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Research paper

Attenuation of implicit motor learning with consecutive exposure to visual errors

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ABSTRACT

Visual errors induced by movement drive implicit corrections of that movement. When similar errors are experienced consecutively, does sensitivity to the error remain consistent each time? This study aimed to investigate the modulation of implicit error sensitivity through continuous exposure to the same errors. In the reaching task using visual error-clamp feedback, participants were presented with the same error in direction and magnitude for four consecutive trials. We found that implicit error sensitivity decreased after exposure to the second error. These results indicate that when visual errors occur consecutively, the sensorimotor system exhibits different responses, even for identical errors. The continuity of errors may be a factor that modulates error sensitivity.

1. Introduction

Individuals correct their movements based on perceived errors (Kim et al., 2021; Krakauer et al., 2019). Learning from errors is a fundamental motor learning process. Many studies have explored the factors that modulate changes in behavior relative to errors, or error sensitivity. Their findings indicated that error sensitivity is modulated by the error magnitude (Kim et al., 2018; Marko et al., 2012; Wei and Körding, 2009), environmental stability (Avraham et al., 2020; Gonzalez Castro et al., 2014; Herzfeld et al., 2014), and uncertainty of visual feedback (Makino et al., 2023; Wei and Körding, 2010).

In our daily lives, it is common to experience errors of similar direction and magnitude consecutively. For instance, this is likely to occur when individuals have a habit ingrained in our movements. How does consecutive exposure to similar errors affect error sensitivity? This question is relevant in reaching experiments conducted by Hutter and Taylor (2018) providing visual feedback rotated in the same direction and magnitude consecutively for two to seven trials. Figures 3A and 6A from Hutter and Taylor (2018) show a trend in which the magnitude of trial-by-trial learning decreased with the continued application of the same visuomotor rotation. Initially, this result appeared to indicate attenuation of error sensitivity. However, as the authors discussed, this result may be attributable to a decrease in visual errors by counteracting rotation. Finally, they believed that the third and subsequent trials would yield an impure measure of error sensitivity and did not conduct statistical analyses using these trials. Thus, it remains unclear how error sensitivity is modulated by continuous exposure to the same error.

How can we predict the modulation of error sensitivity based on prior findings? Herzfeld et al. (2014) proposed the memory of errors model, where the brain memorizes experienced errors and adjusts error sensitivity based on the history of past errors. According to this model, error sensitivity increases when consecutive errors occur in a consistent direction (e.g., deviation to the left of the target). Subsequent research showed that the memory of errors model was related to the implicit learning system, not the explicit one (Albert et al., 2021). In contrast, it is known that implicit adaptation saturates at around 15°–25° even after hundreds of trials, irrespective of the perturbation magnitude (Bond and Taylor, 2015; Kim et al., 2018). The saturation has typically been interpreted as the existence of an upper limit of implicit adaptation (Kim et al., 2021; Krakauer et al., 2019); however, a reduction in error sensitivity may also be involved in the saturation. Therefore, when the same error occurs consecutively, there are two opposing hypotheses: that error sensitivity either increases or decreases.

To investigate the effect of consecutive exposure to the same error, this study employed visual error-clamp feedback in a reaching task. Using this feedback, the cursor consistently follows a trajectory that

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Abbreviations: CCW, counterclockwise; CW, clockwise; STL, single-trial learning; LMM, linear mixed effect model.

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deviates from the target at a fixed angle, irrespective of the hand position (Avraham et al., 2021; Kim et al., 2018; Morehead et al., 2017). Even though participants have full knowledge of the error-clamp feedback and receive instructions to ignore the feedback and reach the target directly, the direction of their reaching movement shifts to counteract the cursor's deviation from the target (Kim et al., 2022; Matsuda and Abe, 2023; Tsay et al., 2022). Thus, error-clamp feedback allows us to measure implicit learning while presenting a fixed visual error, regardless of the participants' performance, although explicit learning cannot be evaluated. By presenting the same error consecutively with error-clamp feedback, we examined the trial-by-trial dynamics of implicit error sensitivity.

2. Materials and Methods

2.1. *Participants*

This study recruited 40 young adults (18 women, 22 men, age: 19.7 ± 1.9 [mean ± standard deviation (SD)]). All participants were right-handed according to the Japanese version of the FLANDERS handedness questionnaire (Okubo et al., 2014) and were healthy volunteers with no history of developmental or neurological disorders. This study adhered to the principles of the Declaration of Helsinki and was approved by the Ethics Committee of the Faculty of Education at Hokkaido University (approval number: 21–08). All participants signed an informed consent statement prior to participation in the study.

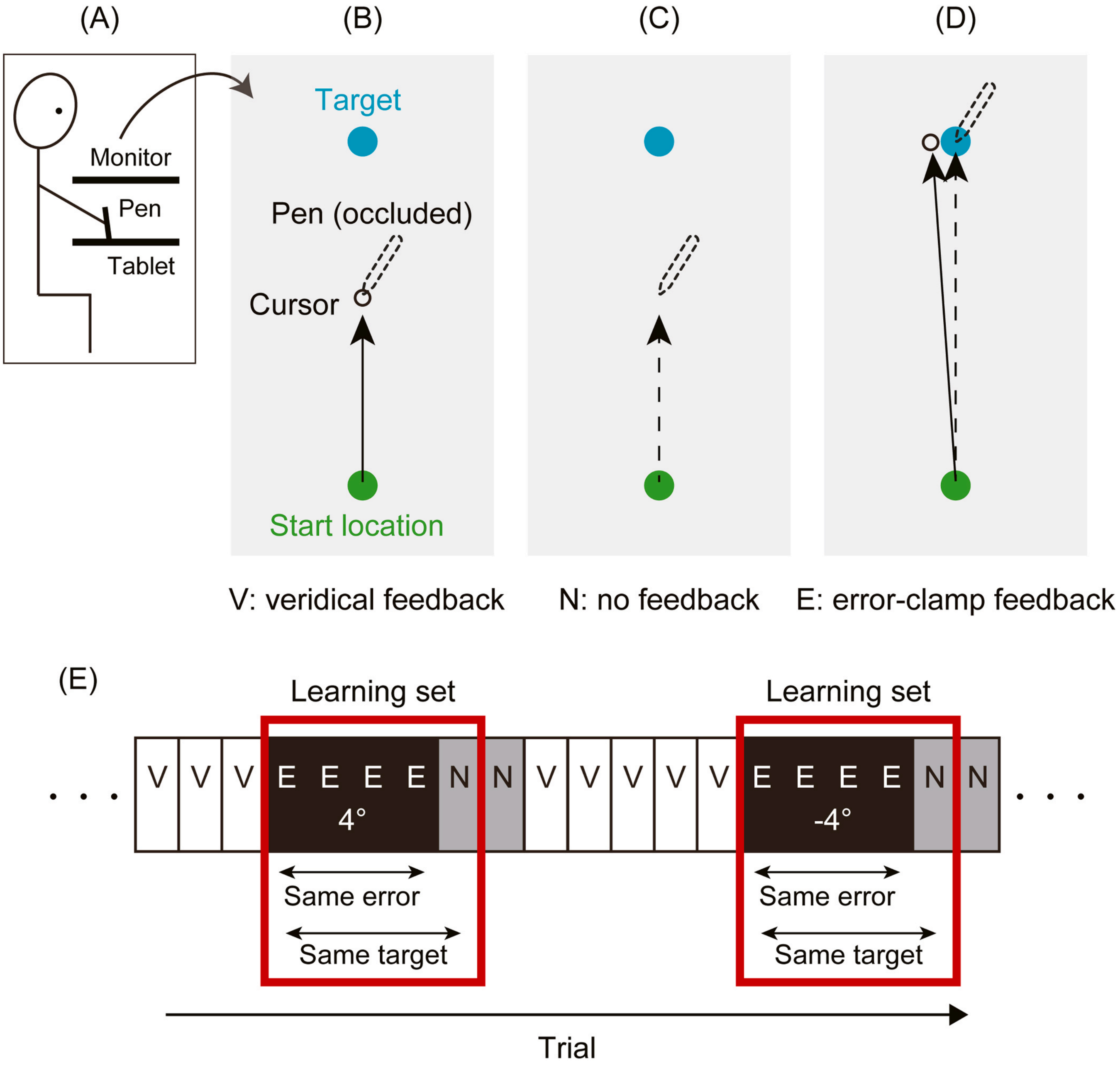

Fig. 1. Experimental setup and visual feedback. (A) Setup. (B) Veridical feedback. (C) No feedback. (D) Error-clamp feedback. Here, the error-clamp feedback with a 4° error is illustrated, where positive and negative values indicate counterclockwise (CCW) and clockwise (CW) deviations from the target. (E) Example of the trial order in the main phase. The learning set consisted of four trials with error-clamp feedback and one trial with no feedback. Within the learning set, the target location did not vary, and the error-clamp feedback consistently provided visual errors of the same sign (-4° or 4°).

2.2. *Shooting task*

The participants held a digitizing pen with their right hand and performed reaching movements across a digitizing tablet (Intuos Pro, Wacom, Japan; Fig. 1A). During the experiment, the hand position was recorded at 120 Hz and visual stimuli were presented on a 25-inch LCD monitor (GigaCrysta, I-O DATA, Japan) positioned 28 cm above the tablet. The monitor obstructed the participants' direct view of their hands. The experimental software was programmed in MATLAB R2019b using Psychtoolbox extensions (Kleiner et al., 2007).

To initiate each trial, participants placed their right hand on a start location (green circle; 0.6 cm diameter). The feedback of the hand position was indicated by a cursor (white circle; 0.3 cm diameter) and was visible when the hand was within 4 cm of the start location. Once the hand position was maintained within 0.25 cm of the start location for 1000 ms, a target (cyan circle; 0.6 cm diameter) appeared. The radial distance of the target from the start location was 10 cm, and for each trial, the target appeared at one of five locations around an invisible virtual circle (40°, 65°, 90°, 115°, or 140°, where 0° represents the right of the start location). Following the appearance of the target, participants made a fast-reaching movement (i.e., "shooting" movement), attempting to slice through the target. During the shooting movement, a visual feedback cursor was provided (i.e., online feedback). When the movement amplitude exceeded 10 cm, the cursor froze for 1000 ms (i.e., endpoint feedback). If movement time (i.e., the interval between the times when the movement amplitude reached 1 cm and 10 cm) exceeded or fell below a predefined time range (120–240 ms), an auditory message of "slow" or "fast" was played.

2.3. *Trial types*

Three types of trials were conducted: veridical feedback, no feedback, and error-clamp feedback. In the veridical feedback trial (Fig. 1B), the cursor accurately corresponded to the hand position. In the no-feedback trial (Fig. 1C), the cursor disappeared when the movement amplitude exceeded 1 cm and endpoint feedback was not provided. In the error-clamp trial (Fig. 1D; Morehead et al., 2017), the cursor always deviated from the target by -4° or 4° regardless of the angular position of the hand; positive and negative values indicated counterclockwise (CCW) and clockwise (CW) deviations from the target. The distance of the cursor from the starting location corresponded to movement amplitude.

Participants were fully briefed on error-clamp feedback and no feedback and were instructed to move their hand directly toward the target regardless of the type of feedback cursor (see also *2.4. Procedures*). Furthermore, they were informed in advance that the clamp feedback would be presented in the upcoming trial through the following procedure: in the middle of returning the hand to the start location after completing the trial preceding each error-clamp feedback trial, the cursor turned magenta, and a "knocking" sound was played. Accordingly, the participants were able to determine in advance whether visual error-clamp feedback was presented.

2.4. *Procedures*

After practicing the shooting movements within the correct time range (Fig. S1A), the experiment proceeded to the familiarization and main phases. The familiarization phase consisted of 100 trials with veridical feedback. The main phase included four blocks, each consisting of 125 trials: 65 with veridical feedback, 20 with no feedback, and 40 with visual error-clamp feedback.

Each block in the main phase began with 25 veridical feedback trials to stabilize the participants' performance, as the blocks were preceded by instructions or a short break. In all blocks, there were ten learning sets in which four error-clamp feedback trials and one no-feedback trial were performed consecutively (Fig. 1E). Within the learning set, the target location did not vary, and the error-clamp feedback consistently provided visual errors of the same sign (-4° or 4°). The sign alternated for each learning set. The learning sets were preceded by three, four, or five trials with veridical feedback, followed by one trial with no feedback. This no-feedback trial aimed to sufficiently wash out implicit learning while minimizing the participants' awareness of the influence of error-clamp feedback on shooting movements. Conversely, the no-feedback trial within the learning set played a role in measuring error sensitivity following four consecutive error presentations.

Before the main phase, the participants were fully briefed on error-clamp feedback and no feedback, and they experienced these trials three times each (Fig. S1B, C). Subsequently, they practiced 20 trials using the same procedure as the main phase and the phase began.

2.5. *Data analysis*

All analyses were performed using MATLAB R2021b, JASP (version 0.18.2.0), and R software (version 4.3.1). From the hand trajectory data, the hand angle was defined as the angle between the lines connecting the starting location to the target and the starting location to the hand position at the peak velocity. The positive and negative angles represent CCW and CW deviations from the target, respectively. Trials where the absolute hand angle was > 45° were excluded from the analysis (0.1 %).

We computed the hand angle in trials within the learning sets. Using the five hand angles in the learning set, single-trial learning (STL) was calculated as follows:

$$STL_n = HA_{n+1} - HA_n, \quad n = 1, \quad 2, \quad 3, \quad 4 \tag{1}$$

where HA_n is the hand angle in nth trial within a learning set. Thus, four types of STL were generated for each learning set according to the number of consecutive exposures to the same error, or repetition number (Fig. 2B). The sign of STL for a 4° error was reversed so that STL was calculated for each absolute error size (aligned with the -4° condition); thus, a positive sign of STL indicates a change in the hand angle in the direction that counteracts the presented error (i.e., occurrence of trial-by-trial learning).

To investigate the effect of repetition number, we first evaluated STL using analysis of variance (ANOVA) with the repetition number (1, 2, 3, and 4) as the within-subject factor. ANOVA was applied to the mean of averaged STLs within each error sign. However, in this analysis, we were concerned about the influence of hand angle in an error-clamp trial (HA_n in Eq. 1): for example, if HA_n is far offset from the target in the CW direction (minus sign) owing to noise and implicit learning driven by visual errors, it may be challenging to shift the hand angle further CW in the next trial (HA_{n+1}), even when provided with a 4° error. To mitigate the influence of HA_n, we also evaluated STL using a linear mixed effect model (LMM). Individual STLs were submitted to LMM with the repetition number and HA_n as fixed factors and participants as random factors; degrees of freedom were estimated using the Satterthwaite approach. The significance level was set at $\alpha = 0.05$ and the false discovery rate approach was applied to post-hoc pairwise comparisons.

3. Results

In the familiarization phase, the mean hand angle was 0.7° ± 0.5°, and the SD of hand angle, labeled as baseline variability, was 3.7° ± 0.9° (Fig. 2A).

Fig. 2B shows that trial-by-trial learning was driven for any repetition number of the same error presentation (one repetition: $t[39] = 12.389$, $p < 0.001$, $d = 1.959$; two repetitions: $t[39] = 6.255$, $p < 0.001$, $d = 0.989$; three repetitions: $t[39] = 2.374$, $p = 0.023$, $d = 0.375$; four repetitions: $t[39] = 4.677$, $p < 0.001$, $d = 0.739$; one-sample t-test against zero). We examined whether the magnitude of this learning, or error sensitivity, was modulated by consecutive exposure to the same error. The ANOVA of the STL revealed a significant main effect of the

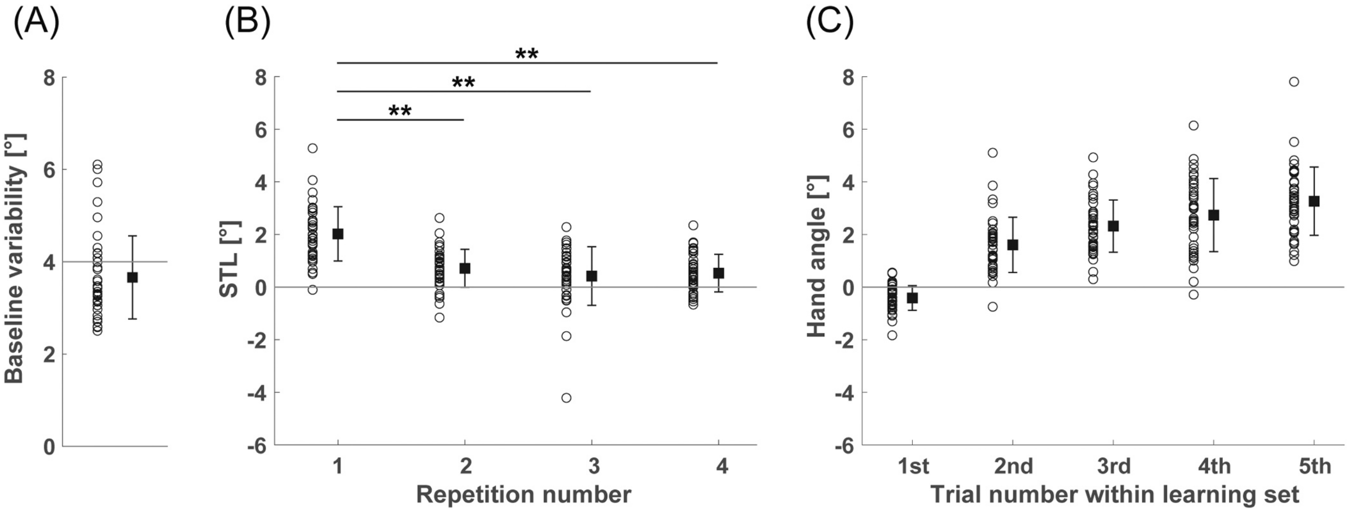

Fig. 2. Results. (A) Baseline variability: SD of hand angle in the familiarization phase. (B) Single-trial learning (STL) as a function of the number of consecutive exposures to the same error, or repetition number. (C) Hand angles collapsed across error signs within the learning set. The dots, squares, and error bars represent individual means, overall means, and standard deviations. **$p < 0.01$.

repetition number ($F[2.544, 99.234] = 23.631$, $p < 0.001$, $\eta 2 = 0.377$; Greenhouse-Geisser-corrected). Post-hoc pairwise comparisons revealed that the STL for the first error was significantly greater than that for the other errors (one vs. two repetitions: $t[39] = 6.019$, $padj < 0.001$, $d = 1.433$; one vs. three repetitions: $t[39] = 6.145$, $padj < 0.001$, $d = 1.755$; one vs. four repetitions: $t[39] = 6.720$, $padj < 0.001$, $d = 1.634$). The other comparisons were not significant (two vs. three repetitions: $t[39] = 1.482$, $padj = 0.219$, $d = 0.322$; two vs. four repetitions: $t[39] = 1.209$, $padj = 0.281$, $d = 0.201$; three vs. four repetitions: $t[39] = 0.477$, $padj = 0.636$, $d = 0.121$).

Considering the influence of hand trajectory in the preceding trial (HA_n in Eq. 1), we also performed an LMM on the STL. The LMM yielded results consistent with those obtained using the ANOVA. Specifically, the main effects of the repetition number and HA_n were significant, and the interaction was not significant (repetition number: $F[3,6327] = 8.654$, $p = 9.958^{-6}$; HA_n: $F[1,6362] = 714.780$, $p < 0.022^{-18}$; interaction: $F[3,6348] = 0.474$, $p = 0.700$). According to post-hoc pairwise comparisons using estimated marginal means, the STL for the first error was significantly greater than that for the other errors (one vs. two repetitions: $t[6326] = 3.964$, $padj = 0.002^{-1}$, $d = 0.151$; one vs. three repetitions: $t[6327] = 4.253$, $padj = 0.001^{-1}$, $d = 0.162$; one vs. four repetitions: $t[6327] = 2.780$, $padj = 0.011$, $d = 0.106$), and the other comparisons were not significant (two vs. three repetitions: $t[6323] = 0.325$, $padj = 0.745$, $d = 0.012$; two vs. four repetitions: $t[6324] = 1.234$, $padj = 0.261$, $d = 0.044$; three vs. four repetitions: $t[6324] = 1.551$, $padj = 0.182$, $d = 0.056$). Therefore, we found that consecutive error presentations modulated error sensitivity despite the significant effect of preexisting movement (HA_n). Moreover, the error sensitivity decreased when the same error was experienced two consecutive times, and the attenuated sensitivity was maintained.

The implicit learning for visuomotor rotation and clamped visual errors has an upper bound. Even after hundreds of trials, learning asymptotes around 15°–25° irrespective of the error magnitude (Bond and Taylor, 2015; Kim et al., 2018). In the present study, the hand angles within the learning set were below these values. Fig. 2C illustrates the hand angles when the sign of the error was collapsed, aligned with the -4° condition. This suggests that implicit learning did not reach its upper bound in this study, and that the attenuation of error sensitivity could not be explained by the saturation of implicit learning.

4. Discussion

In this study, we conducted a shooting experiment with visual error-clamp feedback to examine the modulation of implicit error sensitivity through continuous exposure to the same errors. In the experiment, participants were exposed to visual errors of the same direction and magnitude for four consecutive trials. Following exposure to the second error, the trial-by-trial learning decreased. Thus, our results indicate that consecutive error experiences modulate error sensitivity.

In a study related to our results, Avraham et al. (2021) conducted two experiments involving two learning phases (Experiment 1: 160 trials with 45° rotated feedback per phase; Experiment 2: 400 trials with 15° error-clamp feedback per phase) with a washout phase between the two learning phases. They reported attenuation of implicit adaptation in the second learning phase in both experiments, and additionally verified the robustness of the attenuation by reanalyzing previous studies with an experimental protocol similar to that of Avraham et al. (2021) (e.g., Leow et al., 2020; Stark-Inbar et al., 2017; Yin and Wei, 2020). In the present study, a trial-by-trial learning paradigm was used, and error sensitivity was reduced by two consecutive presentations of the same error. Accordingly, our results suggest that the attenuation of implicit learning occurs not only between phases, but also between trials.

The present results are inconsistent with the memory of errors model proposed by Herzfeld and colleagues, which indicates that implicit error sensitivity increases when errors are consecutively presented in a consistent direction (Albert et al., 2021; Herzfeld et al., 2014). However, assuming that not only the direction but the size of errors is memorized and utilized to adjust error sensitivity, we speculate that the model may provide a potential explanation of our results. Previous studies introduced perturbations, such as visuomotor rotation, that participants could relatively easily counteract (Albert et al., 2021; Herzfeld et al., 2014). Accordingly, the authors focused only on the cases where a presented error is undercompensated or overcompensated in the next trial, consistent or inconsistent errors with respect to direction consecutively occur; they demonstrated that error sensitivity increases and decreases under each circumstance, respectively. In contrast, let us consider cases where the error of the same direction and size, as in this study, or of the same direction and larger size is presented compared to the previous trial. In these cases, the performed action (e.g., correction of shooting movement in the opposite direction of the experienced error) can be regarded as an ineffective approach in reducing the error. Therefore, the reliability of this action may diminish, leading to the attenuation of error sensitivity in this study. Our results may imply the potential for further development of the memory of errors model.

There are other potential factors that contribute the attenuation of implicit error sensitivity by consecutive presentations of the same error.

First is changes in internal states, such as arousal and surprise. Yokoi and Weiler (2022) measured pupil diameter, which is associated with these internal states (Morad et al., 2000; Nassar et al., 2012; Preuschoff, 2011; Yoss et al., 1970), during reaching tasks. They suggested that the baseline pupil diameter before movement or the pupil dilation velocity in response to errors was reduced by an increase in the number of error experiences or a decrease in the intervals between error experiences. Although they did not measure the learning rate, other studies have shown a positive relationship between these eye metrics and the learning rate (Sedaghat-Nejad and Shadmehr, 2021; Yokoi, 2021). Thus, a decrease in arousal and surprise may have caused the attenuation of implicit learning observed in Avraham et al. (2021) and the present study. Second is the shift in the perceived hand position toward the cursor, known as proprioceptive shift (Tsay et al., 2021). According to the proprioceptive re-alignment model (Tsay et al., 2022), implicit adaptation is driven by the proprioceptive error, which is the discrepancy between the perceived and desired hand position (i.e., target); this error is produced by the proprioceptive shift. Ruttle et al. (2021) showed that the proprioceptive shift reached asymptote with only one exposure to visuomotor perturbation. This very sharp emergence of the proprioceptive shift may be related to the highest error sensitivity immediately after the first error presentation. Third is the prediction of motor performance error. Ranjan and Smith (2020) indicated that the response patterns obtained by different paradigms of single-trial learning were well explained by motor performance prediction error (MPPE)-driven learning. MPPE is defined as the difference between actual and predicted performance. Assuming that the direction of cursor movement represents performance in our task, the performance within each learning set could be accurately predicted following the first error-clamp trial. This accurate prediction may cause the decrease in error sensitivity after exposure to the second error.

The limitations of this study and directions for future research are as follows. First, this study employed a visual error-clamp paradigm, not a visuomotor rotation paradigm (Hutter and Taylor, 2018), to investigate the modulation of implicit error sensitivity through consecutive exposure to the same error. However, the visual error-clamp paradigm does not control hand trajectory, resulting in increased noise in measuring error sensitivity. Although we attempted to mitigate the effect of the hand trajectory in the analysis stage, it is preferable to address this issue in the experimental design stage. Therefore, future studies should consider using a manipulandum to fix the hand trajectory in addition to the cursor trajectory (i.e., force channel method; Hayashi et al., 2020). Second, this study did not find any change in error sensitivity after exposure to the third error. Because the STLs for the second, third, and fourth errors were small (Fig. 2B), a floor effect might have been present. Therefore, even if error sensitivity continues to decrease after exposure to the third error, this decrease may go undetected owing to the floor effect. Further studies are required to explore this. Third, the error size presented with error-clamp feedback was only 4°. Thus, we cannot determine whether the present results are dependent on error size. Initially, we also established a group exposed to a larger error (i.e., 12°). However, many participants in the 12° group noticed that error-clamp feedback unconsciously altered their shooting movement. Concerned that the notice could bias their shooting movements (e.g., explicit re-aiming), we ceased data acquisition for the 12° group and decided not to use the data in this study (Fig. S2). It is likely that the participants' notice of the impacts of error-clamp feedback was caused by the insertion of veridical feedback trials between the learning sets to motivate them. Therefore, to investigate the modulation of error sensitivity through consecutive exposure to larger errors, it may be necessary to insert only no-feedback trials there.

5. Conclusion

This study investigated how implicit error sensitivity changes with consecutive exposures to the same error. In the shooting task, visual errors of the same direction and magnitude were presented for four consecutive trials using visual error-clamp feedback. Error sensitivity was attenuated following exposure to the second error. These results indicate that when visual errors occur consecutively, the sensorimotor system exhibits different responses, even for identical errors. The continuity of the error may be one of the factors modulating the error sensitivity.

Compliance with ethical standards

This study adhered to the principles of the Declaration of Helsinki and was approved by the Ethics Committee of the Faculty of Education at Hokkaido University (approval number: 21–08). All participants signed an informed consent statement prior to participation in the study.

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CRediT authorship contribution statement

Masaki O. Abe: Project administration, Resources, Supervision, Writing – review & editing, Conceptualization, Validation. **Naoyoshi Matsuda:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft.

Declaration of Competing Interest

None

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Data statement

The data presented in this study are openly available in FigShare at 10.6084/m9.figshare.25263613.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ibneur.2024.05.004.

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