# Implicit adaptation processes promoted by immediate offline visual and numeric feedback

Beverley C Larssen[1,2]

Sarah N Kraeutner[3]

Nicola J Hodges[1,*]

[1]School of Kinesiology, UBC

[2] Department of Physical Therapy, UBC

[3] Department of Psychology, UBC-Okanagan

THIS IS A PRE-PRINT VERSION OF THE MANUSCRIPT WHICH IS NOW PUBLISHED WITH THE JOURNAL OF MOTOR BEHAVIOR:

https://www.tandfonline.com/doi/full/10.1080/00222895.2022.2088678

THERE MAY BE SMALL DIFFERENCES BETWEEN THIS VERSION AND THE FINAL PUBLISHED VERSION; Published online: 03 Jul 2022

* = corresponding author

School of Kinesiology

210-6081 University Blvd

The University of British Columbia

Vancouver, BC

V6T 1Z1

Email: nicola.hodges@ubc.ca

Tel: 604 822 5895

Declarations of Interest: none

## Abstract

In adaptation learning, visual feedback impacts how adaptation proceeds. With concurrent feedback, a more implicit/feedforward process is thought to be engaged, compared to feedback after movement, which promotes more explicit processes. Due to discrepancies across studies, related to timing and type of visual feedback, we isolated these conditions here. Four groups (N = 52) practiced aiming under rotated feedback conditions; feedback was provided concurrently, immediately after movement (visually or numerically), or visually after a 3s delay. All groups adapted and only delayed feedback attenuated implicit adaptation as evidenced by post-practice after-effects. Contrary to some suggestions, immediately presented offline and numeric feedback resulted in implicit after-effects, potentially due to comparisons between feedforward information and seen or imagined feedback.

Keywords: Adaptation learning, Internal models, Knowledge of results, Implicit processes

**Implicit adaptation processes promoted by immediate offline visual and numeric feedback**

When we act in novel environments our movements are often quite errorful and unstable. In such scenarios, we must learn to adapt known relationships between motor commands and movement outcomes to reduce error. This adaptation has been proposed to be accomplished via a combination of two different processes: an unintentional, implicit process, which reflects recalibration of the sensori-motor system and a more strategic, explicit process (e.g., Mazzoni & Krakauer, 2006; McDougle et al., 2015; 2016; Taylor et al., 2014). Although there have been studies investigating how feedback impacts adaptation in reference to these two processes, there are discrepancies across studies (e.g., Brudner et al., 2016; Hinder et al., 2008; 2010; Mazzoni & Krakauer, 2006; Taylor & Ivry 2011; Taylor et al., 2014; Schween & Hegele, 2017). Furthermore, feedback timing and type (i.e., visual or numeric) have not been considered within the same study. In the following experiment, we compared concurrent feedback to feedback provided immediately at movement end; either visually or numerically, as well as after a 3 s delay. Our aim was to inform understanding of how feedback is used to adapt goal-directed movements and to determine what conditions best promote adaptation and the development of implicit planning processes.

In visuomotor adaptation paradigms, a visual perturbation is applied, creating a mismatch between what is seen and the actual felt or expected position of the hand (e.g., Bernier et al., 2005; Mikaelian & Held, 1964; Redding & Wallace, 2002). Initial exposure results in errorful trajectories which become more accurate with practice, indexing successful adaptation. Adaptations are thought to be largely a result of an implicit, sensory prediction error, based on comparisons between an internal prediction of sensory consequences and the actual sensory feedback (e.g., Shadmehr & Krakauer, 2008; Wolpert et al., 1995; Wolpert, 1997; yet see

Hadjiosif et al., 2021; Wood et al., 2020). This prediction error is thought to guide and update motor planning processes, in a way that is independent of conscious awareness (e.g., Mazzoni & Krakauer, 2006). After-effects that persist following exposure to a visuomotor perturbation, when the participant is in a known normal environment, allow assessment of this implicit adaptation. Post-practice after-effects represent errors that persist despite being cued that there is no perturbation (e.g., Hadjiosif et al., 2021; Heirani Moghaddam et al., 2021; Larssen et al., 2021; Ong et al., 2012). Presence of after-effects provide evidence that an implicit internal model or sensori-motor mapping has been updated (e.g., Held & Hein, 1958; Redding & Wallace, 1993; Shadmehr & Mussa-Ivaldi 1994), but can also index use dependent learning associated with repetitive aiming during practice that is in the direction of the after-effect (e.g., Diedrichsen et al., 2010; Wood et al., 2020).

Successful adaptation can also be achieved via (or in conjunction with) explicit processes involving the conscious monitoring of movement and/or application of strategies (e.g., Heirani, Moghaddam et al., 2021; McDougle et al., 2016; Taylor et al., 2014). These explicit processes are believed to be sensitive to target error and rewards, impacting action selection (e.g., Benson et al., 2011; Bond & Taylor 2015; Hinder et al., 2008; Izawa & Shadmehr, 2011; Mazzoni & Krakauer 2006; Sarlegna et al., 2007; Schween & Hegele, 2017; Taylor & Ivry 2011). Reaction time (RT) is one measure that has been used to infer a more explicit type of adaptation, due to increased preparation time required to implement explicitly derived plans (Benson et al., 2011; Dang et al., 2019; Hinder et al., 2010; Ong et al., 2012, Saijo & Gomi 2010). Implementation of strategies also typically result in increased performance variability reflecting the testing of strategies (e.g., Benson et al., 2011; McDougle et al., 2016; Ong et al. 2012). Although a distinction is usually made between explicit and implicit processes, these processes are not necessarily independent, they develop concurrently and awareness of a rotation does not prevent implicit learning processes (e.g., Mazzoni & Krakauer, 2006; Modchalingam et al., 2019).

The timing of sensory feedback, relative to the timing of movement execution appears to be important for the type of adaptive process (Brudner et al., 2016; Hinder et al. 2010; Honda et al., 2012a; Schween et al., 2014; Schween & Hegele, 2017; Shabbott & Sainburg, 2010). When visual information is provided after movement completion, “offline” error correction processes involving explicit strategies are thought to be used (e.g., Shabbott & Sainburg, 2010). However, when visual feedback is provided at the same time as movement (“online”), implicit adaptation processes, based on sensory prediction errors, are thought to be activated (Hinder et al. 2010, 2008; Shabbott & Sainburg, 2010). In typical visuomotor adaptation tasks, online feedback encourages a real-time (i.e., concurrent with movement) comparison between visual and proprioceptive input, as well as comparisons between actual and predicted sensory consequences. These comparisons can lead to a sensory prediction error, which is thought to lead to the automatic updating of an internal model for aiming through implicit, feedforward/ predictive mechanisms (Hinder et al., 2008, 2010; Tseng et al., 2007).

Why feedback might not get incorporated into any internal model may be due to the availability of sensory feedback during feedforward predictions. In support of this proposal, post-practice after-effects were only seen in groups that received online visual feedback, rather than endpoint error or delayed (~4s) visual feedback (Hinder et al., 2010, 2008). However, all groups adapted to the rotation. Because the feedback delay was so long in these studies, it is possible that implicit adaptation would have occurred had the feedback been available earlier, thus enabling sensory comparisons. Indeed, others have shown that endpoint feedback, provided immediately at cessation of the movement does result in after-effects, although the magnitude may be moderated (e.g. Barkley et al., 2014; Bond & Taylor, 2015; Honda et al., 2012a; Taylor et al., 2014). Based on these endpoint feedback effects, Honda and colleagues have argued that as the time between action and feedback increases, the relevance of the generated error signal decreases (Honda et al., 2012a; Honda et al., 2012b; Kitazawa et al., 1995; see also Brudner et al., 2016; Schween & Hegele, 2017).

It may well be that the quality of feedback moderates the type of adaptation process engaged. A model has been proposed that describes the moderation of adaptation processes as a result of feedback based on behavioural distinctions between online visual feedback and endpoint feedback about task success (Izawa & Shadmehr, 2011). Only when 'quality' visual feedback is presented, as would be the case when it is provided concurrent with movement, are sensory prediction errors used to fully update implicit, feedforward processes. In contrast, feedback alterations offline, that primarily signal movement success, serve a reward function (see also Nikooyan & Ahmed, 2015). Although this latter information can lead to a change in movement on the next trial due to explicitly-evoked strategies and changes to action-selection, there is no update of the general motor plan and implicit feedforward predictions. However, visual feedback about the sensory consequences of the movement, even if delayed, can still result in some implicit adaptation. In this case, the adaptation would be based on both reward and sensory prediction error.

Another feature of feedback that can impact the type of adaptation processes engaged is whether it is visual or numeric. These two different types of visual feedback can also be thought to differ in the quality of information they provide. Numeric feedback provides the learner with a more abstract, less-salient source of error information than visual trajectory feedback. Because some translation is required of the numeric information into a movement plan, potentially creating a delay, this type of feedback (referred to as Knowledge of Results/ KR, Adams, 1971) is more likely to operate via strategically applied error-correction processes on action selection. Given that it is not strictly speaking sensory information, there would be no discrepancy between predicted and actual sensory consequences that would hinder any updating of feedforward processes. Indeed, Izawa and Shadmehr (2011) have proposed that this numeric KR primarily serves a reward function, impacting action selection (i.e., explicit) processes. Reduced or no implicit adaptation would be expected because of the lack of sensory prediction error. Evidence in support of this reward function has been provided. When numeric feedback was given concurrently, conveying scalar magnitude of distance from the target (but not direction), participants adapted to a rotated environment (Butcher & Taylor, 2018; Nikooyan & Ahmed, 2015). Slower learning rates were observed when adapting with only numeric reward compared to visual feedback (Nikooyan & Ahmed, 2015), and no after-effects were observed (Butcher & Taylor 2018).

In the current study, we sought to further test the effects of delaying the presentation of visual cursor feedback on adaptation processes in a paradigm where movement feedback was rotated 30° in a clockwise direction. If concurrent feedback is essential for implicit adaptation to occur, we expected that delaying visual feedback would negate or attenuate implicit adaptation. This attenuation would be evidenced by smaller magnitude of after-effects for delayed feedback groups. Adaptation was expected to occur regardless of feedback conditions, but for delayed feedback groups, we predicted that adaptation would be achieved by more explicit means. These explicit processes would be evidenced through increased awareness and knowledge of the rotation, increased trial-to-trial variability, and increased action selection/ planning time (i.e., longer RT's). In addition to comparing groups that received feedback either concurrent with movement, immediately at movement end, or after a 3 s delay, we also tested a group that received numeric feedback immediately at movement end. The numeric feedback conveyed both direction and magnitude of error between the target and rotated feedback. We expected that presenting information as a number would cause a more explicit type of adaptation, which would be evidenced by elevated RTs and increased between-trial variability. We did not expect implicit updating of the motor plan (i.e., no after-effects), due to an absence of sensory information to compare to any sensory feedforward prediction.

## Methods

### Ethics Statement

All procedures were conducted according to the regulations of the Behavioural Research Ethics' Board of the University of British Columbia (H09-00717). Written informed consent was obtained from all participants.

### Participants

Fifty-two, self-reported right-hand dominant participants, volunteered to participate after responding to an advertisement.[1] These individuals were naïve to the task and were randomly allocated to one of four groups (n=13/group): an online feedback group (ONLINE, Mn Age = 20.8, SD = 2.3 yr, Female = 8), which received concurrent continuous feedback of their cursor trajectory during each aiming movement; two post-trial feedback groups, which received feedback of their cursor trajectory immediately after movement execution (OFFLINE_VIS, Mn Age = 21.1, SD = 2.3 yr, Female = 9) or following a 3 s delay (OFFLINE+3s, Mn Age = 20.3, SD =2.5 yr, Female = 9); or a numeric feedback group that received signed error feedback immediately after movement execution (OFFLINE_#,  Mn Age = 19.5, SD =1.4 yr, Female = 8).

### Task and Apparatus

Participants performed right-hand aiming movements with a custom mouse connected to a graphics' digitizing tablet (Calcomp Drawing Board IV, 200Hz), as illustrated in Figure 1A. The mouse had a plastic extension with a central crosshair whose coordinates were registered by the tablet. Participants were asked to centre the index finger of their right hand on this crosshair. Aiming movements were made on the graphics' tablet to 5 equally-spaced visual targets. These targets were projected downwards from an upturned monitor (ViewSonic E70f – CRT 17" monitor, 1280 X 1024 resolution, refresh rate: 66Hz) onto a semi-silvered mirror that were held in place by a custom-built box (with openings at the top, middle and bottom, for the up-turned monitor, semi-silvered mirror, and graphics tablet to rest respectively). Note that due to inherent delays with the monitor's refresh rate, in all groups an ~15 ms delay in feedback would be expected. A larger opening on one side of the apparatus allowed the participant to interact with the tablet and view the display. The semi-silvered mirror was positioned between the participant's line of vision and 33.3 cm above their hand in the workspace and the monitor was connected to a desktop computer which afforded control of the display and feedback.

The experimental protocol was run using a PC (Dell Inspiron 531, AMD Athlon™ 64x2, 5600+, 2.9GHz dual core processor; Windows Vista OS) through a custom program using LabVIEW™ software (version 9.0, National Instruments). On the visual display, a central home position (0.6 cm X 0.6 cm square) was situated in the centre of the 5 targets (at a 9.5 cm radius). Target and cursor diameter were both 0.4 cm. The participant's head was supported by a chin rest positioned just outside of the workspace. The distance between the chin rest and the projected image of the central home position was 26.5 cm.

To start a movement trial, participants had to move their cursor back to the central home position, which they could do in their own time. Vision of the cursor was not available until they were within 4.75 cm of home and only as a single point to aid with home position placement (see Hutter & Taylor, 2018 for similar methods). One of the 5 targets then appeared 1.5 s after the cursor was inside the home position. After the completion of each movement (when movements exceeded the 9.5 cm radial distance from the home position to the target), participants were instructed to stop moving and not to return to the home position until after the target and/or feedback had been extinguished from the display. All feedback (cursor or number) remained on the visual display for 1.5 s after it was first shown, with the exception of online feedback which was extinguished immediately when the 9.5 cm radial distance between the home position and the target was surpassed.

**Procedure**

A summary of experimental procedures is provided in Figure 1B and C. Participants first performed a 20-trial familiarization phase, followed by a 20-trial pretest, both consisting of aiming movements to 5 targets in a normal, non-rotated environment with concurrent (online) visual feedback of the cursor trajectory. Within a block of 5 trials (4 blocks for each testing phase) all 5 targets were sampled in a random order. Participants were told that their goal was to guide a green cursor through one of the delineated targets, moving the mouse fast while being accurate at guiding the mouse in a straight trajectory. Errors and movement times were monitored on a separate computer monitor. If movement times exceeded 350 ms, participants were verbally reminded to move quicker on the following trial. This was especially important for the ONLINE group that received concurrent cursor feedback, to minimize the opportunity for online corrections (Tseng et al., 2007). Our aim was to encourage the updating of motor planning processes prior to movement execution, not corrections during. They were also instructed to move the mouse in a straight, uncorrected line, performing shooting movements through the target.[2]

Participants were instructed that the next trial would only begin once their hand was back in the home starting square. The participant was cued to go by the appearance of one of the five targets. As below, although no special instructions were given to constrain reaction time (RT; the interval between target appearance and movement onset), we measured this interval to give an indication of movement planning time.

The adaptation phase immediately followed the pretest and involved either 100 (shorter) or 200 (extended) practice trials. Initially, n=8/group completed the shorter adaptation phase, but then we recruited a further n=5/group to extend practice, due to the higher error at the end of practice for the numeric and delayed feedback groups. This post-hoc decision to extend the practice phase allowed us to account for potential differences in after-effects which could otherwise be explained by accuracy at the end of practice, rather than necessarily feedback-type or timing.

A visuomotor rotation was gradually introduced in increments of 5°, after 5 reach trials to each of the 5 target locations, up to a maximum of a 30° clockwise (CW) rotation of the feedback relative to the position of the participant's index finger. Therefore, participants finished the adaptation phase with either 75 (shorter adaptation) or 175 (extended adaptation) trials of practice in the 30° CW environment (see Figure 1C). The target locations were again presented in a random order within each 5-trial practice-block. Participants were told that they would now be performing in a "new" environment, but they were not given any details concerning the rotation. The ONLINE feedback group received the full continuous cursor feedback trace of the rotated cursor trajectory concurrent with movement. The delayed feedback groups received either a static image of the full trace of their last trial cursor trajectory (OFFLINE_VIS or OFFLINE+3s) or a numeric error score that showed the signed direction and magnitude of their radial error from the target in degrees (OFFLINE_#) (see Figure 1B). Feedback was provided immediately when movements exceeded the 9.5 cm radial distance from the home position to the target (movement end) for the OFFLINE_VIS and OFFLINE_# groups or 3 s after movement end for the OFFLINE+3s group. Feedback remained on the screen for 1.5 s. Participants in the numeric group were told that negative scores indicated errors in the counterclockwise (CCW) direction relative to the target, positive scores indicated error in the CW direction, and a score of zero indicated an accurate hit. They were not told that this feedback was erroneous (rotated by 30°). All participants were instructed that their goal was to achieve accurate aiming while moving as quickly as possible. They were reminded of the instructions after every 5 aiming trials (for the first 30 trials). Participants in the long adaptation protocol were also reminded again after the completion of their 100$^{th}$ trial.

A 20 trial, normal environment posttest was conducted immediately following the adaptation phase to test for after-effects, again consisting of four 5 trial blocks comprising each target. Participants were informed that they were in a different, but now “normal” environment and that they would not see the cursor or receive any feedback about target accuracy. Because only the ONLINE group received feedback of the cursor during practice, withholding any feedback about accuracy during the posttest allowed us to test all groups under the same conditions, which were not specific to only one group during practice. Moreover, without feedback, individuals were not expected to make any corrections on subsequent trials based on awareness of error from the feedback. Participants were told to make normal aiming movements to shoot through the targets. This instruction was provided to discourage application of any previously learned explicit strategy in order to test for unintentional (implicit) after-effects. Participants were continually reminded throughout testing in the posttest to just make normal aiming movements through the targets.

Explicit knowledge and awareness of the rotation was assessed at the end of testing using a pen and paper test accompanied by a questionnaire adapted from Benson et al. (2011). Participants were first shown diagrams of the 5 radially arranged targets that were connected to the start square by 5 black lines. They were told that the lines represented an accurate cursor trajectory for aiming. They were then asked to draw the 5 corresponding trajectories that their right index finger would have had to follow to produce the same cursor trajectories during the adaptation phase (i.e., new environment). Participants were also asked a series of questions about their awareness of both the presence and nature of the rotation and to determine any strategies adopted for reducing aiming error for those who reported awareness of a mismatch between the visual feedback (cursor or number) and their actual movement.

**Measures and Analysis**

Directional, constant radial error (CE; in degrees) was calculated as the angle between the reference trajectory joining the origin (home position) and the intended target and the trajectory joining the origin and the actual cursor position measured at peak tangential velocity. A mean CE value was calculated across blocks of 5 trials for each participant. Positional error at peak velocity has been used as a reliable index of aiming accuracy (adaptation) in previous studies involving similar movement time constraints and the expectation that movements cannot be corrected online (e.g. Larssen et al. 2012; Lim et al. 2014). Indeed, these type of “shooting” movements produce almost identical errors at peak velocity as noted at movement end (as confirmed in this study through graphical comparisons; see also Lim et al., 2014). A positive or negative value for error denotes a CW or CCW error respectively. To assess variability between trials, mean inter-trial variable error (VE; in degrees) was calculated as the standard deviation of the directional constant radial error across 5-trial practice-blocks for each participant. Derivation of kinematic information (magnitude and timing of peak tangential velocity) was performed using the same custom LabVIEW™ program that was used to run data collection.

Reaction time (RT) data were collected as an index of movement planning (time of target presentation to movement onset). Movement onset was defined as the time when the cursor left the central home square and movement completion was determined to be the time when the cursor exceeded the 9.5 cm radius of the target array. Inter-trial variability in aiming accuracy (VE) provided an indirect measure of explicit strategy use. Aiming trials where movement time (MT) exceeded 1000 ms were excluded from analyses to control for potential online corrections. We were less concerned in this experiment about participants moving slowly because in all but one group, visual feedback was provided only once the aiming movement was completed (i.e. reducing the need for online corrections). This resulted in a mean exclusion of a small proportion, ~3.0%, of the total trials (ONLINE = 3.7%, OFFLINE_VIS = 3.1%, OFFLINE+3s = 1.4%, OFFLINE_# = 4.0%).

***Adaptation and After-effects:*** Separate linear mixed effects (LME) models were used to evaluate aiming CE, VE, and RT during adaptation, using the lme4 package (Bates et al., 2015) in R version 3.2.4 (R Development Core Team, 2013). For all LME models, participant was included as a random effect. Model fit of adaptation data was evaluated using Akaike's Information Criterion.[3] All statistical outputs for each LME are presented in Tables S1-7 in Supplementary Materials. To assess change during adaptation, we evaluated CE, RT and VE across all participants (n = 13), comparing across groups and practice-blocks (blocks = 6-20).

Only practice-blocks 6-20 were included in this analysis as practice-block 6 was when the cursor rotation had reached the full 30° and we had complete data for all participants up until practice-block 20. For statistical analyses, practice-block 6 was always used as the reference value in comparing across practice-blocks[4].

For tests of after-effects, a LME model was conducted on CE with Group (all), Time (Pretest vs Posttest) and test-Block (4 blocks) entered as fixed effects. Test-block 1 was used as our reference value in statistical analyses. Given the variations in practice duration in our design (Short/100 trials vs. Long/200 trials), practice duration was entered into the LME as a group-level, fixed effect control variable.

Planned contrast analyses were used to test primary group-level hypotheses. The OFFLINE_VIS group was the reference group, allowing three comparisons corresponding to the three degrees of freedom for each effect and our major hypotheses. Two contrasts, comparing the OFFLINE_VIS group to the ONLINE and to the OFFLINE+3s groups, addressed questions related to feedback timing and hypotheses concerning the importance of online/immediate feedback for sensorimotor adaptation processes. The third contrast, comparing the OFFLINE_VIS group to the OFFLINE_# group, allowed us to make conclusions about feedback type (i.e., visual cursor vs. numeric) and the importance of visual feedback generally for sensorimotor adaptation processes.

After-effect magnitude (difference between mean aiming error in the first block of posttest minus the last block of pretest) was characterized with separate within-subject effect sizes for each group (Cohen's *dz;* Lakens, 2013). These calculations were based on the standard deviation of the posttest minus pretest difference scores for all participants.

***Awareness.*** Explicit awareness was characterized by the mean planned aiming error (in degrees), calculated from measuring the average error of the participant's trajectory drawings to each of the five targets on the post-experiment questionnaire. To assess for group differences in explicit awareness, mean planned aiming errors were again analyzed with pre-planned simple contrasts comparing all feedback groups to the OFFLINE_VIS group as above.

***Relationships between implicit and explicit measures.*** Three separate Pearson correlations were run to evaluate relationships between the magnitude of after-effects and (i) mean RT during adaptation (ii) VE during adaptation and (iii) planned aiming error assessed in the explicit awareness test. After-effect magnitude was calculated as the absolute value of the mean difference between the first 5 trials of posttest and the last 5 trials of pretest (see Larssen et al., 2021 for similar analysis).

# Results

## Adaptation

### *Constant Error*

Mean directional CE for all four feedback groups is shown in Figure 2A. All groups showed a decrease across practice-blocks but this was most pronounced for the ONLINE and OFFLINE_VIS groups, especially in practice-blocks 6-20. At the end of practice-block 20, the groups still looked different, but differences across groups had reduced across extended practice. Full sample analysis based on practice-blocks 6-20 showed that errors decreased significantly over the course of practice for each block relative to practice-block 6 (with the exception of practice-block 7, $p$ =.14). Although none of the contrast comparisons based on group were significant (all $p$s>.10, with the exception of OFFLINE+3s versus OFFLINE_VIS, $p$ = .096), there were Group X practice-Block interactions. As is apparent in Figure 2 (see also supplementary Table 1), the decrease in error relative to practice-blocks 6-12 and 6-17 was more pronounced for the OFFLINE_VIS group compared to the decrease in error at those same blocks for the OFFLINE+3s delay group. The decrease in error for OFFLINE_VIS from practice-blocks 6-17, 6-19 and 20 was also greater compared to OFFLINE_# group[4].

*Reaction Time*

Mean RT data during adaptation is plotted as a function of practice-block in Figure 3 (see also supplementary Table 3). RTs remained relatively consistent across practice-blocks 6-20, although there was more variation in the second part of practice for the extended practice groups, particularly the +3s delayed feedback group[4]. Analysis of practice-blocks 6-20 did not yield differences across blocks when compared to the reference practice-block 6. As predicted, in these first 100 trials, delaying feedback by 3 s resulted in longer RTs than not delaying it (i.e. in comparison to OFFLINE_VIS, $p$ =.03). Mean RTs did not differ between the groups that received cursor feedback during the movement (ONLINE) or immediately after movement completion (OFFLINE_VIS). With respect to feedback type, although RTs were longer for the numeric feedback group compared to the OFFLINE_VIS group as predicted, the difference was not significant ($p$ = .058). Group effects did not vary with practice-block except for the OFFLINE_# group at practice-block 9, where the increase in mean RT relative to practice-block 6 was greater than the increase in RT observed for the OFFLINE_VIS group ($p$ = .043).

*Variable Error*

Group mean VE data during adaptation is plotted as a function of practice-block in Figure 4. In the first part of practice, inter-trial variability in aiming error was relatively consistent across practice, only showing differences from the first block (i.e., practice-block 6) and practice-block 11 ($p$ = .049). With respect to group differences, once again, there was no differences in VE between the OFFLINE_VIS and ONLINE feedback groups, but the timing of feedback did matter when it was delayed by 3s (OFFLINE_VIS vs. OFFLINE+3s, $p$ = .014). The type of feedback also impacted VE, with the numeric group being more variable than the OFFLINE_VIS group ($p$ <.01) (see supplementary Table 5). Significant Group X practice-Block effects, although not predicted, were present at practice-blocks 9 (OFFLINE_#, $p$ =.008), 11 (ONLINE, $p$ = .036), 12 and 19 (OFFLINE+3s, $p$s <.05). These interaction effects reflect the smaller but inconsistent increase in inter-trial variability relative to practice-block 6 for the OFFLINE_VIS group compared to the relatively larger, but also inconsistent increases in VE for the OFFLINE_+3s and OFFLINE_# groups, or the small but inconsistent decrease in VE error for the ONLINE group shown in Figure 4.

**After-effects**

In Figure 2A, pretest and posttest mean CEs across the four no-rotation, no-feedback test-blocks are shown on the far left and far right of the figure. The last block of pretest and the first block of posttest are highlighted in blue and illustrated as bar-graphs in Figure 2B. Individual means are illustrated on the bars, with short duration practice participants shown as circles and longer duration participants as triangles. We included practice duration as a fixed effect control variable in our LME model. Overall, participants with extended practice performed with more error in the posttest than those with shorter practice durations, as evidenced by the significant Practice Duration X Time interaction ($p$ =.012) and Practice Duration X Time X test-Block interactions for test-blocks 2 and 4 ($p$s <.05). Importantly, there were no interactions of Practice Duration with Group (see Supplementary Table 7).

As can be seen from Figure 2, posttest mean CEs were larger than those for the pretest, especially for the ONLINE and OFFLINE_VIS groups. This was confirmed by a significant effect of Time ($p < .001$). The predicted Group X Time interactions were also present. With respect to feedback timing and our preplanned contrasts, the OFFLINE_VIS group showed a greater increase in error across time (i.e., larger after-effects) than the OFFLINE+3s group ($p<.001$), but it did not differ to the ONLINE group ($p = .61$). With respect to feedback type, the OFFLINE_VIS group also showed a greater increase in error across time than the OFFLINE_# group ($p =.007$). Errors across test-blocks were relatively stable and no differences were noted as a function of test-block (all *p*s>.28). All groups showed some decay of after-effects across posttest blocks as evidenced by a Time X test-Block interaction when comparing test-block 1 to block 4 ($p =.01$), but there were no significant interactions with Group (only differences for the OFFLINE+3s group at block 4 approached statistical significance, $p = .052$).

After-effect magnitude is also illustrated by post-hoc effect size calculations, comparing the last block of the pretest to the first block of the posttest. Directional error from pretest to posttest increased (i.e., became more negative) for all groups, but to different magnitudes. As depicted in Figure 2B, large effects were shown for the ONLINE ($d_z = 3.07$) and OFFLINE_VIS groups ($d_z = 3.29$). Although substantially less, relatively large effects were also observed for the OFFLINE_# group ($d_z = 1.73$) and OFFLINE+3s group ($d_z = 1.71$).

**Awareness**

For this measure we were missing data from two participants from the OFFLINE+3s group, due to a procedural error during data collection. As can be seen in Table 1, participants in all groups reported being aware of the rotation applied to the feedback and that it was not a true representation of their actual aiming. However, none of the participants in the ONLINE and OFFLINE_VIS groups and only 2 participants in the OFFLINE_# group showed accurate awareness about the *nature* (direction and magnitude) of the rotation. Nine out of eleven participants were correct in determining the direction in the OFFLINE+3s group but mean estimates of rotation size were still low for this group (~60% of the actual magnitude). Statistical analysis on the estimated magnitude of the rotation, comparing the OFFLINE_VIS group to each of the other feedback groups through simple contrasts, only showed a difference with the OFFLINE+3s group ($t(46) = 7.10$, $p < .001$).

**Relationships between implicit and explicit measures**

We ran Pearson correlations to determine if after-effect magnitude (absolute value of the first block of posttest minus the final block of pretest) was related to indices of explicit awareness; namely mean RT and VE during adaptation and estimated aiming error (awareness). Scatterplots for these analyses are presented in Figure 5. After-effect magnitude was negatively correlated with RT, $r = -.63$, $p <.001$, VE, $r =-.73$, $p <.001$, and estimates of rotation magnitude, $r = -.46$, $p <.001$. As predicted, larger RTs, VE, and better estimates of rotation magnitude, were associated with smaller magnitude after-effects. From inspection of the graphs and the results reported above, these relationships appeared to be driven by individuals in the OFFLINE+3s group, clustered on the right of the graphs (small after-effects, large RT, VE, Awareness), and the ONLINE and OFFLINE_VIS participants, clustered on the left (large after-effects with smaller magnitude RT, VE, Awareness). From inspection of the scatterplots these relationships did not appear to be dependent on practice duration.

## Discussion

We studied how delays in the provision of visual feedback and the type of feedback (visual or numeric) affects adaptation processes. Through measures of after-effects, we inferred the degree of implicit adaptation as a result of feedback provided concurrently with action, immediately at the end of the movement, or after a 3 s delay. We also studied adaptation processes in the absence of visual feedback, when participants were only provided with numeric feedback about their aiming errors. Consistent with previous findings, all four groups were able to use their respective types of feedback to adapt to the rotation. However, this adaptation took longer when the visual cursor feedback was delayed by 3 s or if numeric rather than visual cursor feedback was provided (see Figure 2A). Importantly, after-effects were significantly reduced when feedback was delayed by 3 s but not when it was provided immediately at movement end.

**Immediate feedback**

When visual feedback was provided immediately after movement end, significant large after-effects were noted. Immediate after-effects (test-block 1 of the posttest minus block 4 of the pretest) were of a similar high magnitude for the OFFLINE_VIS ($d_z$ = 3.07) and ONLINE ($d_z$ = 3.29) groups, translating to an increase in error of ~18-20°. These after-effects are consistent with those noted elsewhere based on similar no-feedback methods (e.g., Barkley et al., 2014; Bond & Taylor, 2015, Exp 3; Ong & Hodges, 2010). There was attenuation in the size of the after-effects across blocks in the posttest, evidenced by a Group X Time interaction, but the attenuation was primarily independent of group. Although the longer practice duration generally led to larger errors in the posttest, as noted by a Time X Practice Duration interaction, again this was independent of group.

Similar effects and conclusions concerning online versus terminal feedback comparisons were noted by Barkley et al. (2014). These authors assessed both reach and proprioceptive after-effects following visual feedback provided immediately after target attainment versus during the actual reach (with the latter based on a separately conducted study; Salomonczyk et al., 2011). The after-effects were of a slightly smaller magnitude in the after-target attainment group (~12-15°), versus the during-reach group (~18°), but comparisons were made across different studies.

In these groups, there was no increase in magnitude of the after-effects after extended training (the groups were subdivided based on the amount of training). The findings that sensory predictions were also adapted after practice and that the size of the effects were not dependent on the amount of practice, suggests that the after-effects were related to sensory prediction error rather than use-dependent learning associated with repetitive positioning (cf., Diedrichsen et al., 2010). While we cannot rule out some contribution from use-dependent learning mechanisms in our current data, we saw similar magnitude of after-effects for our ONLINE and OFFLINE_VIS groups, with only small moderation due to the amount of practice. Taken in the context of the literature noted above, we suspect that sensory prediction errors were the driver of after-effects in the ONLINE and OFFLINE_VIS feedback groups.

We had predicted that offline feedback would engage explicit adaptation processes, as evidenced by longer RTs and more variable aiming performance during adaptation compared to online feedback. This prediction was due to previously cited evidence that real-time error detection appeared to be essential for implicit feedforward adaptation to occur (e.g. Hinder et al., 2010; 2008; Shabbott & Sainburg, 2010; yet see Bond & Taylor, 2015). Contrary to this expectation, visual offline feedback provided immediately at movement end resulted in large after-effects, which were also associated with fast RTs. There were no group differences between the OFFLINE_VIS group and the ONLINE group for this measure of planning time.

Online visual feedback and immediate feedback have been compared in two other visuomotor adaptation studies (Bernier et al., 2005; Bond & Taylor, 2015). Like us, these authors showed that both online and offline feedback resulted in significant after-effects. However, in the study by Bernier et al. (2005), the online feedback group actually had smaller after-effects compared to the offline group, which was attributed to a dependence on or guidance-effect of the online feedback during practice (e.g., Winstein & Schmidt, 1990; Salmoni et al., 1984). Because the movements were relatively slow (400-600 ms; compared to less than 300 ms for participants in our study), online corrections were possible, reducing the need to update motor plans and perhaps partially accounting for the dependence that emerged.

In summary, despite, the proposal of Honda et al. (2012b) that remapping of sensory input to action plans requires concurrent comparisons between visual and proprioceptive inputs (i.e. a dynamic error signal), our data suggest that a different conclusion is warranted. Concurrent comparisons were not required for implicitly driven error processing. Rather, congruent with a model of adaptation based on feedback and error processing (Izawa & Shadmehr, 2011), when feedback is considered to be of "high quality" (i.e. feedback is reliable, detailed and available on every trial), the performer can use sensory prediction error to update feedforward control processes even if not available concurrently with movement execution.

**Delaying visual feedback after movement end**

Delaying visual feedback to immediately after movement end did not impact on the type of adaptation observed, compared to feedback provided concurrently. This finding suggests that the quality of the sensory information still allowed for the updating of sensori-motor planning processes. However, consistent with work of Hinder and colleagues (2010), withholding online feedback beyond movement end, markedly attenuated implicit adaptation processes.

Participants who adjusted aiming movements in response to feedback that was delayed by 3 s took significantly longer to initiate their movements compared to the other visual feedback groups. One interpretation of the RT data was that participants in the 3 s delay group required more planning time to formulate an appropriate aiming strategy once a target had been signaled (Hinder et al. 2010). Delayed error information is thought to bring about a compensatory strategy, termed "workspace sampling", particularly evidenced through trial-trial variability, which in early trials would be based on guessing (Shabbott & Sainburg, 2010). This sampling strategy seems to describe the aiming behaviour in our 3 s delay group in view of the large trial-trial variability. Therefore, adaptation to a target rotation following a significant delay in feedback, appeared to take place via explicit, strategy implementation processes. These processes are potentially a result of the absence of "available" augmented sensory consequences of the movement that could otherwise be used to update more implicit, feedforward processes. During the movement itself, individuals are processing veridical proprioceptive feedback and are not guided by visual feedback (cf., Winstein & Schmidt, 1990). Rather, the delayed feedback serves primarily to inform strategies for correcting target errors on subsequent trials rather than informing sensory predictions.

This idea that augmented feedback can create feedback dependence is important to consider as an explanation for our data. The interval between movement completion and the delivery of augmented feedback, in the form of knowledge of results (KR), is important for processing intrinsic (proprioceptive) feedback related to the executed movement (e.g., Carter & Ste-Marie, 2017; Swinnen, 1990). According to the guidance hypothesis (Winstein & Schmidt, 1990), reliable augmented feedback that is provided concurrently with movement or immediately at the end creates a dependence on that source of feedback for judging movement correctness. This dependence on augmented feedback, which can be visual, verbal or numeric, is at the expense of processing of naturally-occurring intrinsic feedback that might otherwise be used if augmented feedback is delayed. Both faster adaptation and low levels of awareness of deviations from normal intrinsic feedback are expected consequences of the guidance effects of augmented feedback. These consequences are consistent with data from our study when comparing the ONLINE and OFFLINE_VIS groups to the delay group (see also Honda et al., 2012a; Kitazawa et al., 1995; yet see Brudner et al., 2016). If the feedforward sensory prediction is coded in terms of the augmented visual feedback and not in terms of veridical proprioceptive feedback, we would expect after-effects to wane quickly when this visual feedback is removed. Indeed, without this sensory comparison in the no visual feedback posttests, all groups showed evidence of decay, with decreasing error between the first and last test-blocks of the posttest. Although error was much reduced for the 3 s delay group, the decay over test-blocks was also less (see Figure 2A). Although we did not have predictions regarding washout of after-effects, there is reason to suspect that the after-effects would have decayed faster and more dramatically if veridical visual feedback had been provided during the posttests, as has been the case in other related work (e.g., Shabbott & Sainburg, 2010; Mazzoni & Krakauer, 2006).

**Manipulating type of visual feedback**

For numeric feedback, significant after-effects were present. However, these after-effects were of a reduced magnitude compared to the group that received immediate post-movement visual feedback of their cursor trajectory, which was matched in terms of feedback timing. Despite elevated RTs and VE for the numeric group, this group significantly underestimated the magnitude of the feedback “rotation” and showed poor awareness of its direction. This was unlike the delayed feedback group (OFFLINE+3s), which showed elevated RTs, VE, and accurate awareness of the magnitude of the rotation. Therefore, numeric feedback was not equivalent to delaying feedback. While longer RTs may have supported interpretation and translation of numeric feedback, these data suggest it is unlikely that this was achieved by explicit adaptation processes alone.

Based on previous research (e.g. Hinder et al., 2008; Butcher & Taylor, 2018), we had not predicted after-effects for the numeric feedback group, even though these were significantly reduced compared to the OFFLINE_VIS group. With respect to the model of Izawa and Shadmehr (2011), it could be argued that numeric feedback served both a reward function, changing or maintaining action selection processes, as well as providing some means of calibrating proprioceptive feedback to outcome. Such calibration could be used to update feedforward processes associated with expected sensory (proprioceptive) consequences. In addition to conveying a metric for how successful (or unsuccessful) participants were at reducing their errors (reward), the numeric feedback in our study also provided information about the direction and magnitude of errors (cf., Butcher & Taylor, 2018; Nikooyan & Ahmed, 2015). Mental imagery processes, involving the reactivation and manipulation of remembered visual images, may have enabled participants to transform the numeric error feedback into a visual error signal or movement vector (see Ganis & Schendan, 2011). In this way participants could have imagined what the feedback would have looked like if it was presented as their finger or visual cursor (like that available in familiarization trials). This imagined feedback would then have been used to calibrate or inform feedforward processes and associated sensory prediction errors (at least later in practice).

After-effect magnitude has been shown in other research to be moderated by reward errors, achieved by manipulation of task success. For example, Leow et al. (2018) showed that target hits (and misses) moderated implicit after-effects when target misses were prevented through alteration of target position to align with the visually rotated cursor. There was a lower rate of adaptation and a reduction in after-effects, despite the fact that the visual cursor feedback and sensory prediction error did not change. Whether this numeric feedback in our study is acting via a reward prediction error that interacts with the implicit adaptation process or via the sensory prediction error based on imagined sensory feedback remains unanswered. It is also possible that the after-effect for this group was one based primarily on use-dependent mechanisms, related to the aiming direction during adaptation trials (Diedrichsen et al., 2010; Wood et al., 2020). Repeatedly aiming in the same direction during adaptation may be partially responsible for the continued bias to aim in the direction of the rotation, despite instructions to aim “normally”. As with all groups, these effects were further amplified by extended practice.

In summary, we have provided further evidence that adaptation processes are sensitive to temporal delays in presentation of augmented visual feedback. Providing augmented feedback immediately (or at least less than 3s) after the end of the movement appears to be important for implicit processes to be activated during adaptation. When augmented feedback is delayed, it is thought that feedforward processes are not updated because concurrent comparisons cannot be made between predicted sensory consequences and actual sensory consequences. In-turn, the process for updating sensory predictions that are proposed to lead to behavioural after-effects is disrupted. However, rather than after-effects being absent in the case of relatively long delays, they are instead significantly attenuated. We argue that the delay serves to reduce the quality or reliability of the delayed feedback signal required for updating feedforward processes. This reduction in quality is then evidenced in terms of a weaker internal model (i.e., smaller after-effects). However, the feedback signal can still be used to inform complementary action selection processes that inform explicit strategies which help to correct movement on the next trial.

Although not included in this study, process dissociation measurement techniques that probe explicit planned aiming during adaptation could be applied in future research (e.g., Modchalingam et al., 2019; Taylor et al., 2014; Werner et al., 2015). Although there is the risk that explicitly generating a prediction could alter how individuals adapt, these methods could further help in understanding how feedback delay impacts the development of explicit and implicit processes.

Finally, with respect to small after-effects as a result of numeric feedback, these implicit effects may be the result of feedforward adaptation processes based on imagined trajectories. Although it is not resolved how such implicit processes develop, there may be insights to be gained through manipulation of the activities in the interval between movement end and feedback provision, perhaps through explicit instructions to engage in visual imagery between trials, or to prevent such imagery.

**References**

Adams, J. A. A closed-loop theory of motor learning. (1971). *J Motor Behav*. *3*, 111–150.

Barkley, V., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2014). Reach adaptation and proprioceptive recalibration following terminal visual feedback of the hand. *Front Hum Neurosci*, *8*, 705.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw*. 67:105931. doi: 10.18637/jss.v067.i01

Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J Neurophysiol, 2214*, 2843–2851. http://doi.org/10.1152/jn.00002.2011

Bernier, P. M., Chua, R., & Franks, I. M. (2005). Is proprioception calibrated during visually guided movements? *Exp Brain Res*, *167*(2), 292–296. http://doi.org/10.1007/s00221-005-0063-5

Bond, K. M, & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J Neurophysiol, 113*(10), 3836-3849. https://doi.org/10.1152/jn.00009.2015

Brudner, S. N., Kethidi, N., Graeupner, D., Ivry, R. B., & Taylor, J. A. (2016). Delayed feedback during sensorimotor learning selectively disrupts adaptation, but not strategy use. *J Neurophysiol* 115: 1499–1511. https://doi.org/10.1152/jn.00066.2015

Butcher, P. A., Ivry, R. B., Kuo, S. H., Rydz, D., Krakauer, J. W., & Taylor, J. A. (2017). The cerebellum does more than sensory prediction error-based learning in sensorimotor adaptation tasks. *J Neurophysiol*, *118*(3), 1622-1636. https://doi.org/10.1152/jn.00451.2017

Butcher, P. A., & Taylor, J. A. (2018). Decomposition of a sensory prediction error signal for visuomotor adaptation. *J Exp Psychol: Hum Percept Perform*, *44*(2), 176-194. https://doi.org/10.1037/xhp0000440

Carter, M. J., & Ste-Marie, D. (2017). An interpolated activity during the knowledge-of-results delay interval eliminates the learning advantages of self-controlled feedback schedules. *Psychol Res*, *81*(2), 399-406. https://doi.org/10.1007/s00426-016-0757-2

Dang, K. V., Parvin, D. E., & Ivry, R. B. (2019). Exploring Contextual Interference in Implicit and Explicit Motor Learning. *bioRxiv*, 644211. https://doi.org/10.1101/644211

Diedrichsen, J., White, O., Newman, D., & Lally, N. (2010). Use-dependent and error-based learning of motor behaviors. *J Neurosci*, *30*(15), 5159-5166. https://doi.org/10.1523/JNEUROSCI.5406-09.2010

Ganis G, & Schendan, HE. Visual imagery. *Wiley Interdiscip Rev Cogn Sci*, *2*(3), 239-252. https://doi.org/10.1002/wcs.103

Hadjiosif, A. M., Krakauer, J. W., & Haith, A. M. (2021). Did We Get Sensorimotor Adaptation Wrong? Implicit Adaptation as Direct Policy Updating Rather than Forward-Model-Based Learning. *J Neurosci, 41*(12), 2747-2761. https://doi.org/10.1523/JNEUROSCI.2125-20.2021

Heirani Moghaddam, S., Chua, R., & Cressman, E. K. (2021). Assessing and defining explicit processes in visuomotor adaptation. *Exp Brain Res*,*239*(7), 2025-2041. https://doi.org/10.1007/s00221-021-06109-5

Held, R., & Hein, A. (1958). Adaptation of disarranged hand-eye coordination contingent upon re-afferent stimulation. *Percept Mot Skills*, *8*, 87–90. https://doi.org/10.2466/pms.1958.8.3.87

Hinder, M. R., Riek, S., Tresilian, J. R., De Rugy, A., & Carson, R. G. (2010). Real-time error detection but not error correction drives automatic visuomotor adaptation. *Exp Brain Res*, *201*(2), 191–207. http://doi.org/10.1007/s00221-009-2025-9

Hinder, M. R., Tresilian, J. R., Riek, S., & Carson, R. G. (2008). The contribution of visual feedback to visuomotor adaptation: How much and when? *Brain Res*, *1197*,123–134. http://doi.org/10.1016/j.brainres.2007.12.067

Holland, P., Codol, O., & Galea, J. M. (2018). Contribution of explicit processes to reinforcement-based motor learning. *J Neurophysiol*, *119*(6), 2241-2255. https://doi.org/10.1152/jn.00901.2017

Honda, T., Hirashima, M., & Nozaki, D. (2012a). Adaptation to visual feedback delay influences visuomotor learning. *PLoS ONE, 7*(5), 1–9. http://doi.org/10.1371/journal.pone.0037900

Honda, T., Hirashima, M., & Nozaki, D. (2012b). Habituation to feedback delay restores degraded visuomotor adaptation by altering both sensory prediction error and the sensitivity of adaptation to the error. *Front Psychol*, *3*, 1–8. http://doi.org/10.3389/fpsyg.2012.00540

Hutter, S. A., & Taylor, J. A. (2018). Relative sensitivity of explicit reaiming and implicit motor adaptation. *J Neurophysiol*, *120*(5), 2640-2648. https://doi.org/10.1152/jn.00283.2018

Izawa, J., & Shadmehr, R. (2011). Learning from sensory and reward prediction errors during motor adaptation. *PLoS Comput Biol*, *7*(3), 1–11. http://doi.org/10.1371/journal.pcbi.1002012, 2011.

Kitazawa, S., Kohno, T., & Uka, T. (1995). Effects of delayed visual information on the rate and amount of prism adaptation in the human. *J Neurosci*, *15*(11), 7644–7652. https://doi.org/10.1523/JNEUROSCI.15-11-07644.1995

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. *Front. Psychol*, *4*, 863. https://doi.org/10.3389/fpsyg.2013.00863

Larssen, B. C., Ho, D. K., Kraeutner, S. N., & Hodges, N. J. (2021). Combining Observation and Physical Practice: Benefits of an Interleaved Schedule for Visuomotor Adaptation and Motor Memory Consolidation. *Front Hum Neurosci, 15*, 614452. https://doi.org/10.3389/fnhum.2021.614452

Larssen, B. C., Ong, N. T., & Hodges, N. J. (2012). Watch and Learn: Seeing Is Better than Doing when Acquiring Consecutive Motor Tasks. *PLoS ONE*, *7*(6), 1–8. http://doi.org/10.1371/journal.pone.0038938, 2012.

Leow, L. A., Marinovic, W., de Rugy, A., & Carroll, T. J. (2018). Task errors contribute to implicit aftereffects in sensorimotor adaptation. *Eur Jn Neurosci*, *48*(11), 3397-3409. https://doi.org/10.1111/ejn.14213

Lim, S. B., Larssen, B. C., & Hodges, N. J. (2014). Manipulating visual-motor experience to probe for observation-induced after-effects in adaptation learning. *Exp Brain Res*, *232*(3), 789-802. https://doi.org/10.1007/s00221-013-3788-6

Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci*, *26*(14), 3642–5. http://doi.org/10.1523/JNEUROSCI.5317-05.2006, 2006.

McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. *J Neurosci*, *35*(26), 9568–9579. https://doi.org/10.1523/JNEUROSCI.5061-14.2015

McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends Cogn Sci*, *20*(7), 535–544. https://doi.org/10.1016/j.tics.2016.05.002

Mikaelian, H., & Held, R. (1964). Two types of adaptation to an optically-rotated visual field. *Am J Psychol*, *77*(2), 257–263. https://doi.org/10.2307/1420132

Modchalingam, S., Vachon, C. M., ’t Hart, B. M., Henriques, D. Y. P. (2019). The effects of awareness of the perturbation during motor adaptation of hand localization. *PLoS One*, *14*(8), e0220884. https://doi.org/10.1371/journal.pone.0220884

Nikooyan, A. A., & Ahmed, A. A. (2015). Reward feedback accelerates motor learning. *J Neurophysiol*, *113*, 633-646. https://doi.org/10.1152/jn.00032.2014

Ong, N. T., & Hodges, N. J. (2010). Absence of after-effects for observers after watching a visuomotor adaptation. *Exp Brain Res, 205*, 325–334. https://doi.org/10.1007/s00221-010-2366-4

Ong, N. T., Larssen, B. C., & Hodges, N. J. (2012). In the absence of physical practice , observation and imagery do not result in updating of internal models for aiming. *Exp Brain Res*, *218*(1), 9–19. http://doi.org/10.1007/s00221-011-2996-1

Redding, G. M., & Wallace, B. (1993). Adaptive coordination and alignment of eye and hand. *J Motor Behav*, *25*, 75–88. https://doi.org/10.1080/00222895.1993.9941642

Redding, G. M., & Wallace, B. (2002). Strategic calibration and spatial alignment: a model from prism adaptation. *J Motor Behav*, *34*(2), 126–138. https://doi.org/10.1080/00222890209601935

Saijo, N., & Gomi, H. (2010). Multiple motor learning strategies in visuomotor rotation. *PLoS One*, *5*, e9399. https://doi.org/10.1371/journal.pone.0009399

Salmoni, A. W., Schmidt, R. A., & Walter, C. B. (1984). Knowledge of results and motor learning: A review and critical reappraisal. *Psychol Bull*, *95*(3), 355–386. https://doi.org/10.1037/0033-2909.95.3.355

Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2011). Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. *Neuropsychologia*, *49*(11), 3053-3062.

Sarlegna, F. R., Gauthier, G. M., & Blouin, J. (2007). Influence of feedback modality on sensorimotor adaptation: contribution of visual, kinesthetic, and verbal cues. *J Motor Behav*, *39*(4), 247–258. doi: 10.3200/JMBR.39.4.247-258, 2007.

Schlerf, J. S., Xu, J., Klemfuss, N. M., Griffiths, T. L., & Ivry, R. B. (2013). Individuals with cerebellar degeneration show similar adaptation deficits with large and small visuomotor errors. *J Neurophysiol*, *109*(4), 1164-1173. https://doi.org/10.1152/jn.00654.2011

Schlerf, J., Ivry, R. B., & Diedrichsen, J. (2012). Encoding of sensory prediction errors in the human cerebellum. *J Neurosci, 32*(14), 4913-4922. https://doi.org/10.1523/JNEUROSCI.4504-11.2012

Schultz, W. (2006). Behavioral theories and the neurophysiology of reward. *Annu Rev Psychol*, *57*, 87 – 115. https://doi.org/10.1146/annurev.psych.56.091103.070229

Schween, R., & Hegele, M. (2017). Feedback delay attenuates implicit but facilitates explicit adjustments to a visuomotor rotation. *Neurobiol Learn Mem, 140,* 124-133. https://doi.org/10.1016/j.nlm.2017.02.015

Schween, R., Taube, W., Gollhofer, A., & Leukel, C. (2014). Online and post‐trial feedback differentially affect implicit adaptation to a visuomotor rotation. *Exp Brain Res*, *232*(9), 3007–3013. https://doi.org/10.1007/s00221-014-3992-z

Shabbott, B.A., Sainburg, R.L. (2010). Learning a visuomotor rotation: simultaneous visual and proprioceptive information is crucial for visuomotor remapping. *Exp Brain Res*, *203*, 75–87. https://doi.org/10.1007/s00221-010-2209-3 Shadmehr, R., & Krakauer, J.W. (2008). A computational neuroanatomy for motor control. *Exp Brain Res*, *185***,** 359–381 (2008). https://doi.org/10.1007/s00221-008-1280-5 Shadmehr, R., & Mussa-Ivaldi, F. (1994). Adaptive representation of dynamics during learning of a motor task. *J Neurosci*, *14*, 3208–3224. https://doi.org/10.1523/JNEUROSCI.14-05-03208.1994

Swinnen, S, P. (1990). Interpolated activities during the knowledge-of-results delay and post-knowledge-of-results interval: Effects on performance and learning. *J Exp Psychol -Learn Mem Cogn*, *16*(4), 692–705. https://doi.org/10.1037/0278-7393.16.4.692

Swinnen, S. P., Schmidt, R. A., Nicholson, D. E., & Shapiro, D .C. (1990). Information feedback for skill acquisition: Instantaneous knowledge of results degrades learning. *J Exp Psychol -Learn Mem Cogn,* 16(4), 706-716. https://doi.org/10.1037/0278-7393.16.4.706

Taylor, J. A., & Ivry, R. B. (2011). Flexible cognitive strategies during motor learning. *PLoS Comput Biol*, 7(3), e1001096. http://doi.org/10.1371/journal.pcbi.1001096

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J Neurosci*, *34*(8), 3023-3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2016). Effective reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. *Brain*, *139*, 101-114. https://doi.org/10.1093/brain/awv329

Tseng, Y., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J* Neurophysio*l*, *98*(1), 54–62. http://doi.org/10.1152/jn.00266.2007

Werner, S., van Aken, B. C., Hulst, T., Frens, M. A., van der Geest, J. N., Strüder, H.K., & Donchin, O. (2015) Awareness of Sensorimotor Adaptation to Visual Rotations of Different Size. *PLoS ONE*, *10*(4), e0123321. https://doi.org/10.1371/journal.pone.0123321

Winstein, C. J., & Schmidt, R. A. (1990). Reduced frequency of knowledge of results enhances motor skill learning. *J Exp Psychol - Learn Mem Cogn*, *16*(4), 677–691. https://doi.org/10.1037/0278-7393.16.4.677

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends Cogn Sci*, *1*(6), 209–16. http://doi.org/10.1016/S1364-6613(97)01070-X

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, *269*(5232),1880–1882. doi: 10.1126/science.7569931

Wood, J. M., Kim, H. E., French, M. A., Reisman, D. S., & Morton, S. M. (2020). Use-dependent plasticity explains aftereffects in visually guided locomotor learning of a novel step length asymmetry. *J Neurophysiol*, *124*(1), 32-39. https://doi.org/10.1152/jn.00083.2020

Table 1: Number of participants (n) who verbally reported a subjective awareness of the rotation or misalignment between their feedback and movement during the adaptation phase is reported on the left of the table. The right three columns are data based on objective assessment of the rotation through completion of schematic diagrams of the target display. These columns contain: the number of participants that consistently marked the correct direction (Dir) of the visual rotation of the cursor (or numeric feedback) for all 5 targets, the mean estimated angle of the rotation from the diagrams (*M* Rotation °), and the mean between-target standard deviations (*M* SD °) across all 5 targets. Between-subject SDs are reported in parentheses for each measure.

| | Subjective report | Objective assessment | | |
|---|---|---|---|---|
| Group | Rotation Present (n) | Dir (n) | *M* Rotation (°) | *M* Between-Target SD |
| ONLINE | 7 / 13 | 0 / 13 | 1.02 (2.70) | 4.84 (5.57) |
| OFFLINE_VIS | 8 / 13 | 0 / 13 | 2.06 (4.15) | 5.57 (5.25) |
| OFFLINE+3S | 11 / 11 | 9 / 11 | 17.15 (7.00) | 7.25 (5.64) |
| OFFLINE_# | 8 / 13 | 2 / 13 | 4.24 (6.16) | 5.36 (5.27) |

**Footnotes**

1: Sample size was informed based on estimates of effect size (Cohen's *d*) and sample sizes used in previous literature, where concurrent and delayed feedback were compared for after-effects in a visuomotor adaptation paradigm ($d$ =5.6, n = 8-9/group; Shabbott & Sainburg, 2010). Based on these large effects, in a 3-group design, a minimum sample size of 18 was estimated (n = 6/gp, $1-\beta$ = 0.80, $\alpha$ = .05). Because we also had a numeric feedback group, we initially constrained our sample size to a minimum of n = 8. This was increased to n = 13/group, based on a post-hoc decision to double the number of practice trials for an additional n = 5/gp. A post-hoc calculation in G*Power for a 4 Group x 2 Time-point mixed design, based on Cohen's $f$ = .25 (a more moderate effect size), yielded a min. sample size of N = 48 (12/gp).

2: After excluding trials where movement times exceeded 1000 ms, the remaining percentage for trials where movement times exceeded 350 ms for the ONLINE group was 2.69%. To confirm that participants in the ONLINE group were not adjusting movements online, we also ran Pearson's correlations comparing mean constant error (binned into 5-trial averages) at peak velocity to error at movement end. There was a large significant correlation between the two measures, $r$ = .96, $p$<.001. There was no difference (based on a dependent t-test), between error at movement endpoint and error at peak velocity, $t(294)$ = .059, $p$ = .95. There was also no evidence that individuals in this group were slowing down (i.e., longer MT) in order to achieve greater accuracy and hence use the feedback to correct (i.e., error at peak velocity), $r$ = -.013, $p$ = .63.

3: Model fit of adaptation data was evaluated using Akaike's Information Criterion (AIC) by modelling trial as a continuous variable (CE and RT). The linear model produced the lowest AIC for measures of CE (AIC = 28639) and RT (AIC = 54525) during adaptation, and for assessment of after-effects (CE, AIC = 14754)

4: We ran secondary analyses on the extended practice duration participants during the adaptation phase (practice-blocks 6-40, n=5/gp). For CE (see supplementary Table 2), significant block differences starting at practice-block 9 were shown on all subsequent practice-blocks (all *p*s <.04). There was only a significant Group X practice-Block interaction for the OFFLINE+3s group at practice-block 10, but no interactions for later practice-blocks. For all extended practice groups, there was a significant reduction in error and for the most part, there were not significant differences in how this was achieved. For RT (supplementary Table 4), no practice-block or group effects were observed, but there were Group X practice-Block interactions for the OFFLINE+3s group (blocks 12, 22, 25, 27, 28, 30, 34, 39, 40; *p*s <.03). Relative to practice-block 6, RT's increased for OFFLINE+3s at these later practice-blocks more so than the increase in RT that was observed for OFFLINE_VIS group at the same practice-blocks. There was also an interaction for the OFFLINE_# group at practice-block 9 and 15 (*ps*<.02; see Figure 3). For VE (supplementary Table 6), a significant group difference was shown when comparing the ONLINE_VIS group to the numeric feedback group (*p*=.001; OFFLINE+3s, *p* = .06). A significant Group X practice-Block effect was again present at practice-block 9 (OFFLINE_#, *p*=.001) and 24 (OFFLINE+3s, *p* = .04), but not in later practice-blocks.

**Figure Headings**

Figure 1: Schematic of experimental apparatus (A) and visual stimuli (B). Panel B illustrates the visual cursor or numeric feedback with full 30 degree clockwise visual rotation for each feedback group. Cursor feedback was provided to the ONLINE, OFFLINE_VIS, AND OFFLINE+3S groups as a green line representing their cursor trajectory. OFFLINE_# participants received their numeric feedback in a box located next to the illuminated target. The grey dashed line in panel B represents the unseen hand trajectory. Participants never have vision of their hand. A timeline of procedures, including experimental conditions and number of trials (t), is presented in C.

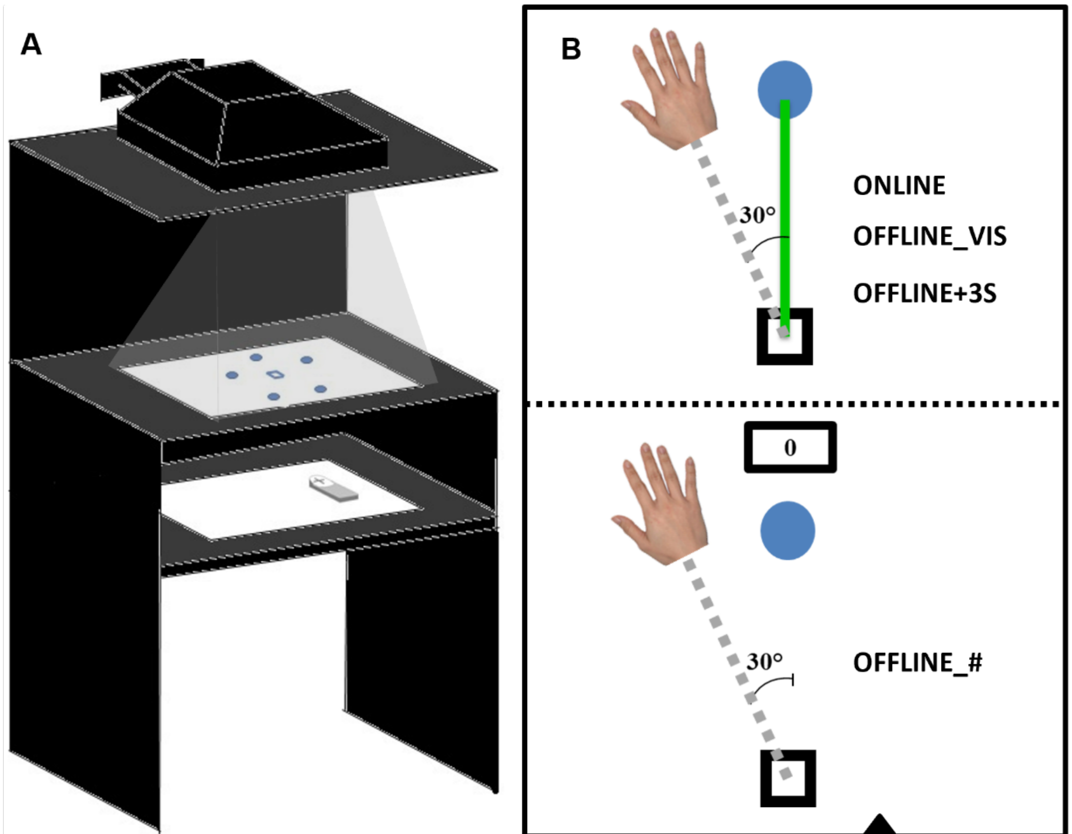
Figure 2: Adaptation and After-effects. (A) Group Mean directional constant aiming error (CE; in degrees) reported as a function of time (Pretest, Adapt, Posttest), and practice-block (5 trials/block) for each feedback group. Error bars represent standard error of the mean. During Adaptation, data from practice-blocks where participants experienced the full 30 degree feedback rotation (Blocks 6-40) are presented for illustrative purposes. Only practice-blocks 6-20 were included in the full sample LME model. The dashed vertical line represents the end of adaptation practice for all participants that received 20 blocks of practice. Sample sizes (*N*) that contributed to each group mean are listed in the graph. (B) Mean directional CE (in degrees) of spatial aiming errors during the last block of Pretest (5 trial average) and the first block of in the test for after-effects (Posttest; 5 trial average) for all feedback groups. Group means are presented as columns. Individual participant means are presented as separate data points for visual comparison to demonstrate variability within each group. Participants that received extended practice are represented by triangle-shaped data points. Cohen's *dz* effect sizes are presented for the difference between the mean error of block 4 of the Pretest and block 1 of Posttest.

Figure 3: Group mean Reaction Time (ms) reported as a function of practice-block (5 trials/block) for each feedback group. Error bars represent standard error of the mean. Data from practice-blocks where participants experienced the full 30 degree feedback rotation (blocks 6-40) are presented for illustrative purposes. Only practice-blocks 6-20 were included in the full sample LME model. The dashed vertical line represents the end of adaptation practice for the short practice group. Sample sizes (*N*) that contributed to each group mean are listed in the graph.

Figure 4: Group mean inter-trial Variable Error (in degrees) reported as a function of practice-block (5 trials/block) for each feedback group. Error bars represent standard error of the mean. Data from practice-blocks where participants experienced the full 30 degree feedback rotation (blocks 6-40) are presented for illustrative purposes. Only practice-blocks 6-20 were included in the full sample LME model. The dashed vertical line represents the end of adaptation practice for the short practice group. Sample sizes (*N*) that contributed to each group mean are listed in the graph.

Figure 5: Absolute value of mean after-effect magnitude (Mean aiming error in degrees of the first 5 trials of Posttest – mean error of the last 5 trials of Pretest) reported as a function of mean Reaction Time during adaptation (RT, ms; Panel A), mean inter-trial Variable Error during adaptation (VE, degrees; Panel B), and mean aiming angle during the post-experiment assessment of rotation awareness (degrees; Panel C). Participant means are represented by individual data points. Pearson correlation coefficient (*r*) and p-values are reported for each correlation.

Figure 1:




C

| Familiarization (0°) | Pretest (0°) | Gradual Adaptation (5 - 30° CW) | Posttest (0°) |
|---|---|---|---|
| t=20 | t=20 | t= **100** or **200**<br>t **= 5** x 5°, 10°, 15°, 20°, 25°;<br>t **= 75** (n=8/gp) <u>or</u> **175** (n=5/gp) x 30° | t=20 |
| Feedback: ✓ cursor | No Feedback | Feedback: as above | No Feedback |

Figure 2:

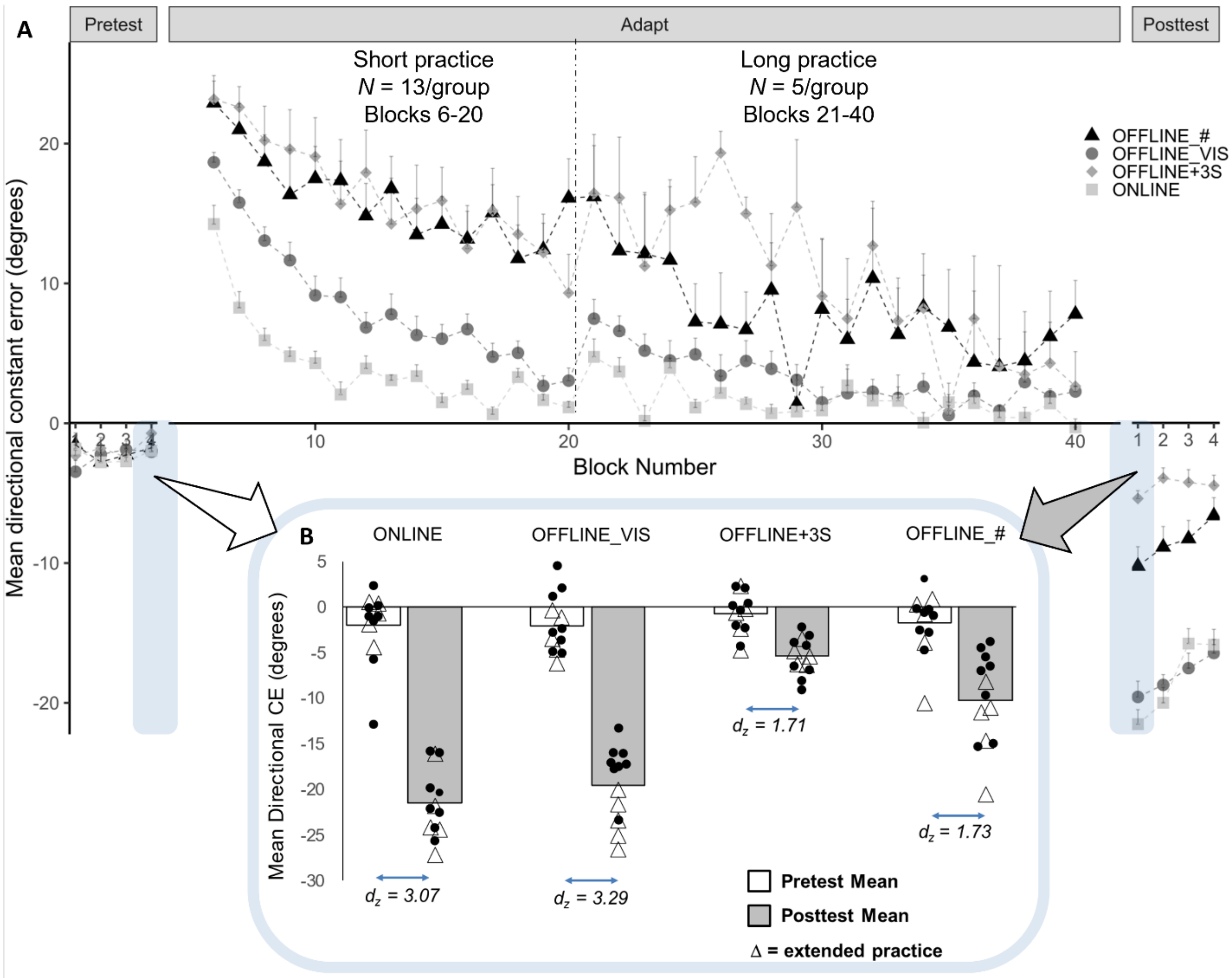

A
Pretest
Adapt
Posttest
Short practice
N = 13/group
Blocks 6-20
Long practice
N = 5/group
Blocks 21-40
OFFLINE_#
OFFLINE_VIS
OFFLINE+3S
ONLINE
Mean directional constant error (degrees)
Block Number
B
ONLINE
OFFLINE_VIS
OFFLINE+3S
OFFLINE_#
Mean Directional CE (degrees)
d_z = 3.07
d_z = 3.29
d_z = 1.71
d_z = 1.73
Pretest Mean
Posttest Mean
Δ = extended practice

Figure 3:

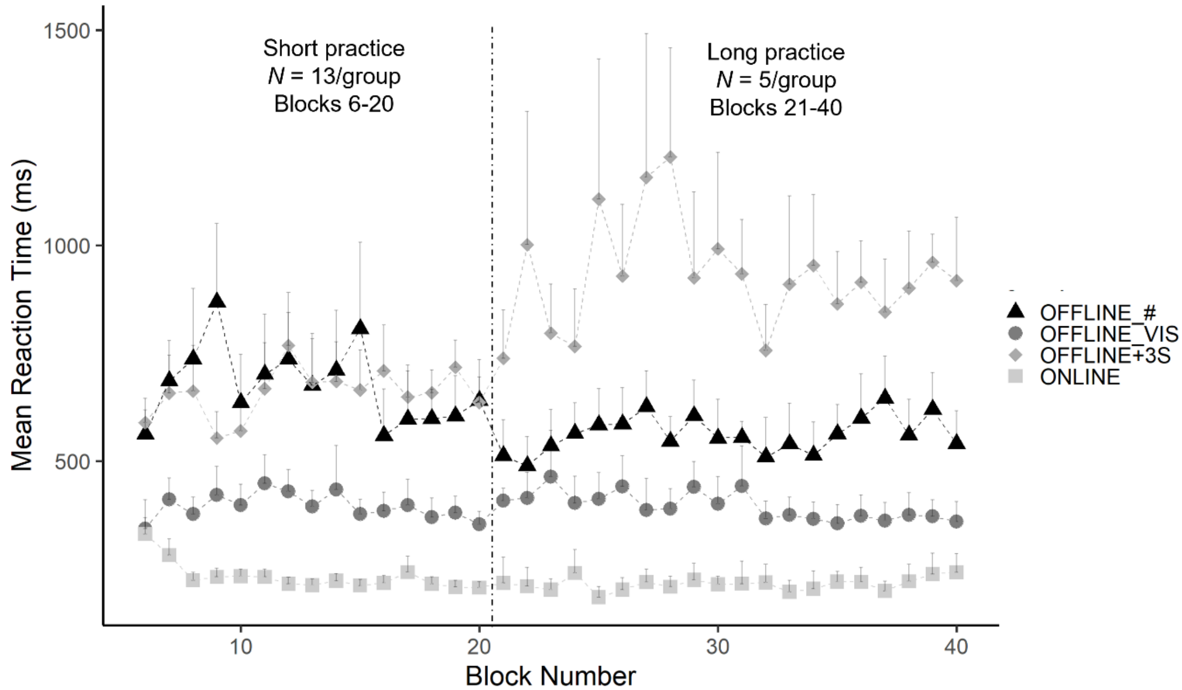

1500
1000
500
Mean Reaction Time (ms)
Short practice
N = 13/group
Blocks 6-20
Long practice
N = 5/group
Blocks 21-40
OFFLINE_#
OFFLINE_VIS
OFFLINE+3S
ONLINE
10
20
30
40
Block Number

Figure 4

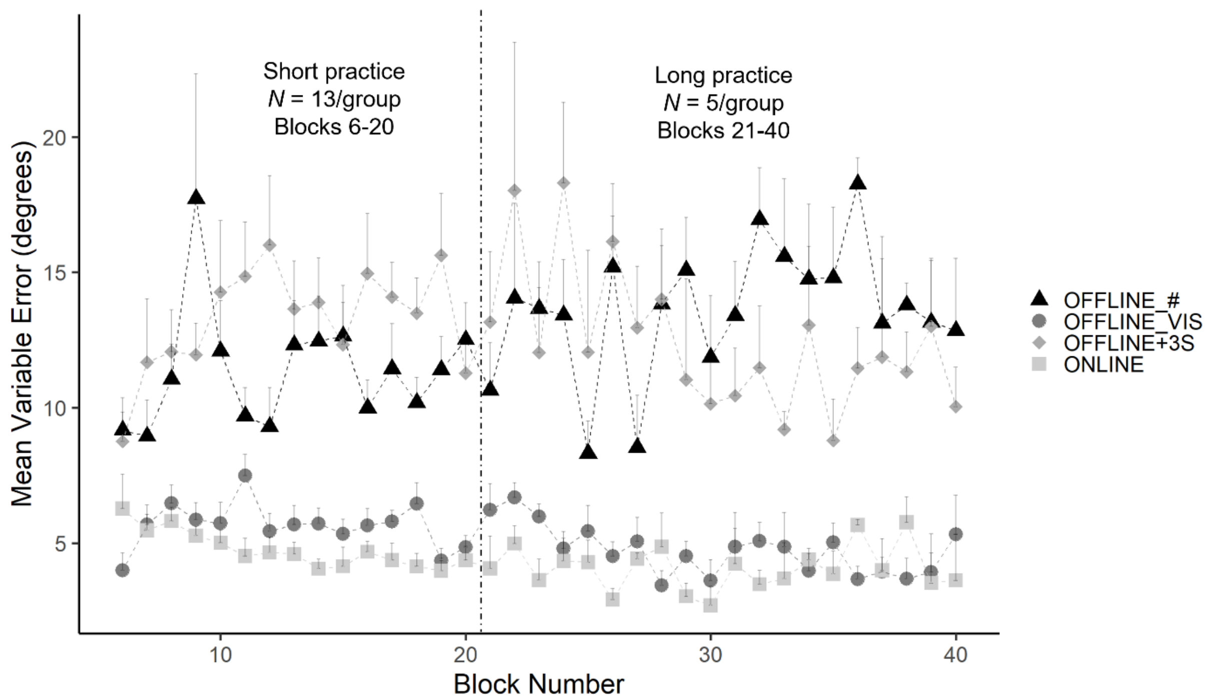
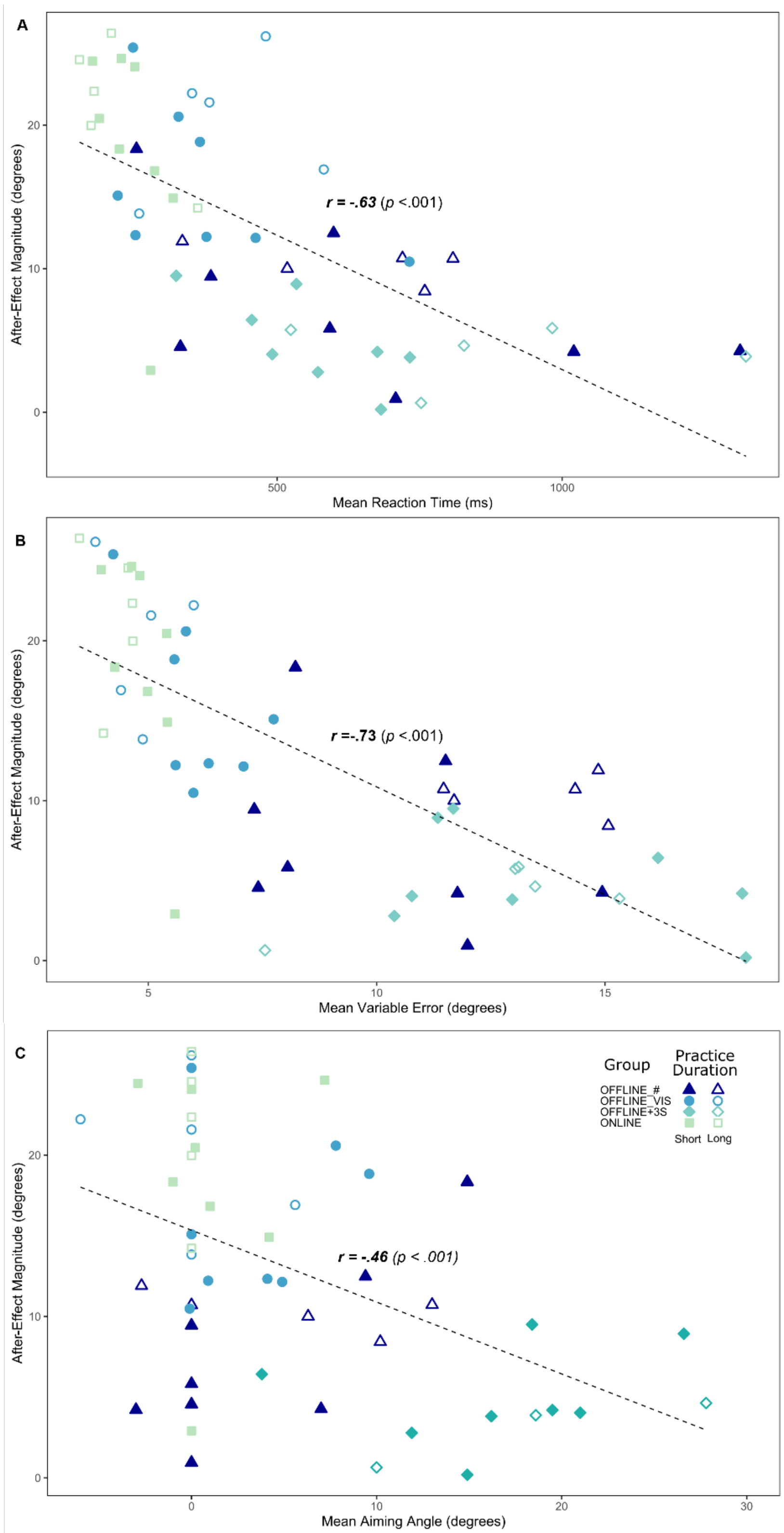

Short practice
N = 13/group
Blocks 6-20
Long practice
N = 5/group
Blocks 21-40
Mean Variable Error (degrees)
Block Number
OFFLINE_#
OFFLINE_VIS
OFFLINE+3S
ONLINE
5
10
15
20
10
20
30
40

Figure 5


A
r = -.63 (p <.001)
After-Effect Magnitude (degrees)
Mean Reaction Time (ms)
B
r =-.73 (p <.001)
After-Effect Magnitude (degrees)
Mean Variable Error (degrees)
C
r = -.46 (p < .001)
After-Effect Magnitude (degrees)
Mean Aiming Angle (degrees)
Group
Practice Duration
OFFLINE_#
OFFLINE_VIS
OFFLINE+3S
ONLINE
Short
Long