugita, 1996). The reversed feedback conditions in our experiment only reverses the image of the forearm arm, so that the targets (and the rest of the visual field) are not reversed, and thus our subjects adapted quickly and improved significantly within the training period. Furthermore, these reversing-prism studies addressed different issues than those in the current study: they did not measure nor compare bimanual transfer of visual alteration, nor did they chart the time course of learning, nor did they compare learning and transfer across different distortions of visual feedback of the arm. While arm-movement

their right hand and were tested with their left (RL group) in terms of their initial or final adapted performance in the training period (blocks 1 and 3) or their initial performance in the testing period (block 4). This was true for all feedback conditions ($p < .05$).

Transfer also did not seem to be related to the initial hand path deviations or the magnitude of learning. Both initial and final hand path deviations during training did not differ between the 105° rotated and the rotated-reversed conditions (the slopes in Figure 4B nearly overlap), yet only the latter showed significant bimanual transfer.

Feedback condition	Trial set	Absolute angle at peak vel. (°)	Absolute maximum deviation (cm)	Averaged deviation (cm)	Pathlength (cm)	MT (s)
45° Rotated	1st 10 adapted trials	16.8 ± 11.6	1.8 ± 1.1	0.9 ± 0.5	11.7 ± 2.3	3.5 ± 1.3
	Last 10 adapted trials	7.6 ± 5.6	0.9 ± 0.6	0.5 ± 0.3	10.8 ± 1.2	3.5 ± 1.4
	1st 10 transfer trials	16.9 ± 12.1	1.8 ± 1.1	0.9 ± 0.5	11.8 ± 2.0	3.5 ± 1.4
	Adaptation %	54.5%**	47.3%**	47.4%**	8.3%**	1.2% NS
	Transfer %	−0.9% NS	0.5% NS	4.2% NS	−0.7% NS	2.0% NS
105° Rotated	1st 10 adapted trials	31.4 ± 18.9	2.2 ± 1.2	1.9 ± 0.9	22.7 ± 2.7	5.0 ± 0.8
	Last 10 adapted trials	15.2 ± 9.6	1.3 ± 0.3	0.6 ± 0.3	13.8 ± 3.3	3.9 ± 1.2
	1st 10 transfer trials	29.0 ± 19.0	1.8 ± 0.9	2.0 ± 1.1	22.7 ± 12.7	4.5 ± 1.0
	Adaptation %	51.5%**	39.9%**	67.0%**	39.3%**	22.2%**
	Transfer %	7.5% NS	19.1% NS	−2.9% NS	0.3% NS	8.9%**
Strictly reversed	1st 10 adapted trials	27.5 ± 25.7	3.1 ± 2.8	1.5 ± 1.4	15.5 ± 7.8	3.4 ± 1.7
	Last 10 adapted trials	9.3 ± 10.9	0.9 ± 0.7	0.5 ± 0.3	10.0 ± 1.5	1.8 ± 0.9
	1st 10 transfer trials	19.4 ± 21.8	2.0 ± 1.8	1.0 ± 0.8	12.1 ± 3.8	2.2 ± 1.0
	Adaptation %	66.2%**	70.7%**	67.0%**	35.3%**	45.9%**
	Transfer %	29.5%**	37.3%**	35.8%**	21.6%**	34.4%**
Rotated-reversed	1st 10 adapted trials	31.5 ± 23.6	4.1 ± 2.6	1.8 ± 1.1	19.8 ± 8.3	4.4 ± 1.2
	Last 10 adapted trials	11.9 ± 13.7	1.4 ± 1.1	0.6 ± 0.4	11.5 ± 2.1	3.7 ± 1.3
	1st 10 transfer trials	22.4 ± 19.1	3.6 ± 2.7	1.4 ± 1.0	19.7 ± 10.5	4.3 ± 1.2
	Adaptation %	62.4%**	67.1%**	65.9%**	41.8%**	16.2%**
	Transfer %	29.0%**	11.3%*	20.5%**	0.2% NS	3.7% NS

Table 1. Means ±*SD* for each feedback condition illustrating performance in the first and last 10 trials of training and the first 10 trials with the untrained hand across five kinematic measures. Percentage of adaptation and transfer are also shown. *Note*: **$p < 0.01$, *$p < 0.05$, *$p \sim 0.05$.

studies have been done using displacing (non-reversing) prisms, only some of these studies show transfer of adaptation across arms (i.e., Cohen, 1967) and others have not (Choe & Welch, 1974; Taub & Goldberg, 1973). Yet, these results do not extend to tasks such as ours chiefly because prisms produce a shift (or an inversion) of the entire visual field rather than providing altered visual feedback of the hand alone, and so prism adaptation likely entails different learning algorithms than those required when only the view of the hand is altered (either by using a cursor to represent the hand or altering the visual image of the hand).

Although in this experiment we did not find that learning transferred to the untrained limb in our rotated conditions, many visuomotor adaptation studies have found significant bimanual transfer (Sainburg, 2002; Sainburg & Kalakanis, 2000; Sainburg & Schaefer, 2004; Sainburg & Wang, 2002). These studies involve people reaching with their hand misrepresented by a cursor. Why should adapting to a misaligned cursor lead to bimanual transfer while adapting to a rotated view does not? We are addressing this question in another ongoing experiment where we tested subjects using the same setup and with the same rotated visual feedback of the hand, but this time we provided them with a cursor that misrepresented the hand rather than a rotated view of their hand and forearm (Siegel, Budge, Gill, & Henriques, 2008). In this case, we found significant bimanual transfer like those

found in these other studies. Specifically, after learning to reach with a cursor whose motion was either rotated 45° or 105°, these subjects showed a significant reduction in initial hand path deviations of about 39% and 17% made with their untrained left hand compared to those initially produced by their trained right hand. Even when we programmed the cursor to both rotate 45° and mirror reverse (the equivalent to our rotated-reversed hand condition in the current study), we found significant transfer of about 30% to the untrained hand. We interpret these results as perhaps suggesting that different learning processes, or internal models, may be involved in learning to manipulate a cursor versus learning using actual feedback of the arm (Clower & Boussaoud, 2000; Siegel et al., 2008; Sober & Sabes, 2005).

Siegel et al. (2008) also found that overall reaching with rotated cursor-feedback lead to initial hand path deviations that were about 40% larger than those produced when reaching with a rotated view of the forearm in this study. The discrepancy is likely because the image of the arm configuration prior to and during the trial provides better visual state information (Clower & Boussaoud, 2000; Sober & Sabes, 2005) which in turn may be useful in adjusting the motor plan even prior to movement onset (Ghez, Gordon, & Ghilardi, 1995; Ghez, Gordon, Ghilardi, Christakos, & Cooper, 1990), although further work needs to be done to tease apart the contribution of initial view of the arm configuration compared to online

view of the hand during visuomotor adaptation. Yet, this view of starting arm position cannot explain our differences in bimanual transfer across the different feedback conditions in the current study since this information was available for both hands and for all 4 feedback conditions.

Learning strategies may also account for some of the disparity in learning rates between the four visual feedback conditions, in that subjects in the reversed conditions or 105° rotated condition may have used more of a cognitive strategy during initial learning. But this cannot explain differences in transfer since only the reversed-viewing conditions elicited bimanual transfer. In fact, we included the rotated-reversed hand view because we thought that in the strictly reversed condition, that within a couple of trials subjects may realize that anti-reaching was required, which would have lead to very few errors (e.g., Johnson, Van Beers, & Haggard, 2002), and likely to complete bimanual transfer. But this is not what we found: while deviations in hand paths in the reversed condition were reduced when reaching with the opposite, untrained hand, these deviations were not small enough to imply that subjects implemented an anti-reach (cognitive) strategy. Similarly, the discrepancy in hand path deviations between the strictly reversed and rotated-reversed decreased across trials (Figure 4) suggesting that subjects were learning both the rotation component as well as the reversal component. Thus, differences in initial learning strategies do not exclude the possibility that the brain does use ambiguous visual information (i.e., what looked like the opposite hand) provided during the reversed conditions to adjust motor commands to the untrained arm.

Overall, vision is such a reliable and dominant sense that it seems even ambiguous visual error signals can trigger the arm controller to recalibrate the motor commands of an arm that is unnecessary for the task. In our study, visual ambiguity did not preclude our subjects' ability to adapt their reaches; they were able to use mirror-reversed visual feedback to minimize their hand path deviation during the training. But more importantly, our findings suggest that the mirror-reversed visual feedback provided to subjects while they learned the reaching task resulted in offline adjustments being made to the motor commands of the opposite, untrained hand. This implies that the nature of the visual information available during the learning period has an effect on recalibrating the motor commands not only for the trained arm but also for the unused arm.

Learning by observation

The process of learning by observation implies that by watching a task being performed, people can learn not only what movement to make but also the pattern of motor commands required to execute the movement. The process of motor adaptation may reflect the acquisition of a neural representation of a novel environment, which is then used to generate the appropriate motor commands for the

environment (Mattar & Gribble, 2005). Studies of learning by imitation or observation have shown that neural representations of novel environments can be acquired visually through observation by engaging motor planning circuits (Buccino et al., 2004; Iacoboni, 2005; Miall, 2003). Recently Mattar and Gribble (2005) found that subjects performed initially better on a novel force-field reaching task after observing a video of another person learning the same task, compared to subjects who observed nothing. Specifically, initial hand path deviation was smaller after seeing a video of someone reaching a hundred times within the force field, but not as small as if the person had themselves already reached the same number of times. This is similar to our results, subjects initially produce smaller hand path deviations after training with the reversed view of the opposite hand (block 4 vs. block 1), although these deviations were not nearly as small as those final reaches during training (block 4 vs. block 3). Moreover, results on learning by observation, like those of our study, suggest that arm motor system can figure out the appropriate motor adjustment based on vision alone.

Studies of learning by observation build on the neurophysiological findings of Rizzolatti, Fadiga, Gallese, and Fogassi (1996) and others: when people and primates observe someone else performing an action it produces the same patterns of neural activation that are seen when people/primates perform the task themselves, activating specific cells referred to as mirror neurons (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, 2005; Rizzolatti et al., 1996; Rizzolatti, Fogassi, & Gallese, 2001). These mirror neurons can be found in areas involved in visuomotor learning such as the premotor area (e.g., Gallese et al., 1996) and the inferior parietal lobule (e.g., Fogassi & Luppino, 2005). In terms of explaining our results, it is possible that "mirror" neural activity during the reversed-viewing condition in the present study may have responded to the visual error signals that led to adjustments in the control of the untrained (e.g., left) arm during learning with the right arm. That is, when our subjects learn to reach with their right limb under reversed-viewing conditions, mirror-neurons associated with left arm control would also be activated and possibly be used to adjust motor commands to the left limb when it is subsequently used to perform the same task. In support of this, Berndt, Franz, Bülthoff, Gotz, and Wascher (2005) found that arm-related EEG activity produced when humans learned to point with reversing prisms showed a decrease in arm-related lateralization in the premotor and motor areas during movement planning. The authors interpret their results as suggestive that reversal of vision leads to simultaneous activity of the left arm and right arm specific neurons.

Another possibility for explaining our results could be that the motor system uses the reversed visual feedback (i.e., the image of the left arm) to estimate what the left arm would need to do correct for the reaching errors and then transfers this information to the right arm motor system

during training. In this case, the right arm learns the visuomotor adaptation during mirror-reversal training by having the left-arm circuitry simulate the observed action and figure out the appropriate motor adjustments. The left motor system could then use this information not only to train the right arm but to adjust itself during the testing condition when it is the left arm that does the reaching. In this case, it is the training (e.g., the right) hand that would benefit from the bimanual transfer during the training reaches, and the tested (e.g., left) hand merely benefits from its previous simulations during the observed training.

From our results, we can infer that the brain is not only relying heavily on visual feedback during performance of the task but is also using (and interpreting) these ambiguous visual signals to form a neural representation of the required pattern of motor commands for both the trained and untrained limbs. We conclude that sensory signals that guide learning are inherently ambiguous, and so that identical sensory feedback, such as a visual image of the left hand misreaching, may call for an adjustment to the control of the left arm in some circumstances and of the right arm in others.

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