Scientific Research Publishing

Journal of Behavioral and Brain Science, 2023, 13, 127-141
https://www.scirp.org/journal/jbbs
ISSN Online: 2160-5874
ISSN Print: 2160-5866

Effects of Different Feedback Conditions on Sensorimotor Adaptation Revealed in a Mirror Reversal Paradigm

Jingyue Xu[1]*, Chen Yang[2]*, Mengzhan Liufu[3,4]*, Shuai Chang[2], Jinpeng Chen[5], Feng Lu[5], Alkis M. Hadjiosif[6], Adrian M. Haith[6], Xueqian Deng[6]#

[1]Department of Cognitive Science, University of California San Diego, La Jolla, California, USA
[2]School of Psychology, Center for Studies of Psychological Application, Guangdong Key Laboratory of Mental Health and Cognitive Science, South China Normal University, Guangzhou, China
[3]The University of Chicago Neuroscience Institute, University of Chicago, Chicago, IL, USA
[4]Institute of Mind and Biology, University of Chicago, Chicago, IL, USA
[5]Department of Applied Mathematics and Statistics, Johns Hopkins University, Homewood Campus, Baltimore, MD, USA
[6]Department of Neurology, Johns Hopkins University School of Medicine, Baltimore, MD, USA
Email: #denghokin@gmail.com

How to cite this paper: Xu, J.Y., Yang, C., Liufu, M.Z., Chang, S., Chen, J.P., Lu, F., Hadjiosif, A.M., Haith, A.M. and Deng, X.Q. (2023) Effects of Different Feedback Conditions on Sensorimotor Adaptation Revealed in a Mirror Reversal Paradigm. *Journal of Behavioral and Brain Science*, **13**, 127-141.
https://doi.org/10.4236/jbbs.2023.137009

Received: June 4, 2023
Accepted: July 28, 2023
Published: July 31, 2023

Abstract

Humans are able to overcome sensory perturbations imposed on their movements through motor learning. One of the key mechanisms to accomplish this is sensorimotor adaptation, an implicit, error-driven learning mechanism. Past work on sensorimotor adaptation focused mainly on adaptation to rotated visual feedback—A paradigm known as visuomotor rotation. Recent studies have shown that sensorimotor adaptation can also occur under mirror-reversed visual feedback. In visuomotor rotation, sensorimotor adaptation can be driven by both endpoint and online feedback [1] [2]. However, it's not been clear whether both kinds of feedback can similarly drive adaptation under a mirror reversed perturbation. We performed a study to establish what kinds of feedback can drive adaptation under mirror reversal. In the first two conditions, the participants were asked to ignore visual feedback. In the first condition, we provided mirror reversed online feedback and endpoint feedback. We reproduced previous findings showing that online feedback elicited adaptation under mirror reversal. In a second condition, we provided mirror reversed endpoint feedback. However, in the second condition, we found that endpoint feedback alone failed to elicit adaptation. In a third condition, we provided both types of feedback at the same time, but in a conflicting way: endpoint feedback was non-reversed while online feedback

---

*Equal contributions.

#Corresponding author.

was mirror reversed. The participants were asked to ignore online visual feedback and try to hit the target with help from veridical endpoint feedback. In the third condition, in which veridical endpoint feedback and mirror reversed online feedback were provided, adaptation still occurred. Our results showed that endpoint feedback did not elicit adaptation under mirror reversal but online feedback did. This dissociation between effects of endpoint feedback and online feedback on adaptation under mirror reversal suggests that adaptation under these different kinds of feedback might in fact operate via distinct mechanisms.

Keywords

Endpoint Feedback, Online Feedback, Motor Learning, Implicit Adaptation, Mirror Reversal

1. Introduction

In everyday life, we face constantly changing external and internal conditions affecting our movements, and motor learning is essential for maintaining performance in this dynamic environment [3]. Sensorimotor adaptation is known as one of the key mechanisms of motor learning [2], usually studied by examining how performance is regained under an imposed perturbation. Behaviorally defined, sensorimotor adaptation has the following characteristics. First, participants do not seem to counter the perturbation in a single trial; rather, they engage in a gradual learning process [4] [5]. Second, implicit sensorimotor adaptation tends to saturate [6] [7] [8]. Third, participants always show an aftereffect when the perturbation is removed [9] [10] [11]. Finally, implicit sensorimotor adaptation seems to be parallel with explicit cognitive strategies [1] [12] [13] [14].

Adaptation has mostly been investigated with the visuomotor rotation paradigm. In visuomotor rotation, the participant typically makes reaching movements without direct knowledge of his hand position and instead observes a cursor that is initially veridical to the hand position but is later rotated by 30˚ relative to the true hand position [2]. Past studies have shown that both online feedback and visual feedback can drive sensorimotor adaptation [15] [16]. Also, online feedback seems to have a larger contribution in sensorimotor adaptation in comparison to endpoint feedback [1] [17]. It remains unclear, however, whether these different forms of feedback lead to stronger or weaker versions of the same learning, or whether they act through qualitatively different mechanisms.

A potential way to dissociate the different effects from endpoint and online feedback is by imposing a more extreme perturbation: mirror reversal [18] [19]. Under mirror reversal, the visual feedback is mirror reversed rather than rotated. Hadjiosif and colleagues have utilized mirror reversal to dissociate different learning architectures [20]. Given the more drastic nature of the mirror reversal perturbation, we speculated that this paradigm might allow us to dissociate the effects of online and endpoint feedback on motor adaptation [12] [20] [21]. We performed an experiment to test this conjecture which examined three conditions. In the first condition, we provided online feedback and endpoint feedback under mirror reversal as participants generated upward or downward reaching movements. We replicated results by Hadjiosif *et al.*, showing that this kind of feedback led to implicit adaptation that amplified errors [20]. In the second condition, we provided only mirror reversed endpoint feedback and no online feedback. We found that providing endpoint feedback alone did not elicit adaptation. We considered the possibility that participants might have been insensitive to endpoint feedback because they discounted unnaturally large errors in this case. In a third condition, therefore, we provided veridical endpoint feedback, while still providing mirror reversed online feedback. In this case, adaptation still occurred, driven by the mirror-reversed online feedback, despite the availability of veridical endpoint feedback. These results reveal a dissociation between effects of endpoint feedback and online feedback on sensorimotor adaptation using mirror reversal paradigm.

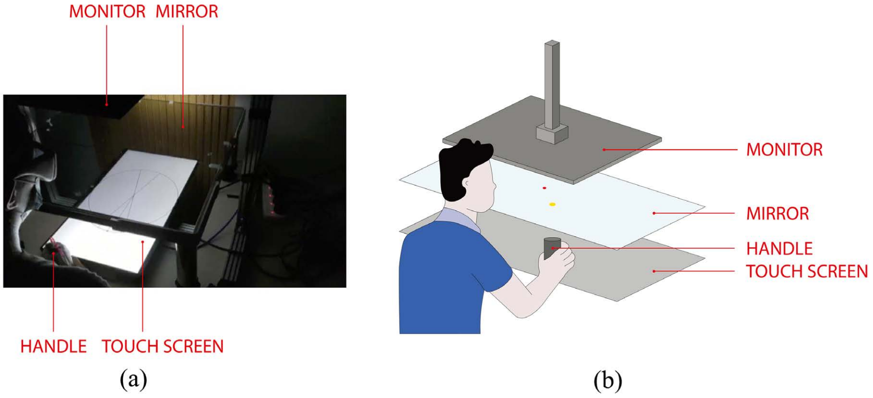
2. Methods

2.1. Participants

There were 24 right-handed participants (7 males and 17 females between age 18 - 23) in total recruited from South China Normal University split into three groups of 8 participants (one for each experiment condition). The study was conducted following the ethical standards laid down in the 1964 Declaration of Helsinki. The study was approved by the Institutional Review Board of South China Normal University. All participants gave informed consent to participate in the study before the start of their experimental session. Recruitment of participants took place from June to October in 2021. No personal identifiers were maintained for the study.

2.2. Apparatus

The participants sat on a chair and held a handle moving on a touch screen (**Figure 1(a)**). The apparatus consisted of an aluminum frame supporting an LCD monitor at the top and a touch screen (Dell P2418HT) at the bottom, with a mirror held in the middle to reflect the top monitor (**Figure 1(b)**). The distance between the mirror and both the monitor and the touch screen was 250 mm so that the image of the monitor appeared in the same plane as the touchscreen. Participants reached towards targets (diameter: 8 mm) that appeared randomly on one of two 30˚ fan-shaped areas (diameter: 220 mm). The generation of targets was pseudo-random and all participants shared the same pseudo-random sequence. The two areas where targets could appear were symmetrical both horizontally and vertically, with an angular range of 30˚ (**Figure 2**). Below the mirror, the participants used their right hand to grasp a handle and to



(a) (b)

Figure 1. Experiment apparatus. (a) Photo, (b) Illustration. The participants sat on a chair and held a handle with their right hand, which was in the shape of bottle with a stylus contacting a touch screen attached to the handle's bottom center. The targets (diameter: 8 mm) were presented on the mirror with the help of a monitor located above the mirror. Two identical fan-shape regions (diameter: 220 mm) were displayed, one upward and one downward from the start position. Below the mirror, the participants completed center-out movement on the touch screen while grasping the handle. The distance between the mirror and both the monitor and the touch screen was 250 mm.

complete center-out movements on the touch screen. The hand's trajectory was recorded at 80 Hz. The program was coded in MATLABR2021a (The MathWorks, Natick, Massachusetts), using Psychtoolbox, and run on an HP Z2 Tower G5 Workstation.

2.3. General Procedure

There were 3 different conditions in the study. Each condition consisted of 7 blocks. Each block included 30 trials. No break was given between blocks. The first 3 blocks were baseline blocks and the following 4 blocks were perturbation blocks. In the third baseline block, no visual feedback was provided at all in order to test the stability of the participant's behavior. The first condition provided participants with online and endpoint mirror-reversed feedback in order to replicate the findings in Hadjiosif *et al.* (2021)—that sensorimotor adaptation would lead to error amplification in shooting movements under mirror reversal [20]. The second condition provided no online feedback but instead provided mirror-reversed endpoint feedback. The third condition provided mirror-reversed online feedback but veridical endpoint feedback. In the first two conditions, the participants were asked to ignore visual feedback. In the third condition, the participants were asked to ignore online visual feedback and try to hit the target with help from endpoint feedback. Each condition had 8 participants and no participants completed more than one condition.

2.4. Condition 1

In each trial, the participant was first required to reach to the starting position (diameter: 8 mm) centered on the touch screen. A "Beep" sound (0.6 second) was played when the participant's handle touched the starting position on the

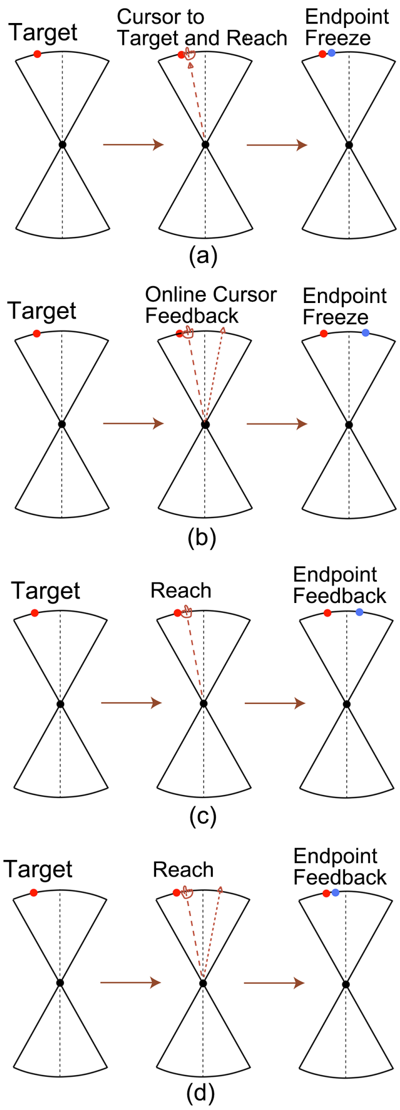


Figure 2. Task design and experimental conditions. (a) Baseline (common for all conditions): Two fan-shape regions were visible at all times. First, the target (represented as red circle) was presented and the participant was asked to make straight shooting movement of the hand towards the target (represented by the thin dashed line). The hand was not directly visible by the participant. The thick dashed line shows the cursor trajectory that would be visible to the participant. After the participant reached across the end of the fan-shaped region, the cursor froze in place at the point where the cursor crossed the arc (represented as the blue circle). This was shown to indicate the veridical position of the movement across the arc. (b) Condition 1: Trials followed same procedure as in baseline, but the online cursor feedback (dashed line) and frozen endpoint (blue circle) were mirror reversed relative to the true hand position (dashed line) across the mid-line of the fan-shaped region (indicated by the vertical black dashed line). (c) Condition 2: Trials followed the same procedure as in Condition 1, except that no online cursor was displayed during movement. Only the frozen endpoint was visible. (d) Condition 3. Trials followed the same procedure as in Conditions 1 & 2, except that participants viewed mirror-reversed online feedback and veridical frozen endpoint feedback (*i.e.* the endpoint feedback indicated the veridical position where the hand cross the target arc). Throughout Condition 3, participants were instructed to make shooting movement to bring the hand towards the target, while ignoring the mirror-reversed online cursor.

screen. After the “Beep” sound ended, two 30˚ fan-shaped regions would appear together with a target positioned along the ending arc of one of them. The target could appear either on the top arc or the bottom arc, randomized across trials. An online cursor (diameter: 8 mm) was shown on the mirror to represent the veridical position of the handle held by the participant. Then, a “Beep” sound (0.6 seconds) was played to prompt the participant to make a straight shooting movement to bring the participant’s hand through the target. When the cursor reached beyond the end of fan-shaped region, another “Beep” sound (0.6 second) was played to indicate the end of reaching. At the same time, the online cursor froze at the location where the cursor’s trajectory intersected the arc, giving the participant endpoint feedback about their performance (**Figure 2(a)**). The same procedure was identical for baseline and perturbation blocks, except that the online cursor and endpoint feedback were both mirror-reversed across the mid-line of the fan (**Figure 2(b)**). Participants were instructed to ignore visual feedback. The next trial began when the participant returned to the original position, which indicated their readiness to the experimenter to start the next trial.

2.5. Condition 2

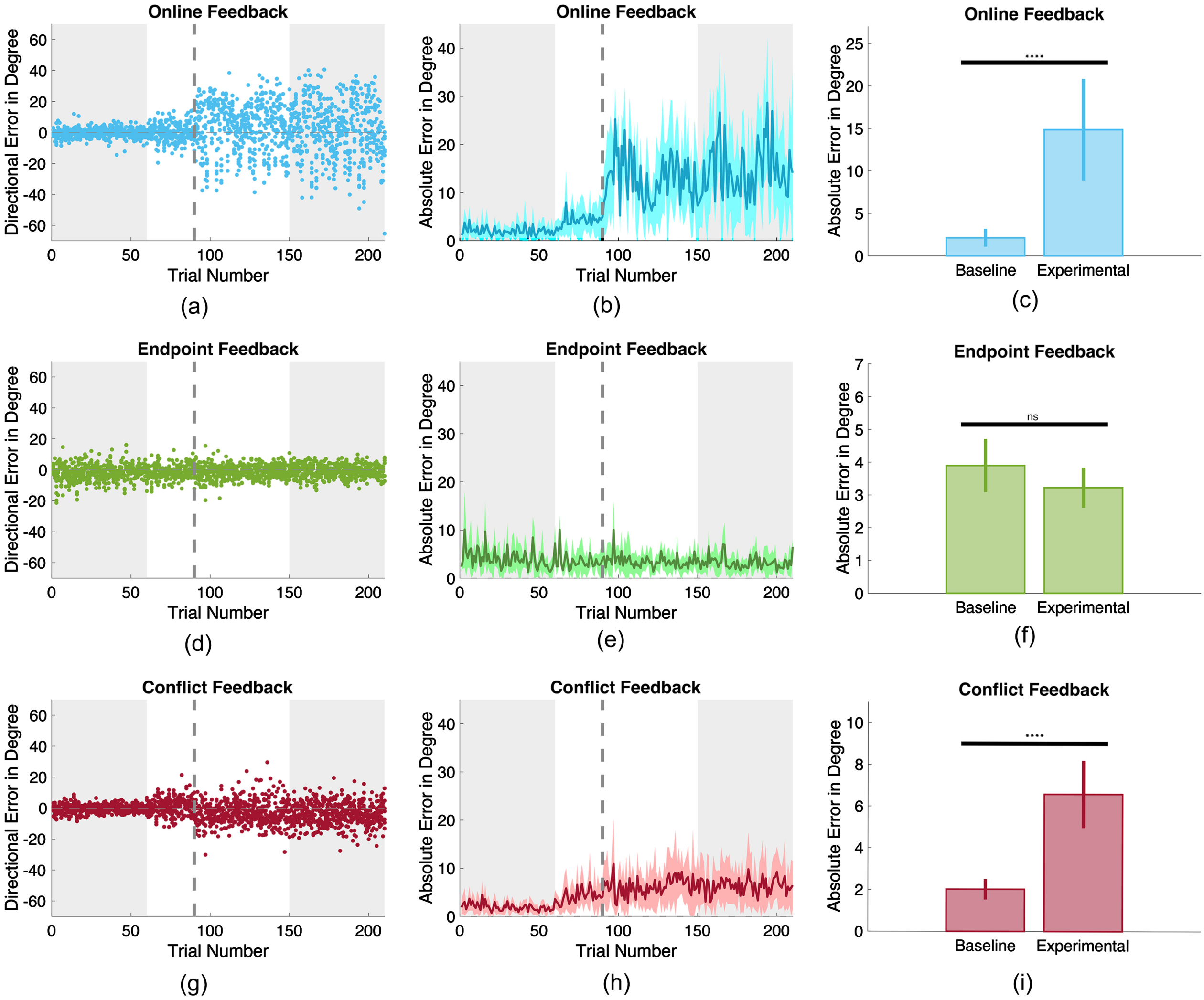
The Condition 2 followed the same procedure as in Condition 1. The only difference between Condition 1 and Condition 2 was that no online cursor feedback was provided, but endpoint feedback was provided. As in Condition 1, baseline blocks were non-reversed (**Figure 2(a)**). In perturbation blocks, the endpoint feedback was mirror reversed (**Figure 2(c)**).

2.6. Condition 3

In baseline trials of Condition 3, the participant was asked to return to starting position at the beginning. In baseline trials, veridical online cursor feedback and endpoint feedback were both provided (**Figure 2(a)**). However, during the perturbation blocks of Condition 3, the online cursor feedback was mirror reversed while the endpoint feedback remained veridical. Participants were told to ignore the online cursor feedback and were instructed to bring their hand to the target with the help from veridical endpoint feedback (**Figure 2(d)**).

2.7. Data Analysis

Analysis was performed using MATLAB (MathWorks). The experimental program was written using Psychtoolbox in MATLABR2021a running on the touch screen Dell P2418HT. The handle gave the touch screen the raw position and the data was saved by Psychtoolbox into a MATLAB file format. The analysis code was written in MATLAB. The reach direction on each trial was taken as the angle at which the handle trajectory intersected the arc. No participants were excluded. For analysis, we selected the first two baseline blocks as baseline data group, and we selected the last two blocks of perturbation blocks as perturbation data group (**Figure 3** grey-shaded areas).



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

Figure 3. Experimental Results: (a), (d), (g), Directional errors for all participants, computed as the reaching angle minus the target angle; every single data point is plotted for each condition; vertical dashed lines indicate the start of the perturbation blocks. (b), (e), (h), Absolute errors for each condition. The thick lines show average absolute errors across participants in the condition. The green, blue, and red shaded areas describe the standard deviation of absolute errors in reaching across participants. Vertical dashed lines indicate the start of the perturbation blocks. (c), (f), (g), Average absolute errors across participants in three conditions in the first two baseline blocks and the last two perturbation blocks. Data are mean ± SEM, ****statistically significant ($p \leq 0.0001$); ns, not significant.

3. Results

Our experiment included three different feedback conditions. In Condition 1, the participants were provided online feedback during movement, as well as endpoint feedback after the movement via the cursor freezing in place as it crossed the target line. In Condition 2, only the endpoint feedback was given, with no online feedback. The participants were instructed to ignore visual feedback and bring their hands to the targets. In Condition 3, both the endpoint feedback and the online feedback were given, but they were in conflict as the endpoint feedback remained veridical while the online feedback was mirror reversed. The participants were instructed to ignore the online cursor and bring their hand to the target with the help from veridical endpoint feedback.

In Condition 1, we provided participants with online feedback during reaching movements, with an endpoint freeze at the end (**Figure 2(a)** and **Figure 2(b)**). **Figure 3(a)** shows directional errors from all participants (in total 8 × 210 data points were plotted in **Figure 3(a)**). During baseline, directional errors remained in a narrow range (around −5˚ to +5˚; **Figure 3(a)**, before the dashed line). Directional errors steeply increased once the mirror reversal was imposed, spreading from −40˚ to +40˚ (**Figure 3(a)**, after the dashed line). This error amplification recapitulated previous observations [20]. To quantify this effect, we calculated the average absolute error across participants in every trial (**Figure 3(b)**). We compared the absolute errors from first two baseline blocks and last two perturbation blocks (grey-shaded areas in **Figure 3(b)**). The data were grouped over all trials for each participant. The average absolute error across participants in baseline blocks was 2.12˚ ± 0.86˚, while the average absolute error across participants in perturbation blocks was 14.85˚ ± 5.79˚ (**Figure 3(c)**). This difference was highly significant (one way ANOVA: $F(1,8) = 33.16$, $p = 9.04 \times 10^{-5}$). Importantly, the increased variability in **Figure 3(a)** was not simply due to individual participants becoming more variable. Most of the increased variability was attributable to a difference in mean (signed) error across participants. The standard deviation in mean reach direction across participants increased from 0.53˚ during baseline blocks to 6.18˚ in the last two perturbation blocks. This result showed that mirror reversal perturbation did elicit error amplification when online feedback and endpoint feedback were given, reproducing the results of Hadjiosif and colleagues [20].

In Condition 2, endpoint cursor feedback was provided, but no online cursor feedback. As in Condition 1, the participants were instructed to ignore the visual feedback. In this case, we did not observe error amplification under mirror reversal. As can be seen in **Figure 3(d)**, the directional errors of all participants were in the range of −10˚ to +10˚ throughout all trials in baseline blocks (trials before the dashed line in **Figure 3(d)**). This trend was maintained in the perturbation blocks in which a mirror reversal was imposed (trials after the dashed line in **Figure 3(d)**). This contrasted the large error increases observed in Condition 1. We then computed the absolute values of directional errors for all participants. We calculated the average absolute error across participants, indicated by the thick green line in **Figure 3(e)**. As can be seen, the absolute error maintained a consistent level throughout both baseline and perturbation trials. To quantify the effect of mirror reversal in this condition, we compared the absolute errors between the first two baseline blocks and the last two perturbation blocks (indicated by two grey-shaded areas in **Figure 3(e)**). The average absolute error in the baseline blocks across all participants was 4.01˚ ± 0.78˚ (**Figure 3(f)**). The slightly worse performance during baseline blocks compared to Condition 1 was likely attributable to the fact that online correction was possible when online feedback was available [22]. The average absolute error in the perturbation blocks across all participants was 3.27˚ ± 0.58˚ (**Figure 3(f)**), which was not significantly different from the baseline condition (one way ANOVA: F(1,8) = 3.57, p = 0.0833). The results from Condition 2 therefore showed that mirror reversal under endpoint feedback did not elicit sensorimotor adaptation, which would have been evidenced by error amplification over time [20]. To establish that the behavior was different between Condition 1 and Condition 2, we further performed two way ANOVA: there was an effect between baseline versus perturbation blocks (F(1,8) = 28.98, $p << 10^{-5}$), and an effect between Condition 1 and Condition 2 (F(1,8) = 19.35, p = 0.002). Critically, there was a significant interaction effect (F(1,8) = 35.83, $p << 10^{-5}$), confirming that the extent of implicit adaptation was greater in Condition 1 than Condition 2.

The results of Conditions 1 and 2 show that implicit adaptation to a mirror reversal occurred when participants were provided both online and endpoint feedback, but not when they were provided only endpoint feedback. However, it's unclear why endpoint error alone failed to elicit adaptation. One possibility is that participants were less confident in endpoint feedback that represented a large error [23]. It could also be that effects of online feedback and endpoint feedback are qualitatively different, but only become dissociable under mirror reversal. In order to more clearly dissociate the effects from online and endpoint feedback, we designed Condition 3, in which participants received conflicting online and endpoint feedback. In this condition, both endpoint feedback and online feedback remained veridical in baseline blocks. However, in perturbation blocks, online feedback was mirror-reversed while endpoint feedback remained veridical. The participants were asked to ignore the online cursor and bring their hands towards the targets with the help from veridical endpoint feedback. Condition 3 provided a stronger test of the implicit component of learning, since the endpoint error gives a very clear way to perform the task explicitly. In baseline blocks in Condition 3, the directional errors of the participants remained around −5˚ to +5˚ (**Figure 3(g)**, before dashed line). However, imposing a mirror reversal perturbation on online feedback, but not endpoint feedback, during perturbation blocks led to error amplification. Participants' directional errors became larger and larger (**Figure 3(g)**, after dashed line). The same trend was seen when we calculated average absolute errors across participants for each trial (**Figure 3(h)**). The average absolute error in baseline blocks was 2.02˚ ± 0.17˚, and the average absolute error for perturbation blocks was 6.57˚ ± 2.36˚. Like for previous conditions, we compared the absolute errors of the first two baseline blocks and the last two perturbation blocks, which showed a significant difference (one-way ANOVA, F(1,8) = 57.20, $p = 6.64 \times 10^{-6}$). Therefore, when participants were provided with mirror-reversed online feedback, but veridical endpoint feedback, they still exhibited strong error amplification, indicative of sensorimotor adaptation. Further, we performed two-way ANOVA to compare performance between Condition 3, with conflicting endpoint and online feedback, and Condition 1, with congruent (but mirror-reversed) endpoint and online feedback: there was a significant main effect of baseline versus perturbation blocks (F(1,8) = 30.7, $p << 10^{-5}$), and there was also an effect of condition (F(1,8) = 4.46, $p = 0.0452$). Critically, there was significant interaction (F(1,8) = 55.78, $p \ll 10^{-5}$), indicating that the extent of adaptation was significantly greater in Condition 1 than Condition 3. Thus, we could say that providing veridical endpoint feedback still had a modulating effect on implicit adaptation to online feedback. We confirmed that the variability in **Figure 3(g)** was primarily due to variability in mean behavior across participants rather than within participants: for baseline blocks, the standard deviation in mean directional error across participants was 0.68˚; for perturbation blocks, it was 2.95˚. These data strongly suggest that online feedback and not endpoint feedback caused sensorimotor adaptation under mirror reversal. Collectively, the results from all three conditions show conclusively that online feedback but not endpoint feedback, led to error amplification of sensorimotor adaptation under mirror reversal.

4. Discussion

Previous studies have argued that online and endpoint feedback might be qualitatively different [16] [24]. The effects of different feedback conditions on sensorimotor adaptation have been hard to distinguish and investigate since, under the classical visuomotor rotation paradigm, both endpoint feedback and online feedback could lead to similar adaptive changes. We speculated that the mirror reversal paradigm might provide a way to dissociate effects of endpoint and online feedback in sensorimotor adaptation. We first examined the effects of endpoint feedback and online feedback together. Our first experiment showed that providing both online and endpoint feedback elicits error amplification, a signature of sensorimotor adaptation under mirror reversal consistent with previous studies [18] [19] [20]. Our second experiment showed that removing online feedback and providing only endpoint feedback led to no error amplification. We further designed a conflict condition in which endpoint feedback remained veridical but online feedback was mirror reversed to further dissociate the two different feedback effects and found that sensorimotor adaptation still occurred, albeit to a lesser extent than when endpoint and online feedback were congruent. These results illustrate a powerful dissociation between online and endpoint feedback: the former, but not the latter, elicits sensorimotor adaptation.

Past experiments in visuomotor rotation have shown that endpoint feedback and online feedback could both contribute to sensorimotor adaptation; however, past results also have suggested that online feedback and endpoint feedback perhaps contribute to adaptation through distinct parallel processes [16]. Their participants received either online visual feedback, with verbal instructions to correct or not to correct online errors, or only visual feedback provided as a static hand-path at the end of each trial in visuomotor rotation. They showed that online error corrections were inconsequential to the adaptation process. The endpoint group showed smaller reductions in mean error with practice, but had increased variability, and generalized less across target distances and workspace. Our experiments under mirror reversal support this conjecture. Another pair of parallel processes that is known for sensorimotor adaptation is learning from sensory prediction error and learning from task error [25] [26]. Sensory prediction error (SPE) refers to the signal that designates the difference between predicted sensory feedback and actual sensory feedback, and this signal updates the internal model for sensorimotor control and thus contributes to adaptation [27]. Task error (TE) refers to the signal reflecting the overall task performance, whether or not the task goal has been achieved, *i.e.* hitting the target in visuomotor rotation and mirror reversal [28]. Leow and colleagues report that task errors enhance sensorimotor adaptation [28]. Recently, Tsay and colleagues have used a clamped visual feedback paradigm, in conjunction with target jumps to demonstrate that both sensory prediction error and task error contribute to sensorimotor adaptation. However, with task error only, sensorimotor adaptation did not happen. When the size of sensory prediction error was fixed, task error seemed to modulate the extent of sensorimotor adaptation. In short, task error has a modulating effect on sensorimotor adaptation when sensory prediction error is present [26]. We observed sensorimotor adaptation under mirror reversal only when online feedback was provided. We did not observe sensorimotor adaptation in the endpoint feedback condition, but we did find that providing incongruent endpoint feedback attenuated the extent of adaptation driven by online feedback. It remains a puzzle if there is a relationship, or only an analogy, between endpoint versus online feedback and sensory prediction error versus task error. While endpoint feedback could contribute to sensorimotor adaptation in the forms of both sensory prediction error and task error, online feedback intuitively should contribute mostly in the form of sensory prediction error. Whether and how these different feedback modalities interact is an interesting topic for future investigation [29].

It has also been established that there exists an explicit process and an implicit process for sensorimotor learning [30]. Mazzoni and Krakauer have shown that the explicit and implicit processes could be dissociated by instructing the participants explicitly and asking them to follow an explicit strategy. Meanwhile, their implicit process would still adapt and thus lead to deterioration of performances in general [12]. Taylor and colleagues further examined the effects of implicit and explicit processes by asking the participants explicitly reporting their aiming positions [1]. There were pronounced differences between the time courses of explicit and implicit processes, making them clearly distinguishable. They demonstrated that the explicit process was mainly driven by task error while implicit process by sensory prediction error. In addition, they compared endpoint feedback and online feedback conditions in their experiments. Their prediction was that online feedback would favor forward-model-based learning that was based on sensory prediction error whereas endpoint feedback would favor learning toward explicit learning that was based on task error. This hypothesis was based on the assumption that endpoint feedback was more associated with task error while online feedback was more associated with sensory prediction error. However, they did not find any differences between the two feedback conditions in either explicit or implicit processes. This result suggested that the association of task error with explicit learning with endpoint feedback on the one hand, and the association of sensory prediction error with implicit learning with online feedback on the other hand, might not be right. This question remains not investigated to now and our work may have shed light on a possible approach. While ways to distinguish explicit-implicit and SPE-TE have been successfully demonstrated in previous experiments, our study has shown a possible approach to dissociate endpoint feedback and online feedback. Nevertheless, it has been shown that both task error and sensory prediction error have more intricate relations with implicit and explicit processes [28]. Taken together, it's often hard to discern people's internal objectives during adaptation, and it's hard to know whether seemingly implicit learning is truly implicit [31]. Thus, the conflict approach in general is a promising way to get around these issues, since participants can more obviously follow the instruction to make sure the endpoint hits the target, than they can focus on bringing their hand to the target.

One major concern has been raised is that the current study produced contradictory results to a previous study in endpoint feedback under mirror reversal condition [32]. In the previous study, researchers showed that endpoint feedback was able to elicit sensorimotor adaptation under mirror reversal. However, the effect was not observed in our experiments. We suggest several possibilities here for the discrepancy and present future research concerns. First, in the previous study, the noise in participants planar reaching behavior is comparably smaller to that in our results. The larger noise in our study could be originated from the inherent friction of our apparatus. In the previous study, the participants held a digital pen to perform reaching movements on a tablet. In our study, we made a handle for the participants to grasp and the platform was a touch screen rather than a tablet. Given different settings, it was highly possible that our equipment would produce a larger friction. However, the effect of friction and drag in reaching has been rarely studied. One future research direction would be to conduct experiments with friction and friction-less conditions. Second, the reaching distance in the previous study was 7 centimeters. In our study, the reaching distance was 22 centimeters. Our participants performed much larger reaching movements compared to the participants in the previous study. One possibility would be that larger movements would lead to larger noise and thus effects from endpoint feedback became indistinguishable in our study. In this regard, future research should look into varied degrees of distances in reaching. Lastly, the results in our third condition did show that endpoint feedback has a modulating effect over online feedback. In this regard, our results agreed with the previous study that endpoint feedback was effective under mirror reversal.

5. Conclusion

Our study showed a clear dichotomy whereby endpoint feedback alone did not elicit adaptation under mirror reversal, but online feedback did. Our experiments recapitulated recent findings on sensorimotor adaptation under mirror reversal and highlighted the role of feedback type when investigating sensorimotor adaptation. Future research is needed to clarify remaining questions about the relationship behind the dichotomy we uncover here regarding the role of endpoint vs. online feedback, and other dichotomies regarding the role of sensory prediction error vs. task error, and implicit vs. explicit motor learning.

Acknowledgements

The authors thank Yanzhen Zhang for the beautiful artistic illustrations and John Krakauer, Kunlin Wei and Terry Sejnowski for the critical feedback on the research. The authors would like to express heartfelt gratitude for the generous support provided by Juan Chen's Action Perception Lab at South China Normal University for human subjects and equipment. Without their invaluable sponsorship, this study would not have been possible.

Data Availability

The data of this study are available from the corresponding authors upon reasonable request.

Code Availability

The code used for the analyses is available from https://github.com/JohnLauFoo/PredictorController_Chen.

Conflicts of Interest

The authors declare no competing interests.

References

[1] Taylor, J.A., Krakauer, J.W. and Ivry, R.B. (2014) Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, **34**, 3023-3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

[2] Krakauer, J.W., Hadjiosif, A.M., Xu, J., Wong, A.L. and Haith, A.M. (2019) Motor Learning. In: Terjung, R., Ed., *Comprehensive Physiology*, Wiley, Hoboken, 613-663. https://doi.org/10.1002/cphy.c170043

[3] Sherrington, C.S. (1911) The Integrative Action of the Nervous System. Yale University Press, New Haven. https://doi.org/10.1037/13798-000

[4] Krakauer, J.W., Pine, Z.M., Ghilardi, M.-F. and Ghez, C. (2000) Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *The Journal of Neuroscience*, **20**, 8916-8924. https://doi.org/10.1523/JNEUROSCI.20-23-08916.2000

[5] Shadmehr, R., Smith, M.A. and Krakauer, J.W. (2010) Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*, **33**,

89-108. https://doi.org/10.1146/annurev-neuro-060909-153135

[6] Huang, V.S., Haith, A., Mazzoni, P. and Krakauer, J.W. (2011) Rethinking Motor Learning and Savings in Adaptation Paradigms: Model-Free Memory for Successful Actions Combines with Internal Models. *Neuron*, **70**, 787-801. https://doi.org/10.1016/j.neuron.2011.04.012

[7] Marko, M.K., Haith, A.M., Harran, M.D. and Shadmehr, R. (2012) Sensitivity to Prediction Error in Reach Adaptation. *Journal of Neurophysiology*, **108**, 1752-1763. https://doi.org/10.1152/jn.00177.2012

[8] Hadjiosif, A.M. and Smith, M.A. (2015) Flexible Control of Safety Margins for Action Based on Environmental Variability. *Journal of Neuroscience*, **35**, 9106-9121. https://doi.org/10.1523/JNEUROSCI.1883-14.2015

[9] Bock, O. (2005) Components of Sensorimotor Adaptation in Young and Elderly Subjects. *Experimental Brain Research*, **160**, 259-263. https://doi.org/10.1007/s00221-004-2133-5

[10] Kluzik, J., Diedrichsen, J., Shadmehr, R. and Bastian, A.J. (2008) Reach Adaptation: What Determines Whether We Learn an Internal Model of the Tool or Adapt the Model of Our Arm? *Journal of Neurophysiology*, **100**, 1455-1464. https://doi.org/10.1152/jn.90334.2008

[11] Kitago, T., Ryan, S.L., Mazzoni, P., Krakauer, J.W. and Haith, A.M. (2013) Unlearning versus Savings in Visuomotor Adaptation: Comparing Effects of Washout, Passage of Time, and Removal of Errors on Motor Memory. *Frontiers in Human Neuroscience*, **7**, Article No. 307. https://doi.org/10.3389/fnhum.2013.00307

[12] Mazzoni, P. and Krakauer, J. (2006) An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, **26**, 3642-3645. https://doi.org/10.1523/JNEUROSCI.5317-05.2006

[13] Deng, X.Q., Liufu, M.Z., Xu, J.Y., Yang, C., Li, Z.N. and Chen, J. (2022) Understanding Implicit and Explicit Sensorimotor Learning through Neural Dynamics. *Frontiers in Computational Neuroscience*, **16**, Article ID: 960569. https://doi.org/10.3389/fncom.2022.960569

[14] Albert, S.T., Jang, J., Modchalingam, S., Marius't Hart, B., *et al.* (2022) Competition between Parallel Sensorimotor Learning Systems. *ELife*, **11**, e65361. https://doi.org/10.7554/eLife.65361

[15] Hinder, M.R., Tresilian, J.R., Riek, S. and Carson, R.G. (2008) The Contribution of Visual Feedback to Visuomotor Adaptation: How Much and When? *Brain Research*, **1197**, 123-134. https://doi.org/10.1016/j.brainres.2007.12.067

[16] Shabbott, B.A. and Sainburg, R.L. (2010) Learning a Visuomotor Rotation: Simultaneous Visual and Proprioceptive Information Is Crucial for Visuomotor Remapping. *Experimental Brain Research*, **203**, 75-87. https://doi.org/10.1007/s00221-010-2209-3

[17] Wang, T.H., Avaham, G., Tsay, J.S. and Ivry, R. (2021) Why Is Online Feedback More Effective than Endpoint Feedback for Sensorimotor Adaptation? *Motor Learning and Motor Control*. https://doi.org/10.1101/2022.09.14.508027

[18] Lillicrap, T.P., Moreno-Briseño, P., Diaz, R., Tweed, D.B., Troje, N.F. and Fernandez-Ruiz, J. (2013) Adapting to Inversion of the Visual Field: A New Twist on an Old Problem. *Experimental Brain Research*, **228**, 327-339. https://doi.org/10.1007/s00221-013-3565-6

[19] Wilterson, S.A. and Taylor, J.A. (2021) Implicit Visuomotor Adaptation Remains Limited after Several Days of Training. *Eneuro*, **8**, ENEURO.0312-20.2021.

https://doi.org/10.1523/ENEURO.0312-20.2021

[20] Hadjiosif, A.M., Krakauer, J.W. and Haith, A.M. (2021) Did We Get Sensorimotor Adaptation Wrong? Implicit Adaptation as Direct Policy Updating Rather than Forward-Model-Based Learning. *The Journal of Neuroscience*, **41**, 2747-2761. https://doi.org/10.1523/JNEUROSCI.2125-20.2021

[21] Morehead, J.R., Taylor, J.A., Parvin, D.E. and Ivry, R.B. (2017) Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-Irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience*, **29**, 1061-1074. https://doi.org/10.1162/jocn_a_01108

[22] Schlerf, J.E. and Ivry, R.B. (2011) Task Goals Influence Online Corrections and Adaptation of Reaching Movements. *Journal of Neurophysiology*, **106**, 2622-2631. https://doi.org/10.1152/jn.00301.2010

[23] Liu, Y.J., Jiang, W.Y., Bi, Y.Q. and Wei, K.L. (2021) Sensorimotor Knowledge from Task-Irrelevant Feedback Contributes to Motor Learning. *Journal of Neurophysiology*, **126**, 723-735. https://doi.org/10.1152/jn.00174.2021

[24] Izawa, J. and Shadmehr, R. (2011) Learning from Sensory and Reward Prediction Errors during Motor Adaptation. *PLoS Computational Biology*, **7**, e1002012. https://doi.org/10.1371/journal.pcbi.1002012

[25] Kim, H.E., Avraham, G. and Ivry, R.B. (2021) The Psychology of Reaching: Action Selection, Movement Implementation, and Sensorimotor Learning. *Annual Review of Psychology*, **72**, 61-95. https://doi.org/10.1146/annurev-psych-010419-051053

[26] Tsay, J.S., Haith, A.M., Ivry, R.B. and Kim, H.E. (2022) Interactions between Sensory Prediction Error and Task Error during Implicit Motor Learning. *PLOS Computational Biology*, **18**, e1010005. https://doi.org/10.1371/journal.pcbi.1010005

[27] Tseng, Y.-W., Diedrichsen, J., Krakauer, J.W., Shadmehr, R. and Bastian, A.J. (2007) Sensory Prediction Errors Drive Cerebellum-Dependent Adaptation of Reaching. *Journal of Neurophysiology*, **98**, 54-62. https://doi.org/10.1152/jn.00266.2007

[28] Leow, L.-A., Marinovic, W., de Rugy, A. and Carroll, T.J. (2020) Task Errors Drive Memories That Improve Sensorimotor Adaptation. *The Journal of Neuroscience*, **40**, 3075-3088. https://doi.org/10.1523/JNEUROSCI.1506-19.2020

[29] Deng, X., Yang, C., Xu, J., Liufu, M., Li, Z. and Chen, J. (2023) Bridging Event-Related Potentials with Behavioral Studies in Motor Learning. *Frontiers in Integrative Neuroscience*, **17**, Article ID: 1161918. https://doi.org/10.3389/fnint.2023.1161918

[30] Huberdeau, D.M., Krakauer, J.W. and Haith, A.M. (2015) Dual-Process Decomposition in Human Sensorimotor Adaptation. *Current Opinion in Neurobiology*, **33**, 71-77. https://doi.org/10.1016/j.conb.2015.03.003

[31] Hadjiosif, A.M. and Krakauer, J.W. (2021) The Explicit/Implicit Distinction in Studies of Visuomotor Learning: Conceptual and Methodological Pitfalls. *European Journal of Neuroscience*, **53**, 499-503. https://doi.org/10.1111/ejn.14984

[32] Wang, T. and Taylor, J.A. (2021) Implicit Adaptation to Mirror Reversal Is in the Correct Coordinate System but the Wrong Direction. *Journal of Neurophysiology*, **126**, 1478-1489. https://doi.org/10.1152/jn.00304.2021