Updating of implicit adaptation processes through erroneous numeric feedback

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Abstract

There is debate about how implicit and explicit processes interact in sensorimotor adaptation, implicating how error signals drive learning. Target error information is thought to primarily influence explicit processes, therefore manipulations to the veracity of this information should impact adaptation but not implicit recalibration (i.e. after-effects). Thirty participants across three groups initially adapted to rotated cursor feedback. Then we manipulated numeric target error through knowledge of results (KR) feedback, where groups practised with correct or incorrect (+/-15°) numeric KR. Participants adapted to erroneous KR, but only the KR+15 group showed augmented implicit recalibration, evidenced by larger after-effects than before KR exposure. In the presence of sensory prediction errors, target errors modulated after-effects, suggesting an interaction between implicit and explicit processes.

Keywords: Adaptation learning, Knowledge of Results, Sensory Prediction Errors, Target Errors

Introduction

Performing motor tasks in novel environments requires a period of calibration of existing relationships between motor commands and their sensory outcomes to accuracy constraints required to minimize performance errors. In sport, this might be adapting striking actions to novel racquets, or could be adapting to immersive virtual environments when playing video games. One proposal for how our nervous system allows us to adapt to different environments is through the development of adaptive internal models (Wolpert, 1997; for more recent reviews see Albert et al., 2022; Shadmehr et al., 2010). We can recalibrate both through implicit processes, that we are mostly unaware of, and through more strategically driven explicit processes. The relationship between these processes in adaptation is currently of interest, due to debate regarding their independence or interactive nature (Kim et al., 2019; Leow et al., 2018; Mazzoni & Krakauer, 2006; Tsay et al., 2022). In this experiment, we study how adaptation processes develop and interact at different stages of practice in the presence of sensory prediction errors and reliable (correct) and unreliable (erroneous) numeric target feedback.

One method used to investigate adaptation learning processes is the visuomotor adaptation paradigm (for recent reviews, see Morehead & Orban De Xivry, 2021; Spampinato & Celnik, 2021). A visual rotation creates a mismatch between the predicted and actual sensory consequences of a movement, creating a sensory prediction error (SPE), which is used to update future motor commands (e.g. Albert et al., 2022; Butcher & Taylor, 2018; Shadmehr et al., 2010; Tsay et al., 2022; Tseng et al., 2007). In addition to SPEs, there are also target errors indicating performance accuracy (e.g. Kim et al., 2019). A distinction can also be made between a binary measure of target success (i.e. hit/miss) and performance error (e.g. Kim et al., 2019; Leow et al., 2018; Morehead & Orban De Xivry, 2021). Because we do not have a binary signal of hit/miss in our current experiment, we restrict our discussion of errors to two primary sources: SPEs and target errors. Initial exposure to a visual rotation will result in errorful movement trajectories and both SPEs and target errors. With practice, participants use both types of errors to improve aiming, resulting in successful adaptation. Although these types of errors typically co-occur, as below, they can be dissociated.

How we learn to use different sources of error to compensate and adapt to rotated visual feedback is thought to be achieved via an unintentional implicit process that is primarily driven by the resolution of SPEs, as well as an explicit process that appears to be driven by target errors (for a review see Albert et al., 2022). Explicit adaptation processes are characterized by an awareness of a mismatch between augmented visual feedback and actual movement position, which leads to the implementation of an aiming strategy or strategies to compensate for the mismatch (e.g. McDougle et al., 2015, 2016; Taylor et al., 2014).

Evidence that implicit adaptation has occurred can be probed through an assessment of post-practice after-effects, seen when the participant returns to a known "normal"/no rotation environment (e.g. Butcher & Taylor, 2018; Held & Hein, 1958; Modchalingam et al., 2019; Redding & Wallace, 1993; Ruttle et al., 2016). If after-effects are present, performance accuracy is unintentionally biased in the opposite direction of the original perturbation (e.g., Hadjiosif et al., 2020; Heirani Moghaddam et al., 2021; Larssen et al., 2022). Since the effects persist despite participants being aware that they are in a "normal" environment, after-effects are considered a robust indicator of implicit (unintentional) motor recalibration (Henriques & Cressman, 2012; Modchalingam et al., 2019).

Presence of explicit processes is typically evidenced by explicit strategy use (e.g. McDougle et al., 2016) and related hypothesis-testing (Hinder et al., 2008, 2010). Although explicit adaptation processes can be evoked by giving individuals a verbal aiming strategy (e.g. Benson et al., 2011; Mazzoni & Krakauer, 2006; Neville & Cressman, 2018; Sarlegna et al., 2007; Taylor et al., 2014), strategies can also develop spontaneously (e.g. Neville & Cressman, 2018; Werner et al., 2015). Engagement of the explicit process is thought to result in faster improvement (i.e. reduced target error), relative to implicit adaptation (e.g. Lee et al., 2018; Mazzoni & Krakauer, 2006; Taylor & Ivry, 2011). The relative contributions of explicit processes to adaptation can be assessed through various measures including post-practice questionnaires (e.g. Larssen et al., 2022) and probes of planned/strategic aiming during adaptation (e.g. Ayala & Henriques, 2021; Bond & Taylor, 2015; Modchalingam et al., 2019). Increased contributions of explicit aiming processes to adaptation have also been associated with increased rotation awareness (Neville & Cressman, 2018), increased preparation time (i.e. reaction time; Benson et al., 2011; Hinder et al., 2010; Ong et al., 2012), workspace sampling (i.e. increased inter-trial variability in aiming error; Shabbott & Sainburg, 2010), and a reduction or absence of after-effects (e.g. Ayala & Henriques, 2021; Mazzoni & Krakauer, 2006; Neville & Cressman, 2018).

There is debate about the relative independence of implicit and explicit adaptation processes and the role of SPEs, target errors, and their potential interaction during adaptation. Some authors have shown evidence that implicit and explicit processes are independent, even though they develop simultaneously (Mazzoni & Krakauer, 2006; McDougle et al., 2016; Sülzenbrück & Heuer, 2009; Taylor & Ivry, 2011). In a seminal study by Mazzoni and Krakauer (2006), despite immediate reductions in target error following implementation of an explicit strategy, hand movements drifted from the target, indexing the independent operation of implicit processes to adjust for the SPE. This unintentional implicit drift has been replicated in other work (Lee et al., 2018; Taylor & Ivry, 2011). In the study by Lee et al. (2018), target errors attenuated the magnitude of this unintentional drift, but did not moderate decay of post-practice after-effects. These data suggest not only an independence of implicit and explicit processes, but that each process potentially operates using different sources of error.

There is also research that questions this story of independence, providing evidence that explicit processes influence the magnitude of implicit sensorimotor recalibration. For example, Benson et al. (2011) showed that a group provided with a strategy had longer reaction times early in learning (reflective of increased planning time), yet attenuated after-effects. They suggested that the explicit process interfered with the development of the implicit process, providing evidence of interdependence (see also Tsay et al., 2022). However, because there was no immediate reduction in error after the strategy was introduced, it may have been that SPEs had been prioritized at the expense of target error information.

In addition to the idea that explicit and implicit processes are interdependent, is the idea that target errors can also promote an implicit type of adaptation (e.g. Brudner et al., 2016; Hinder et al., 2008, 2010; Larssen et al., 2022; Nikooyan & Ahmed, 2015). When visual feedback is not provided online, then there is no immediate discrepancy or SPE and hence adaptation should be driven by target errors. However, Larssen et al. (2022) showed evidence of implicit adaptation to target errors in groups that adapted through immediately presented numeric feedback, as well as through delayed visual feedback. Use-dependent learning (e.g. Diedrichsen et al., 2010; Wood et al., 2020) from repetitive aiming, is one implicit mechanism that may lead to unintended after-effects following target errors, although when aiming to five radial targets in a random order this type of implicit learning is unlikely. It is also possible that visual consequences can be anticipated and covertly imagined from numeric feedback, whereby an error between imagined sensory consequences and feedback engage different adaptation processes than what would be predicted based solely on target error (Larssen et al., 2022).

In previous investigations of the independence of implicit and explicit processes and the role of target error information in this process, adaptation processes were only tested on first exposure to a novel rotation. One method for testing the potential interdependence of explicit and implicit processes is to first adapt individuals implicitly, such that an internal model is established and then manipulate target errors in a second adaptation phase. This method allows testing of this earlier implicit model to modifications via competing explicit processes and was therefore adopted in the current experiment. Individuals were first gradually introduced to a 30˚ clockwise (CW) rotation, where only partial concurrent cursor feedback (i.e. 50% of their movement trajectory) was provided (Adapt 1). This procedure eliminated target hits and misses, but still allowed us to later provide and manipulate numeric performance error about target success. Adapt 1 was followed by a first test of after-effects to provide an index of implicit adaptation. In a second adaptation phase (Adapt 2) we continued to provide partial visual cursor feedback of the 30º rotation, now coupled with numeric feedback (i.e. knowledge of results, KR). This feedback was either accurate (Correct KR) or erroneous. Erroneous KR was designed to bias future movement of the cursor away from the target in the counter-clockwise (CCW; KR+15°) or CW (KR-15°) directions. Post-trial numeric KR has repeatedly been shown to significantly influence motor skill learning (e.g. Swinnen et al., 1990; Winstein & Schmidt, 1990), even when the KR is erroneous (Buekers et al., 1992). A final test of after-effects was conducted after Adapt 2 to test for modulation of implicit processes, followed by a final adaptation, retention test.

We predicted that all participants would adapt to the rotated visual feedback in Adapt 1, reducing error from early to late practice. In Adapt 2, only the erroneous KR groups were expected to (re)adapt to the numeric feedback, and any group differences were expected to remain in a final retention test. All groups were expected to increase error from pre- to post-test 1, after Adapt 1, indexing after-effects. If target errors created by the erroneous numeric KR in Adapt 2 modulate implicit processes, then when comparing the two tests of after-effects (post-test 1 and 2), there would be (greater) modulation of after-effects in the erroneous KR groups in post-test 2, relative to the first test of after-effects, and in comparison to the Correct KR group.

To index explicit adaptation, measures of rotation awareness, reaction time (RT), and variable error (VE) were calculated during both adaptation phases. Group differences were expected to emerge in Adapt 2 only, as evidenced by longer RTs and increased VE across blocks in the erroneous KR groups, as well as greater awareness of the size and direction of the KR-induced rotations Because the KR +15 group would produce a net 45° rotation (i.e. 30° +15°) if they adapted to the feedback, rather than de-adapt to a smaller 15° rotation (30°-15°) for the KR -15 group, we anticipated some asymmetry in how the erroneous KR would work in terms of these explicit processes.

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 and groups

Thirty self-reported right-hand dominant participants that were naïve to the adaptation task, were randomly allocated to three groups (n=10/group). Groups differed depending on the type of KR provided in a second adaptation phase (after adapting to a 30° rotation). A correct KR group (Correct KR, Mn Age = 22.4 yr, SD = 6.8 yr, Females = 7) received correct numeric post-trial KR of their reaching accuracy to the pre-adapted 30° CW rotation. Two erroneous KR groups received post-trial KR that augmented their actual performance error to the 30° rotation by an additional 15°. For one group, the performance error was augmented by +15° in the same direction as the initial cursor rotation (KR+15°, Mn Age = 20.8 yr, SD = 3.3 yr, Females = 4). For the second erroneous KR group, KR served to augment performance error -15˚ in the opposite direction to cursor rotation (KR-15°, Mn Age = 19.5 yr, SD = 1.6 yr, Females = 8). A further n = 5 participants were tested last, who never received any KR (No KR, Mn Age = 21 yr, SD = 2.1 yr, Females = 4)[1]. A schematic of KR conditions is provided in Figure 1.

Sample size was informed by previous work (Larssen et al., 2022), where a numeric KR group (n=13) demonstrated large post- versus pre-adaptation after-effects (Cohen's *dz* = 1.73), after practice with 30° mismatch between hand position and numeric target feedback. This comparison was chosen as our best approximation of any additional after-effect following adaptation to erroneous KR relative to our novel "baseline" condition (where participants had already adapted to a 30° rotation). A power analysis was performed using G*Power (version 3.1.9.7; Faul et al., 2009) to detect the same within-group effect size (*dz* = 1.73, α = .05), which resulted in a sample size estimate for a single group of n=6, although we acknowledge the risk of overestimating effect sizes from studies based on small samples (Albers & Lakens, 2018). Since we did not have any past effect sizes to determine how re-adaptation would impact after-effect size based on KR, but assuming the re-adaptation would be smaller, sample size was increased to n=10/group.

Task and Apparatus

Using their right hand, participants performed aiming movements with a computer cursor that was aligned with their unseen index finger using a custom mouse connected to a graphics' digitizing tablet (Calcomp Drawing Board IV, 200Hz). All task conditions and visual stimuli were generated using a custom program designed using LabVIEW™ software (version 9.0, National Instruments). For a description and diagram of the experimental apparatus and hardware, see Larssen et al. (2022). Aiming movements were made to five peripheral visual targets (0.4 cm diameter circles), arranged around a central start target (0.6cm X 0.6 cm square) that were projected onto a semi-silvered mirror positioned between the participant's line of vision and their hand in the workspace. Peripheral circular targets were presented at 18˚, 90˚, 162˚, 234˚, and 306˚ positions relative to horizontal. The distance between the centre of the central start target and the centre of any one of the 5 circular peripheral targets was 9.5 cm. Participants were asked to perform fast shooting movements through the target as soon as the target appeared. Participants were encouraged to move beyond the target to help keep movements fast. Shooting movements reduce the opportunity for participants to use cursor feedback to inform online movement corrections (Tseng et al., 2007). After each aiming trial, participants moved the cursor back to the central start target, however vision of the cursor was not made available until they were within 4.75 cm of the central home position. A new target was presented after the cursor was inside the central start target for 1.5 seconds.

Procedure

Procedures were similar to those adopted in previous studies (e.g. Larssen et al., 2022; Ong et al., 2012). For a summary of experimental feedback conditions, see Figure 1. For all experimental conditions, participants were asked to perform accurate aiming movements through the targets as quickly as possible. All participants first performed ten familiarization trials with veridical cursor feedback during the full movement trajectory. They were instructed that this was a “normal” environment. This was performed to expose participants to “normal” feedback mapping and give them an opportunity to practice performing shooting movements within the movement time constraints. All groups then performed a 20-trial pretest to provide a baseline measure of normal aiming without any visual feedback. Participants were once again instructed that this was a “normal” environment. Targets were presented randomly to prevent the participants from anticipating future target positions.

The pretest was followed by initial exposure to the adaptation environment (Adapt 1; 30° CW rotation) where the online cursor trajectory was rotated 30° CW relative to actual hand position. At the start of Adapt 1, participants were told they were in a “new environment”. No group-based manipulations occurred in this first adaptation phase. Only the first 50 % of the cursor trajectory trace from the centre position to the target was visible during this phase so that endpoint numeric KR could be manipulated when provided during the second adaptation phase (Adapt 2). The visuomotor rotation was gradually increased by 5° CW every 5 trials up to a maximum of 30° CW such that participants finished Adapt 1 with 75 trials of practice in the 30° CW environment. This method of gradual adaptation leads more reliably than immediate introduction to implicit (unaware) adaptation (e.g. Ingram et al., 2000; Kagerer et al., 1997; Klassen et al., 2005; Yin & Wei, 2020).

To test for immediate after-effects (Post-test 1), participants completed 20 trials without visual feedback of the cursor and were told that they had returned to a normal environment and instructed to aim their movement straight through the target. After this first test of after-effects, participants' explicit awareness of the visuomotor rotation implemented during Adapt 1 was assessed through a pen and paper test (for similar methods see Larssen et al., 2021, 2022). Participants were presented with a schematic diagram of the central target with straight lines connecting the centre of the start target to each of the five surrounding target positions. Participants were told to assume that the black lines represented an accurate cursor trajectory for aiming. They were then asked to draw the trajectory that their right index finger would have had to follow to produce the same cursor trajectory depicted by the diagram.

The group manipulation occurred in a second adaptation phase involving 100 trials, where endpoint target error in the form of numeric KR was provided. Participants continued to perform aiming movements with their cursor rotated 30° CW relative to their index finger and hence the rotation was introduced immediately on the first trial. In addition to the online cursor feedback for 50% of the movement, the groups received their respective post-trial KR manipulations in the form of numeric error scores (illustrated in Figure 1). This KR was provided immediately after the cursor exceeded 9.5 cm, which was the radius of the circle that subtended all 5 targets. The KR appeared beside the intended target on a blank screen as a positive or negative value after each trial. Participants were informed on two occasions (before the start of Adapt 2 and after completion of 50 trials) that: negative scores indicate error (in degrees) in the CCW direction of the cursor relative to the target, positive scores indicate error in the CW direction between the rotated cursor and the target, and a score of zero (0°) indicates an accurate hit of the target. They were instructed to use this error information about the magnitude and direction of their performance error to achieve an error score of 0° for each target. Participants were provided with a compensatory strategy to correct their movements based on their KR feedback (promoting explicit adaptation). They were told that if they received a negative value, they were to adjust their aiming movements by moving in the CW direction (and in the CCW direction for positive values). Participants were never told that the numeric KR was erroneous.

A final test of after-effects (Post-test 2, 20 trials) was conducted, followed immediately by a second test of explicit awareness of the rotation experienced during Adapt 2 (same procedures as previous). This was then followed by a retention test of the 30° CW rotation. During this immediate retention test, participants received online visual feedback of their cursor trajectory but no KR. They were asked to aim using the same strategy that they used to get their KR to 0° during Adapt 2. This was included to assess short-term retention of the aiming strategy that was applied during Adapt 2.

After experimental testing, a final questionnaire of explicit awareness of the adaptation conditions was completed to determine if the KR provided during Adapt 2 was believed to be attributed to self-produced movement. This was included to control for differences that may be attributable to "believability of KR" (see Supplementary Materials for full debrief questionnaire adapted from Benson et al., 2011).

Measures

Derivation of kinematic information (magnitude and timing of aiming errors) was performed using the custom LabVIEW™ program that was used to run data collection. All subsequent statistical analyses were performed using IBM SPSS Statistics software (version 28.0) and R version 4.1.0 (R Core Team, 2021). The primary dependent variable of interest was directional constant error (CE, in degrees) of the cursor from the target. A positive or negative value for error denotes a CW or CCW error respectively. CE was measured at peak tangential velocity of the movement trajectory. This method was based on previous experiments where peak velocity occurred at ~75% of the distance to the target (e.g. Larssen et al., 2012; Bernier et al., 2005). In the current study, peak velocity occurred at 76% of the target distance (averaged across all participants and conditions; range: 69-87%). Error at peak velocity is highly correlated with error at movement end when performing shooting movements (e.g. Larssen et al., 2022). This was also true in the current study (Spearman *rho* = .99).

Variability in aiming accuracy between trials (VE, standard deviation of constant error across a 10-trial block, in degrees) was calculated for each participant as an indirect measure of explicit strategy use (Shabbott & Sainburg, 2010). Reaction time (RT, in milliseconds) data were collected as a measure of movement planning, even though we did not explicitly encourage individuals to react/move as soon as possible on seeing the next target appear. RT was calculated from the time of target presentation to movement onset. Movement onset was defined as the point in time when the cursor left the central start target.

Movement time was calculated as the time between movement onset and when the cursor exceeded a radial distance of 9.5 cm from the central target. Aiming trials where movement time (MT) exceeded 350 ms were excluded from analyses to control for potential online corrections. After exclusion, post-hoc pairwise comparisons of mean movement times did not differ between groups. Aiming trials where reaction times exceeded 1000 ms were also excluded from analysis. Together, this resulted in a mean exclusion of 3.9% of the total trials (Correct KR = 4.9%, KR+15 = 8.0%, KR-15 = 5.2%).

To assess explicit awareness of the rotation, mean planned aiming error (in degrees) was calculated as the average error of the participant's hand trajectory drawings to each of the five targets on the pen and paper rotation awareness task (measured with a protractor). A separate mean value was calculated following Adapt 1 and following Adapt 2.

Statistical analyses

Prior to all analyses, data were assessed for normality with Shapiro-Wilk's tests and homogeneity of variance was assessed with Levene's tests (α = .05 for both). In most cases, distributional analyses showed some evidence of skewness, kurtosis or heterogeneity of variance. Therefore, we chose to use mixed effect regression (MER) analysis, rather than traditional F-tests, as MER is robust against violations to distributional assumptions required by parametric tests, especially with small sample sizes (Schielzeth et al., 2020). MER also accounts for random variation due to participants, through modeling of multiple intercepts for each participant as a random effect, rather than a single mean intercept (Baayen et al., 2008; Magezi, 2015; Nimon, 2012).

Adaptation and After-effects. For analysis, mean values for each dependent variable were calculated for every 10 consecutive trials. Each 10-trial average represents a "Block" of practice within each feedback exposure condition. For measures of CE, RT, and VE, separate linear mixed effects regression (LMER) analyses were conducted using the lme4 package (Bates et al., 2015). Model fit for adaptation data was evaluated using Akaike's Information Criterion.[2] The linear model was used for all analyses. All statistical outputs for each MER are presented in Supplementary Analyses, including regression equations, parameter estimates, and 95% confidence intervals. For all analyses, Group (Correct KR, KR+15, KR-15) was entered as a between-participants' fixed effect and participant was included as a random effect.[2] Pre-planned contrast analyses were used to test group-level hypotheses. The Correct KR group was the reference group, allowing two comparisons with the KR+15 and KR-15 groups. Repeated measures (RM) were treated as categorical factors and entered as fixed effects. For adaptation, these RM factors were Testing Phase (Adapt 1 vs. Adapt 2) and Block (4 vs. 10 for Adapt 1, when the full 30˚rotation was introduced, and 1 vs. 10 for Adapt 2). A 3 Group X 2 Testing Phase X 2 Block LMER was conducted. Interaction terms between RM factors and Group were included due to the predicted 3-way interaction. Group differences between the correct and erroneous KR groups at the end of practice in Adapt 2 were expected in CE, VE and RT.

For tests of After-effects on measures of CE, the fixed effect RM factors were Testing Phase (Pretest vs. Post-test 1 and Post-test 1 vs. Post-test 2) and Block (1 vs 2), resulting in two 3 Group X 2 Testing Phase X 2 Block LMER analyses. We included both the 2-way and 3-way interaction terms in the models. For comparison of Pretest and Post-test 1, no group-based interactions were expected, just differences in testing phase, that might be moderated by block (i.e., errors decreasing across blocks in Post-test 1). For Post-test 1 versus Post-test 2, group-based interactions were expected; with the erroneous KR groups increasing error across Testing Phase (again potentially moderated by testing block). For immediate retention, data were analyzed in a 3 Group X 2 Block LMER. Group differences in aiming due to the lasting, yet unintended impact of erroneous KR conditions, were expected on return to a no-KR, cursor feedback only 30° environment. We tested for the interaction as there was reason to think that the effects of KR would decrease across testing blocks without it.

Awareness. To test for predicted group differences in mean planned aiming error, a 3 Group X 2 Testing Phase (Adapt 1 vs Adapt 2) LMER was conducted with the 2-way interaction alerting to increased awareness in Adapt2 for the erroneous KR groups. We also present frequency data regarding overall awareness of the rotation and veracity of the KR. We characterized rotation awareness as correctly drawing the direction of the rotation for all 5 targets, independent of the magnitude. Answering “no” to the question that the KR was an accurate representation of their aiming error led to a designation as aware that the KR was erroneous.

Results

Adaptation

Constant Error (CE)

As illustrated in Figure 2, all groups decreased CE during Adapt 1 (after the full rotation was introduced) and Adapt 2 (when KR was introduced) as evidenced by the main effect of Block ($ß$ = -6.72, 95% CI [-9.19 – -4.25], p <.001). Across blocks in Adapt 2, CE became more negative (i.e., error increased) for the KR+15 group relative to the Correct KR group. This group-related difference in error in Adapt 2 was confirmed through the predicted 3-way interaction for the KR+15 group ($ß$ = -7.85, 95% CI [-12.79 - -2.91], p = .002), but not the KR-15 group ($ß$ = 1.02, 95% CI [-3.92 – 5.96], p = .68). There were no other group-related effects (see Supplementary Analyses, Table 1).

Variable Error (VE)

In Figure 3, VE is plotted for all 10 blocks of Adapt 1 and Adapt 2 and the No KR group has been added for visual comparison only. VE decreased for all groups from Block 4 to 10 for Adapt 1. When post-trial KR was introduced in Adapt 2, the change in VE varied by group; whereby VE increased for both erroneous KR groups yet decreased for the Correct KR group. These effects were confirmed by the predicted Testing Phase X Block interaction ($ß$ = -2.70, 95%

CI [-4.61 – -.78], p =.006) and three-way interactions for both the KR+15 group ($ß$ = 7.15, 95% CI [4.44 – 9.86], p <.001) and KR-15 group ($ß$ = 5.31, 95% CI [2.60 – 8.02], p <.001), when compared to the Correct KR group. There were no other statistically significant main effects or interactions (see Supplementary Analyses, Table 2).

Reaction Time (RT)

Mean reaction time is plotted in Figure 4. Based on visual inspection only, there was no change for the No KR group across testing phases. When statistically comparing the three numeric KR groups, as expected, RT was higher in Adapt 2 compared to Adapt 1, which was confirmed by a main effect of Testing Phase ($ß$ = 99.33, 95% CI [36.26 – 162.39], p =.002). There was also a decrease in RT across early and late adapt blocks independent of phase ($ß$ = -79.22, 95% CI [-142.25 – -16.19], p =.014). However, as predicted, RT effects were dependent on both group and block in the second adaptation phase as evidenced by a 3-way interaction for the KR+15 group only ($ß$ = 168.39, 95% CI [49.44 – 287.35], p = .006). There was a larger increase in RT for the KR+15 group from block 1 to 10 in Adapt 2 relative to any change in RT experienced by the Correct KR group in this phase (and relative to Adapt 1). The predicted 3-way interaction for the KR-15 group was not significant ($ß$ = 44.62, 95% CI [-74.33 – 163.57], p = .46). There were no other group-related effects (see Supplementary Analyses, Table 3).

After-Effects

Constant Error: After-Effects 1

Aiming error (CE) during the pretest and the first post-test is illustrated on the left side of Figure 5. All groups increased CE in the CCW direction, indicative of after-effects. This was confirmed by a main effect of Testing Phase ($ß$= -15.07, 95% CI [-17.17 – -12.98], p <.001). The magnitude of after-effects decreased by the second block in the post-test, shown by a Testing

Phase X Block interaction (*ß*= 4.77, 95% CI [2.37 – 7.17], p <.001). As predicted in Adapt 1, there were no group differences based on comparisons between the Correct KR group and the KR+15 group (*ß* = -.52, 95% CI [-2.86 – 1.82], p =.66) or KR-15 group (*ß* = .79, 95% CI [-1.55 - 3.13], p =.504). Although we did not predict any group-related interactions, there was a 3-way interaction when comparing the Correct KR group to the KR-15 group (*ß* = -3.73, 95% CI [-7.13 – -.33], p = .03), which was driven by a smaller reduction in error across blocks in post-test 1 for the KR-15 group as compared to the Correct KR group (for full analysis breakdown see Supplementary Analyses, Table 4).

Constant Error: After-Effects 2

In-line with predictions regarding target errors modulating implicit after-effects, errors increased in the CCW direction during post-test 2 relative to post-test 1 for the KR+15 group when compared to the Correct KR group (see right side of Figure 5). There was a significant Group X Testing Phase interaction for the KR+15 group (*ß*= -8.27, 95% CI [-13.17 – -3.37], p = .001). There was, however, no Group X Testing Phase interaction for the KR-15 group (*ß*= -.75, 95% CI [-5.65 – 4.15], p = .76). There was also a significant block effect (*ß*= 4.32, 95% CI [1.98 – 6.65], p < .001), reflecting the attenuation of error from block 1 to block 2 in both post-tests, but there were no interactions of Block with Group, nor any other main effects or interactions (see Supplementary Analyses, Table 5).

To illustrate after-effect magnitude, in Figure 6 we have plotted the mean group differences between the first block of post-test 2 and the last block of post-test 1, along with individual participant means. Although there was a spread in terms of the size of after-effects across individuals, as noted by the positive bars, there was a general increase in the size of implicit recalibration across Adapt 2 in all groups, especially for participants in the KR+15 group. There was one outlier participant in this group whose error-change score was close to zero. In the post-experiment questionnaire, this individual reported difficulty with using the KR to improve accuracy and that they favoured trajectory information during Adapt 2 to achieve accuracy at the expense of KR. They recognized that the KR was erroneous but they could not articulate the magnitude or direction of the discrepancy. This self-assessment is supported by their mean CE at the end of Adapt 2. The goal mean CE for participants in the KR+15 group was -15˚ (see Figure 2), however, in the last block of practice, this individual's mean CE was +6.8°. Mean CEs for all other participants in the KR+15 group ranged from -1.7 to -13.5˚.

Explicit awareness assessment

Explicit awareness of the 30° CW visual rotation of the cursor trajectory was assessed twice, once following each test of after-effects. The estimated size of the cursor rotation is given in Table 1 along with the number of people (n) who correctly identified that the cursor was rotated clockwise relative to their hand for all 5 targets. Following Adapt 1, only 2 out of 30 participants correctly reported the direction of the visual rotation. Following Adapt 2, this had increased only slightly to n =4/30 (1 participant in the KR correct group and 3 in the KR+15 group).

Analysis of the drawn estimated angle of rotation for the three groups in Adapt 1 confirmed that participants showed little to no awareness of the 30° CW rotation, with groups recording differences between hand and the cursor trajectory of 0 and 2.1° on average. There were no statistical differences between the erroneous KR groups and the Correct KR group ($ß_{KR+15}$ = -.86, 95% CI [-9.14 – 7.42], p = .84; $ß_{KR-15}$ = 2.21, 95% CI [-6.07 – 10.49], p = .601). After Adapt 2 there was some increase in the recorded size of the rotation, particularly for the KR+15 group, but there was no effect of Testing Phase ($ß$ = -1.29, 95% CI [-7.34 – 4.76], p =

.68), and there were no Group X Testing Phase interactions ($ß_{KR+15\ X\ Testing\ Phase}$ = -4.34, 95% CI [-12.90 – 4.22], p = .32; $ß_{KR-15\ X\ Testing\ Phase}$ = .81, 95% CI [-7.75 – 9.37], p = .85).

At the end of testing, we also assessed awareness of the KR manipulation. All participants in the Correct KR group believed the KR to be an accurate representation of their aiming error. In the KR+15 and KR-15 groups, n=8 and 7 participants respectively (out of 10) reported that the KR received was not an accurate representation of their cursor trajectory. Seven of these 8 the participants in the KR+15 group reported that they attempted to apply a corrective strategy by aiming in a more CCW direction to achieve an accuracy score of 0°. Only 4 of the 7 participants in the KR-15 group that said they were aware that the KR was erroneous, reported applying a corrective strategy to reduce errors. Despite reported awareness, when asked, all participants said that they still attempted to reduce their KR error score to 0° to comply with the instructions.

Immediate Retention

Immediate retention of the 30º CW rotation was tested in the absence of post-trial KR as shown on the far right of Figure 5 for CE. As predicted, group differences that were present in Adapt 2 were maintained in retention, although now with different goal-related consequences. The KR+15 group showed the lowest overall error, being close to zero and the desired 30° rotation as a result of their prior practice with the augmented "rotation", again different from the Correct KR group ($ß$ = -8.95, 95% CI [-14.06 – -3.84], p < .001). There was no difference between the Correct KR and KR-15 group ($ß$= 3.94, 95% CI [-1.17 – 9.05], p =.13). There was also a significant reduction in error across blocks ($ß$= -3.57, 95% CI [-6.04 – -1.11], p = .005), but this was not dependent on Group (see Supplementary Analyses, Table 7).

Discussion

To study the interaction of implicit and explicit adaptation processes and how target-related numeric information impacts these processes, we compared correct and erroneous numeric feedback groups. Participants first adapted aiming movements without numeric feedback to a 30° CW visual rotation. Because of the gradual nature of the adaptation, the presence of after-effects, and that only 2/30 participants showed awareness of the direction of the rotation, we considered that this first phase was primarily implicit, achieved via recalibration based on SPEs. In the second adaptation phase, we re-introduced the 30° rotation paired with target error feedback that was either redundant (correct KR) or conflicting (erroneous) with the cursor feedback. Participants were required to use the numeric post-trial KR to adapt away from 30°; either augmenting further to a 45° rotation (KR+15) or attenuating closer to a 15° rotation (KR-15). Although the desired hand angles were not achieved, both erroneous KR groups diverged from the Correct KR group in latter blocks of Adapt 2. However, only the KR+15 group was different from the Correct KR group for CE. Both erroneous KR groups diverged from the correct KR group in terms of variable error (VE). Importantly, there was a moderation of after-effects as a result of the erroneous numeric KR. The KR+15 group showed statistically larger after-effects after practice with erroneous KR than the Correct KR group (the Correct KR and KR-15 groups did not differ).

Post-movement numeric target feedback that acts to augment existing error signals impacts implicit recalibration processes presumed to be based primarily if not solely on SPEs. As such, either target errors impact on SPEs, with more explicit corrective strategies interacting with implicitly generated predictions, or target errors impact implicit processes independently from SPEs. We address the evidence in favour of these explanations below; considering first the

KR+15 group in reference to the correct KR group, then the differences between the two erroneous KR groups.

Numeric target feedback that augments errors engages explicit strategic corrections

Erroneous KR in the form of an additional 15° CW rotation augmenting error (but not reducing error) encouraged increased reaction times and increased aiming variability across blocks in Adapt 2, compared to correct KR. Consistently slower RTs during adaptation are indicative of planned attempts to apply a corrective strategy across trials as is increased trial-to-trial variability in aiming error (e.g. Hinder et al., 2010; Larssen et al., 2021, 2022; Shabbott & Sainburg, 2010). Based on these data and that the KR+15 group increased their aiming "error" in response to the erroneous feedback suggests that this re-adaptation was primarily driven by explicit error-reduction processes designed to get the numeric feedback close to zero. Moreover, participants were explicitly given a strategy to reduce errors in response to KR, by aiming more in the CW direction when errors were negative (and CCW for positive errors).

When we look at the RT and VE data in Adapt 2 for the KR-15 group, this group did not show the same RT slowing or variability in trial to trial aiming as the KR+15 group. This lack of what is thought of to reflect strategic adaptation, perhaps speaks to the strength of the implicitly acquired rotation in Adapt 1 and some asymmetric effects associated with adapting (in a different direction) versus augmenting (in the same direction). The KR-15 manipulation encouraged participants to de-adapt in the direction of a no-rotation/veridical mapping between the hand and the cursor, which might be more difficult than augmenting an already acquired rotation by 15°.

The above result and explanation regarding asymmetries between the two erroneous KR groups also aligns with the awareness data. Although participants were not told that the numeric feedback was incongruent with the cursor feedback, 8/10 participants in the KR+15 group were aware that it did not match. Despite the awareness of a potential conflict, 7 of these 8 participants still reported prioritizing the decrease of target errors by applying a corrective aiming strategy to aim further away from the target. Such dominance of numeric KR in the face of conflicting visual information has been shown in other work on augmented feedback in motor learning paradigms (e.g. Buekers et al., 1992, 1994). Participants in the KR-15 group were also aware that the KR did not match their cursor trajectory (7/10 participants). Despite awareness of this mismatch and the fact that all participants had been provided with a strategy to reduce errors in response to KR, only four participants in the KR-15 group could articulate that they were able to apply a corrective aiming strategy that prioritized numeric feedback accuracy at the expense of cursor feedback accuracy. This further highlights a potential difficulty with translating awareness into action in the KR-15 group.

The magnitude of the error signal created by the erroneous numeric KR was of a sufficient size to surpass awareness detection thresholds associated with distinguishing signal from motor noise (Gaffin-Cahn et al., 2019). Detection thresholds of 13˚or greater have been reported for similar aiming tasks with a mouse-guided cursor (Synofzik et al., 2008). Using similar methods to Gaffin-Cahn and colleagues (2019), we calculated detection thresholds from our data, to give an estimate of the minimum magnitude of error that could be visually detected after the introduction of a cursor rotation (as in Adapt 1) or erroneous numeric KR (as in Adapt 2). Separate detection thresholds were calculated for Adapt 1 and 2. Adapt 1 thresholds were obtained by multiplying the SD of aiming error during no rotation pretest trials by the detection threshold scaling factor reported in Gaffin-Cahn et al. (2019). The resulting detection thresholds ranged from 3.6 to 14.7°. Adapt 2 detection thresholds were based on SD of aiming error during the last 5 trials of Adapt 1 and ranged from 3.7 to 12.5°. These detection threshold ranges may explain why participants were mostly unaware of direction of the cursor rotation that was gradually introduced in 5˚ increments during Adapt 1 (as planned), and why most participants in the erroneous numeric KR groups were aware that the KR (which involved the immediate introduction of a 15˚ error) was indeed erroneous. These data support the proposal that the numeric feedback created target errors of sufficient magnitude to create awareness of an error, but that target errors that augmented error in the same direction as a previously applied rotation (KR+15) could more effectively be translated into an explicit corrective movement strategy.

Numeric target feedback that augments errors impacts implicit processes associated with recalibration

Despite the fact that the KR+15 group appeared to adapt explicitly to the numeric KR to reduce target error, unintentional after-effects were augmented as a result of the numeric feedback. When individuals were asked to aim "normally" to the target without visual or numeric feedback, such that their hand shoots straight through the target, the KR+15 group showed significantly larger after-effects during the second post-test compared to the first post-test and when compared to the Correct KR group. Although awareness of the direction of the visual rotation was low across all groups in both adaptation phases, the KR+15 group showed a non-significant trend to judge the magnitude of the rotation to be greater in Adapt 2 than the other groups and in the direction of the KR (*Mean* = ~6.6° vs 1.4° for the Correct KR group; -1.7° for the KR-15 group). These data suggest that the numeric feedback had a small biasing effect on the KR+15 group's perceptions of the mismatch between hand and cursor position, even though this never changed across adaptation phases. This suggestion is further confirmed by the fact that in immediate retention, the KR+15 group continued to aim accurately to the 30°

rotation in the absence of KR, whereas the KR-15 and correct KR groups showed more of a washout towards veridical aiming.

How does numeric feedback work? An interdependence of explicit and implicit processes

While our evidence suggests that numeric KR that further augments error can modify a pre-existing implicitly acquired model for aiming, what is unclear is how this is achieved? Based on the VE, RT and awareness data for the KR+15 group, we have reason to suspect that adaptation was happening via explicitly mediated corrections. If implicit adaptation via SPEs was impervious to explicit modification, there would be no change in after-effects for the erroneous KR groups. However, moderation of the after-effect suggests that these explicit processes were interacting with the implicit processes, perhaps moderating the perceived SPE or independent of SPE.

An interactive explanation of target reward feedback impacting SPEs is congruent with conclusions of others. Target reward signals were thought to weaken implicit recalibration arguably through a reduced attentional focus on SPEs (e.g. Kim et al., 2019; Leow et al., 2018; Shmuelof et al., 2012; Tsay et al., 2022) and increased reliance on frequently available rewarding feedback (van der Kooij et al., 2018). We did not, however, see evidence of a weakened recalibration following target error feedback, but instead an augmentation in the KR+15 group. Hence, a "distracted" attention explanation cannot explain the current data. Another explanation that we discussed in prior work, is that numeric feedback gets reinterpreted into a visual image that influences sensory recalibration (Larssen et al. 2022). In this past work, gradual adaptation to a 30° rotation signalled only by post-trial numeric feedback, resulted in post-practice after-effects. In the current study, participants always had some visual feedback pertaining to the 30°

rotation, but this may have led to imagined sensory predictions as larger or smaller depending on the erroneous KR. It is also possible that use-dependent implicit mechanisms played some role in recalibration, where repetitive aiming during practice in the direction of the after-effects led to a carry-over of unintended movement biases when feedback was removed and participants were asked to aim in a “normal” environment (e.g. Diedrichsen et al., 2010; Wood et al., 2020). However, individuals were aiming to five different targets across only 100 trials (i.e. 20 trials to each target in a random order) and they did not show adaptation until at least the 4th or 5th block of practice, which would result in a relatively low amount of target repetition.

Future work could help identify if the target error signal from numeric KR has the capacity to drive implicit adaptation in isolation from SPEs. For example, had participants again adapted to the SPE, then in a second phase been told to ignore the KR and keep reaching, we could see if unintentional adaptation to the target error would occur and whether this would impact tests of after-effects (c.f., Tsay et al., 2022). We do know that irrelevant/erroneous visual feedback (i.e. clamped cursor feedback), still leads to unintentional implicit adaptation (e.g. Morehead et al., 2017), so this proposal may be valid if KR has to the potential to act in a similar way to visual cursor feedback.

Differential directional effects of erroneous target errors on implicit recalibration

A somewhat unexpected effect of the erroneous KR conditions on adaptation was the differential effects from augmenting error rather than reducing error. There is some work on target jumps, where target errors are put in conflict with SPE-driven errors, which may support such asymmetric target direction effects (Tsay et al., 2022). Although target jumps both towards and away from the rotated cursor feedback attenuated implicit processes, the attenuation was reduced when the target jumped in the opposite direction of the cursor (towards the target, like our KR-15 condition) as opposed to in the same direction but even further (as in our KR+15 condition). Although we saw increased augmentation of after-effects rather than increased attenuation when errors were in the same direction, these interactive effects of target errors on implicit processes may be underpinned by similar mechanisms, with differences driven by methods. Unlike Tsay and colleagues who imposed competing SPE and target error signals simultaneously (where attentional mechanisms may be at play), we first allowed adaptation via minimization of SPEs before introducing the erroneous target error. Perhaps when competing error signals are introduced simultaneously (as in Tsay et al., 2022) the central nervous system has difficulty prioritizing, resulting in interference and attenuation of the implicit process. When SPEs are already minimized, target error does not attenuate. Why it augments is unclear, but our data are congruent with the suggestion that SPE-related processes are more sensitive to target errors in the same direction as the initial rotation (Tsay et al., 2022).

It is also possible that individuals are more sensitive to increasing error in the direction of an initial rotation, such that increased error values are indicative that further adaptation is required. Changes in the error signal in the opposite direction either get ignored and/or coded as noise associated with normal performance variability. One way to test this would be to have the initial adaptation in either the CW or CCW direction and then compare the KR+15 (and KR-15) groups, where now one would augment the original rotation (CW), whereas the same KR would attenuate the rotation. When learning consecutive opposing visuomotor rotations, the rotation that is practiced first often interferes with initial acquisition of the opposing rotation (e.g. Hinder et al., 2007; Krakauer et al., 2005; Larssen et al., 2012; Wigmore et al., 2002). By acquiring the

30° CW rotation first, participants may have developed a strong internal model that was more resistant to interference by an “opposing” CCW rotation, dictated by the KR-15 condition.

Numeric KR and motor learning

The fact that individuals were able to minimize target errors alerted by numeric KR, at the expense of accurate task-relevant sensory information (in this case, the cursor trace and associated SPE) is not new. There is a considerable history on the role of augmented feedback and specifically information concerning outcome errors (i.e. KR) in the motor learning literature (for historical reviews see Adams, 1978, 1987; Salmoni et al., 1984; Swinnen et al., 1990). Providing KR immediately after movement completion can block processing activities thought to be important to learning (e.g. Lee et al., 1990; Swinnen et al., 1990). For example, providing feedback on every trial can lead to a guidance type effect, where individuals rely on the KR at the expense of processing their own intrinsic, response-produced feedback and predicting outcomes. This guidance shows up in poor delayed retention when individuals are later tested without KR (e.g. Schmidt et al., 1989; Swinnen et al., 1990). Although we tested retention in a test without numeric KR immediately after practice, there was no evidence of KR dependence. The group effects associated with the KR manipulation were still evident in retention. Moreover, the lack of apparent difference between the Correct KR and No KR group in retention[1], lends support to the hypothesis that the Correct KR group did not become dependent on post-trial numeric KR (see also Supplementary Analysis, Table 10).

Limitations and future research

As a stand-alone study, based on a relatively small sample size, there is an obvious need for further testing and replication. These data were based on a two-phase adaptation protocol where individuals adapted to a visually-induced SPE before being given the numeric KR. There would be some value in future research to remove this initial adaptation phase (where KR and visual feedback would now immediately be in conflict). We suspect that much like Tsay et al. (2022), we would see attenuation of after-effects when target errors and SPEs are processed at the same time (supporting a conflicting attention hypothesis). It would be of interest to also study delayed retention under no-KR conditions to assess for effects of potential dependence on KR and whether both after-effects and direct learning effects dissipate more quickly when KR is also provided during adaptation practice.

There is also reason to think that increasing practice amount might provide a more complete picture of how individuals use KR to adapt and whether this process of adaptation takes longer in the face of potentially conflicting visual feedback (or when de-adaptation is required). Even with KR available, the Correct KR group did not improve their aiming in the second adaptation phase (in comparison to Adapt 1, see Figure 2 and compared to the no-KR group). Extended practice may be necessary for a more thorough adaptation or re-adaptation following a no-KR initial adaptation phase, especially since no groups actually performed the required 15°, 30° or 45°, for the KR-15, Correct and KR+15 groups respectively. Inspection of Figure 2 and the last 2 blocks of Adapt 2 show that both the KR+15 and KR-15 groups were an equal distance (approximately +/- 7°) from their required target (+15 or -15° CE), which also represents the average reach error for the Correct KR group. This would signal that all groups were attempting to achieve their explicit goal, but likely needed more practice to continue to improve accuracy. A potential contributing factor is the variability in aiming error that may come with mouse-guided cursor aiming tasks. The SD of aiming error (VE) for participants at baseline ranged between 2.5˚-10.3˚, which is higher when contrasted against some free-pointing paradigms (e.g. Gaffin-Cahn et al., 2019; Urbán et al., 2019).

One interesting, yet unexpected result in the immediate retention data was the accuracy of the KR+15 group when retention was tested in the absence of KR. The augmentation of error through numeric KR produced a beneficial learning effect when subsequent retention was examined in the absence of feedback. The KR+15 group was more accurate than both the correct KR group and the KR-15 group in this test, supporting other work showing transfer benefits from augmenting error during practice on subsequent re-testing (e.g. Patton et al., 2013).

Summary/Conclusions

Competing target error information in the form of erroneous numeric endpoint KR can alter the adaptation of an implicitly acquired rotation, updating a previously acquired internal model. This was only true when numeric feedback was augmented in the same direction as the initial rotation. This result suggests that potentially explicitly-driven adaptation informed by target errors interacts with implicitly-driven processes to update a motor plan and produce unintentional after-effects. It is unclear if the assumed explicitly-driven adaptation during Adapt 2, which led to increased after-effects in the KR+15 group, was modifying the existing implicitly acquired internal model for aiming in the presence of a 30° CW visual rotation or if implicit processes were also working concurrently to update the internal model in response to the KR. This second scenario would be possible if post-trial target feedback leads to after-effects (Bernier et al., 2005; Larssen et al., 2022). These results are at odds with the suggestion that implicit adaptation processes are impervious to concurrent, explicitly driven strategies and that implicit and explicit processes operate in a modular fashion (e.g. Mazzoni & Krakauer, 2006). Rather, our data are mostly congruent with more recent data showing that in the presence of SPEs, target errors also modulate implicit processes (e.g. Tsay et al., 2022). Different from current interactive models, we have shown after-effects and evidence of implicit recalibration both when SPEs are already reduced or nullified (following an initial adaptation phase) and in prior work, when no simultaneous sensory information is provided (Larssen et al., 2022). Moreover, target errors alerted via numeric KR in our current study augmented rather than attenuated implicit processes evidenced by after-effects. This goes against an attention distraction explanation for target error interactive effects and instead suggests that numeric KR is impacting implicit processes outside of SPEs (such as use-dependent mechanisms) or through SPEs, perhaps via imagined visual outcomes. Manipulations to the amount of practice and number of targets might help tease apart these explanations.

Authors' Contributions

BCL and NJH were involved in the conceptualization of the project, study hypotheses, and experimental methods. BCL collected data and completed data analysis. BCL and NJH both contributed to writing of the manuscript and both authors read and approved the final version.

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Footnotes

1: A fourth group (n=5) of participants was later tested under the same testing conditions but no numeric KR was provided during Adapt 2. In Figures 2, 5 and 6 we have added this group to visually demonstrate the similarity of this group to the Correct KR group. Despite the low sample size, we ran an exploratory statistical analyses to compare these groups in a 2 Group X 2 Block (1 vs 10) LMER for Adapt 2 CE, where both the group-level contrast ($ß$ = -1.58, 95% CI [-5.50 – 2.35], p = .41) and the Group X Block interaction were not statistically significant ($ß$ = 2.02, 95% CI [-2.10 – 6.15], p = .32). There were also no significant differences between the No KR and Correct KR groups in the patterns of errors for these groups in measures of after-effects after Adapt 2 ($ß_{Group}$ = .44, 95% CI [-4.25 – 5.12], p = .85; $ß_{Group\ X\ Testing\ \mathrm{Phase}}$ = .94, 95% CI [-2.12 – 3.99], p = .54), and in Retention ($ß_{Group}$ = -.14, 95% CI [-2.80 – 2.51], p = .91; $ß_{Group\ X\ Block}$ = .25, 95% CI [-2.39 – 2.88], p = .85) . For full analysis breakdown see Supplementary Analyses, Tables 8-10).

2: The linear model was chosen for all mixed effects analyses. Model fit was evaluated using Akaike's Information Criterion (AIC). For all analyses involving CE and VE, inclusion of the 3-way interaction produced the lowest AIC compared to the base model, with the exception of analysis for RT. However, due to predictions and to be consistent across measures, we kept the interaction term in the model for all analyses. All fixed effects models were then compared to the mixed effects' model that included participant as a random effect. All mixed effects models produced the lowest AIC. For crossed random effects we specified a random intercept for each participant within each testing phase and block. In two cases (analysis of adaptation CE and VE data) the term for the random effect of participant within block was removed, because it produced random effect variance estimates of zero. This was informed by recommendations to fit the most complex model that permits a non-singular fit (Barr et al., 2013).

Table 1: Number of participants (out of 10) who correctly reported (on schematic diagrams of the target display) the correct direction (Dir) of the visual rotation of the cursor for reaching to all 5 targets during Adapt 1 and Adapt 2. Mean estimated angle of the rotation of the cursor measured from the diagrams (Mean Size) is reported in degrees (°) across all 5 targets. Between-subject SDs are reported in parentheses.

Group	**Adapt 1**		**Adapt 2**	
	Dir (n)	*Mean Size (SD)*	*Dir (n)*	*Mean Size (SD)*
Correct KR	1	0.07 (8.93)	1	1.36 (8.48)
KR + 15	1	0.93 (3.49)	3	6.56 (15.28)
KR - 15	0	-2.14 (8.14)	0	-1.66 (8.51)

Figure Captions

Figure 1: Procedures and number of trials (t) for all experimental feedback conditions experienced by all groups. All participants experienced the same conditions except for the second adaptation phase (Adapt 2). Depending on group allocation, in Adapt 2, participants received post-trial numeric KR (knowledge results) that was either correct (Correct KR) or erroneous (either KR+ 15° or KR-15°). Schematics of desired (accurate) aiming trajectories for each feedback condition during Adapt 2 are provided in the bottom panel as well as examples of errorful aiming (Erroneous KR groups only).

Figure 2: Group mean directional CE of cursor trajectory reported as a function of Block during both adaptation phases (Adapt 1 and Adapt 2). Shaded areas represent standard error of the mean. Arrows indicate blocks that were included in statistical analysis. A negative value indicates an error in the CCW direction to the intended target. A 30° CW visual rotation was gradually introduced during Adapt 1 and immediately during Adapt 2. Correct adaptation in Adapt 2 for the KR+15 group would be indexed by -15° CE (blue dashed line) between the rotated cursor and target (hand aiming 45° CCW to the circular target) and for the KR-15 group by +15° CE between the cursor and target (green dashed line; hand aiming 15° CCW relative to the target). The No KR group (n=5) is included for visual comparison. Red and purple dashed lines represent desired CE for the Correct KR and No KR groups. The corresponding figure of individual participant data is presented in Supplementary Materials.

Figure 3: Mean Variable Error (VE; degrees) of manual aiming accuracy (i.e. SD of mean CE) reported as a function of Phase (Adapt 1 or Adapt 2) and Block for all groups. Shaded areas represent standard error of the mean. Arrows indicate blocks that were included in statistical

analysis. The No KR group (n=5) is included for visual comparison. The corresponding figure of individual participant data is presented in Supplementary Materials.

Figure 4: Group mean reaction time (milliseconds) reported as a function of Testing Phase (Adapt 1 or Adapt 2) and Block for all groups. Shaded areas represent standard error of the mean. Arrows indicate blocks that were included in statistical analysis. The No KR group (n=5) is included for visual comparison. The corresponding figure of individual participant data is presented in Supplementary Materials.

Figure 5: Mean directional CE of cursor trajectory reported as a function of Block during the Pretest, first test of after-effects (Post-test 1 following Adapt 1), the KR adaptation phase (Adapt 2; Blocks 1 and 10), the second test of after-effects (Post-test 2), and immediate retention test. Shaded areas and error bars represent standard error of the mean. There was no rotation or KR in the Pre- and Post-tests. No KR was provided in Retention. A negative value indicates an error in the CCW direction to the intended target. A 30° CW visual rotation was introduced immediately during Adapt 2 and Retention phases. Displayed means were included in key statistical comparisons. The No KR group (n=5) is included for visual comparison.

Figure 6: Group mean after-effect magnitude (in degrees) following Adapt 2. After-effect magnitude is the calculated mean difference between the mean aiming error in Block 1 of Post-test 2 and Block 2 of Post-test 1. Group means are represented by shade grey bars. Data points represent individual participant means. The No KR group (n=5) is included for visual comparison. Participants who correctly reported consistent awareness of the direction of the cursor rotation to all 5 targets are outlined and participants in the Erroneous KR groups who reported being aware that KR was erroneous are marked with a single dot.

Figure 1

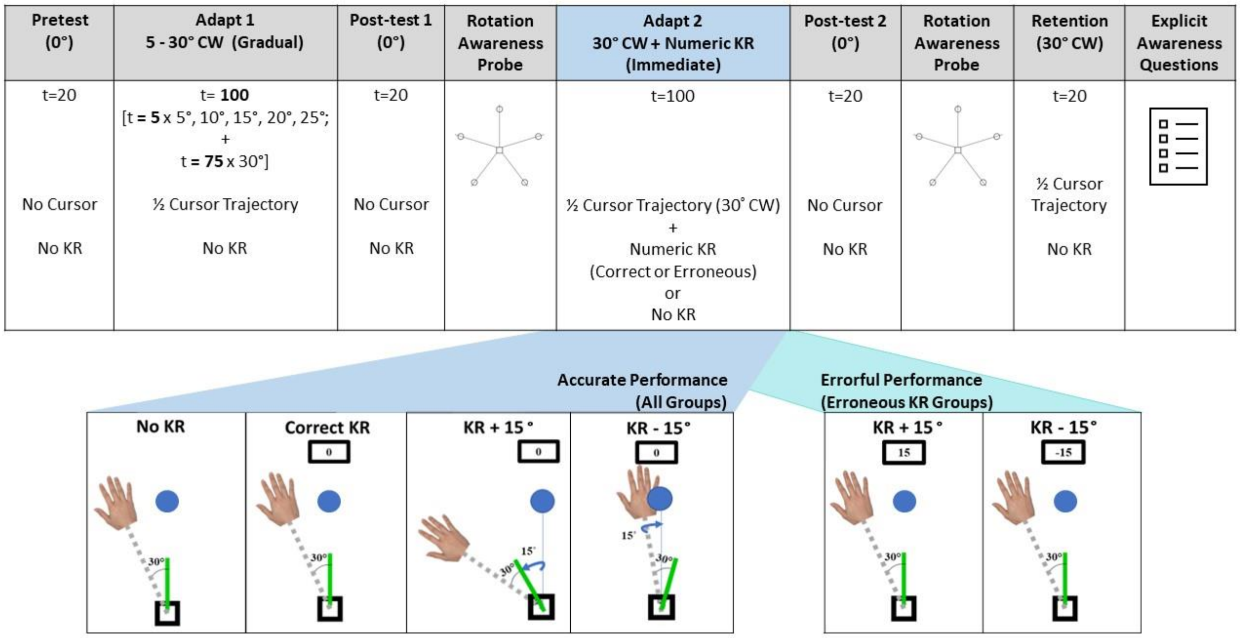


Figure 2

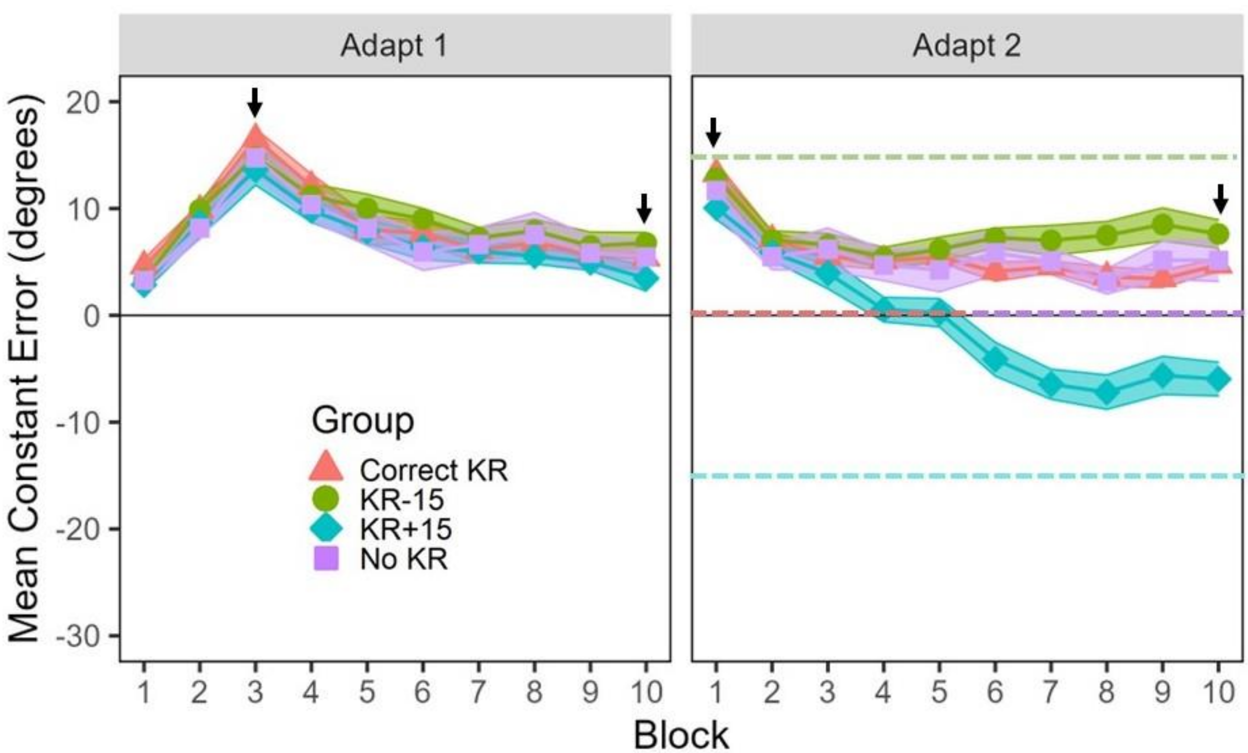


Figure 3

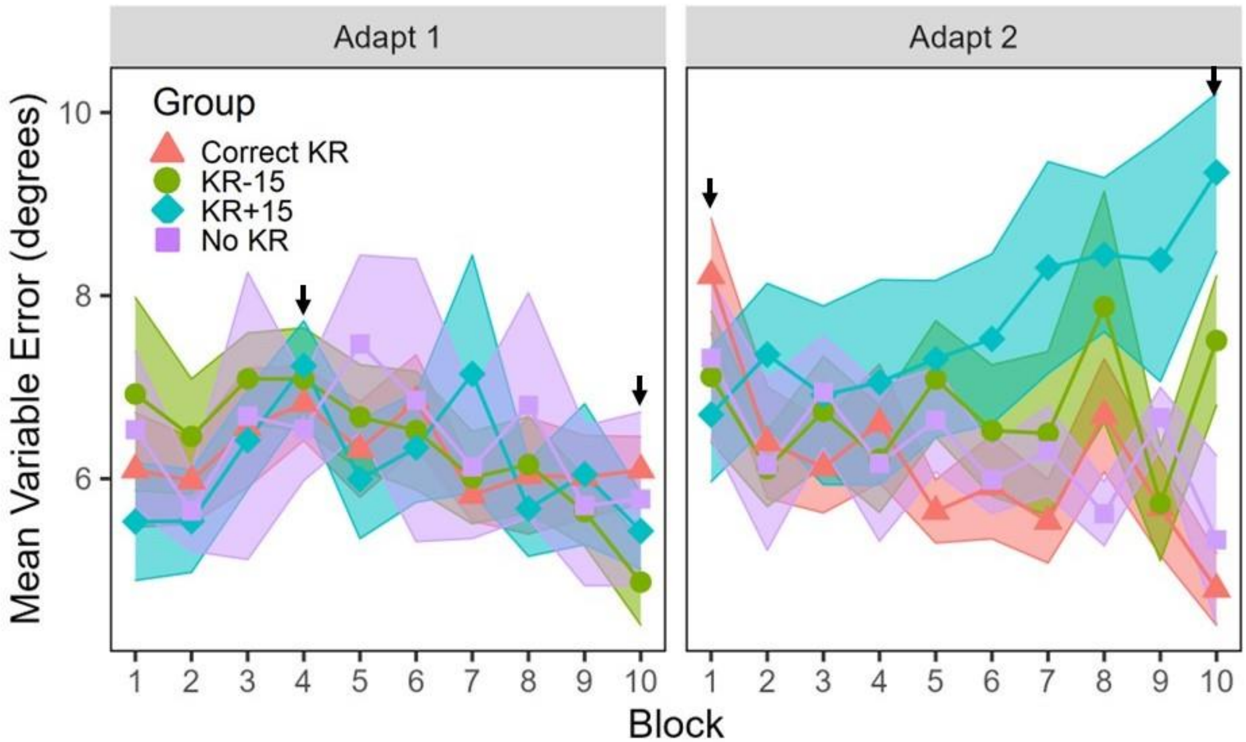


Figure 4

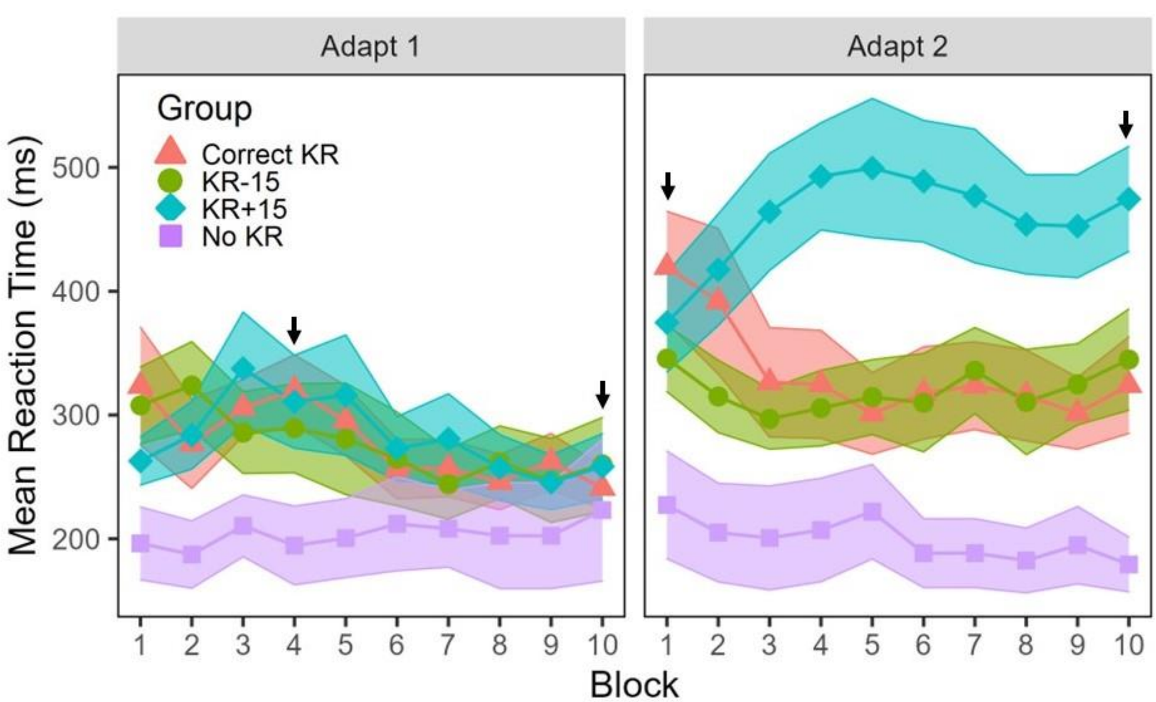


Figure 5

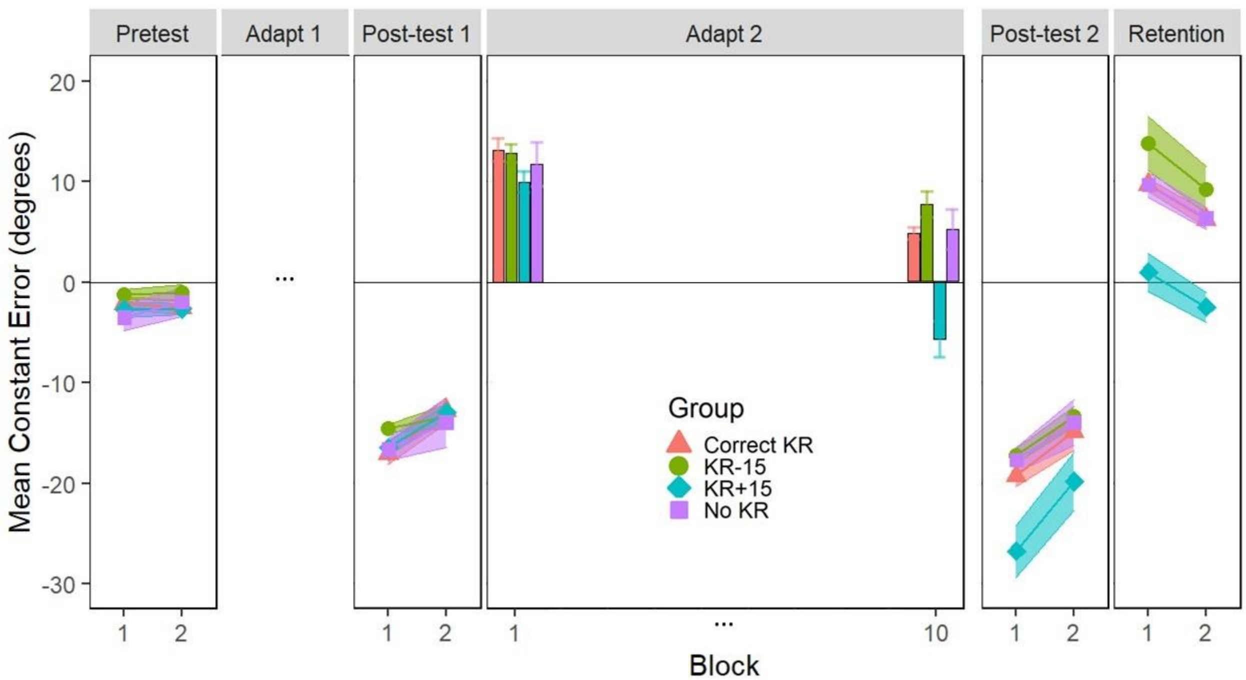
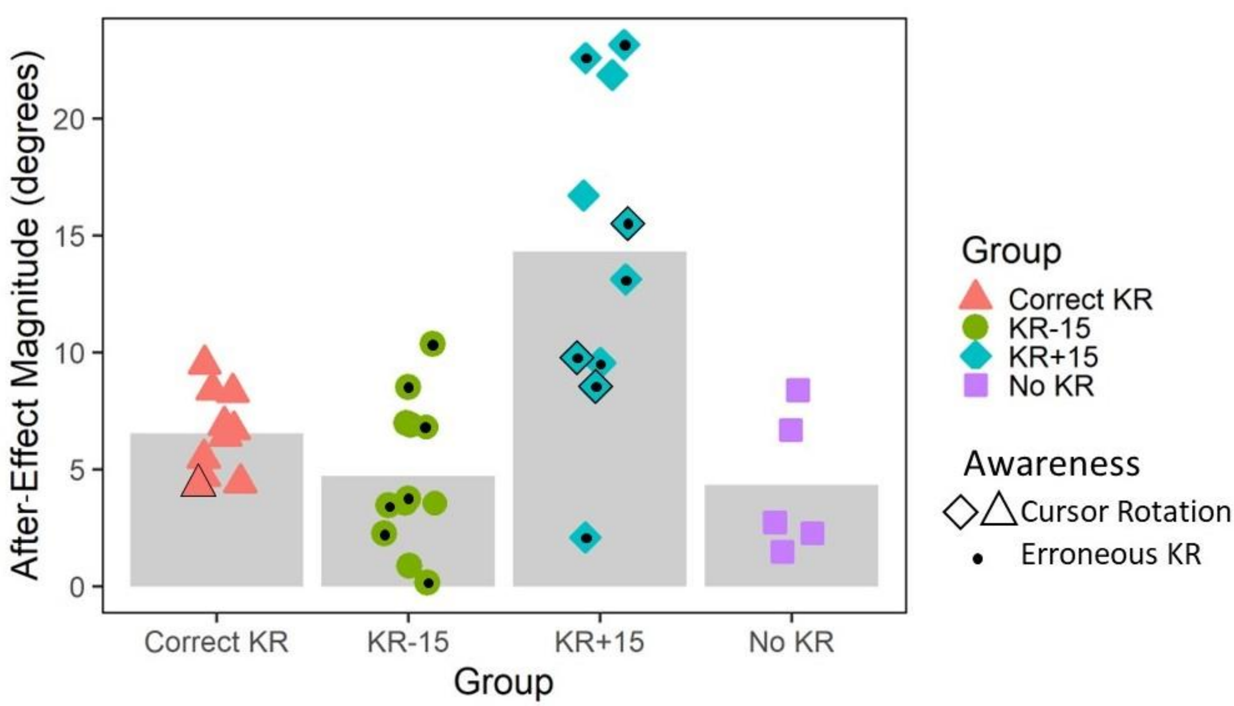


Figure 6



Supplementary Analyses: Analysis output tables for each LMER analysis

Table 1: Adapt 1 vs 2, Constant Error (CE): 3 Group X 2 Testing Phase X 2 Block (Adapt 1: Block 4 vs 10, Adapt 2: Block 1 vs 10)

Regression model equation: CE ~ 1+ Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block and their interactions (see below); Random effects = Participant, Participant*Testing Phase. Participant*Block not included because random effect error variance = 0.

		CE	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	12.08	9.85 – 14.32	**<0.001**
Group [KR-15]	-0.89	-4.06 – 2.27	0.576
Group [KR+15]	-2.28	-5.44 – 0.89	0.156
Testing Phase [Adapt 2]	1.18	-1.50 – 3.85	0.385
Block [10]	-6.72	-9.19 – -4.25	**<0.001**
Group [KR-15] * Testing Phase [Adapt 2]	0.47	-3.31 – 4.25	0.805
Group [KR+15] * Testing Phase [Adapt 2]	-0.92	-4.71 – 2.86	0.629
Group [KR-15] * Block [10]	2.31	-1.18 – 5.81	0.192
Group [KR+15] * Block [10]	0.38	-3.11 – 3.88	0.829
Testing Phase [Adapt 2] * Block [10]	-1.83	-5.33 – 1.66	0.300
Group [KR-15] * Testing Phase [Adapt 2] * Block [10]	1.02	-3.92 – 5.96	0.683
Group [KR+15] * Testing Phase [Adapt 2] * Block [10]	-7.85	-12.79 – -2.91	**0.002**

Random Effects

σ^2	7.76
τ_{00} Testing Phase*Participant	1.34
τ_{00} Participant	3.63
ICC	0.39
N Participant	30
N Testing Phase	2
Observations	120
Marginal R^2 / Conditional R^2	0.678 / 0.803

Table 2: Adapt 1 vs 2, Variable Error (VE): 3 Group X 2 Testing Phase X 2 Block (Adapt 1: Block 4 vs 10, Adapt 2: Block 1 vs 10)

Regression model equation: VE ~ 1+ Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block and their interactions (see below);
Random effects = Participant, Participant*Testing Phase. Participant*Block not included because random effect error variance = 0.

		VE	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	6.82	5.66 – 7.98	**<0.001**
Group [KR-15]	0.27	-1.37 – 1.90	0.746
Group [KR+15]	0.41	-1.22 – 2.05	0.619
Testing Phase [Adapt 2]	1.40	-0.09 – 2.88	0.065
Block [10]	-0.73	-2.08 – 0.63	0.289
Group [KR-15] * Testing Phase [Adapt 2]	-1.37	-3.47 – 0.73	0.198
Group [KR+15] * Testing Phase [Adapt 2]	-1.93	-4.03 – 0.17	0.071
Group [KR-15] * Block [10]	-1.49	-3.41 – 0.42	0.126
Group [KR+15] * Block [10]	-1.08	-2.99 – 0.84	0.267
Testing Phase [Adapt 2] * Block [10]	-2.70	-4.61 – -0.78	**0.006**
Group [KR-15] * Testing Phase [Adapt 2] * Block [10]	5.31	2.60 – 8.02	**<0.001**
Group [KR+15] * Testing Phase [Adapt 2] * Block [10]	7.15	4.44 – 9.86	**<0.001**
Random Effects			
σ^2	2.33		
$\tau_{00\ \text{Testing Phase*Participant}}$	0.46		
$\tau_{00\ \text{Participant}}$	0.61		
ICC	0.31		
$N_{\text{Participant}}$	30		
$N_{\text{Testing Phase}}$	2		
Observations	120		
Marginal R^2 / Conditional R^2	0.325 / 0.537		

Table 3: Adapt 1 vs 2, Reaction Time (RT): 3 Group X 2 Testing Phase X 2 Block (Adapt 1: Block 4 vs 10, Adapt 2: Block 1 vs 10)

Regression model equation: RT ~ 1+ Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant) + (1|Block:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block and their interactions (see below);
Random effects = Participant, Participant*Testing Phase, Participant*Block

	RT		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	320.24	249.53 – 390.96	**<0.001**
Group [KR-15]	-30.93	-130.94 – 69.08	0.541
Group [KR+15]	-9.51	-109.52 – 90.51	0.851
Testing Phase [Adapt 2]	99.33	36.26 – 162.39	**0.002**
Block [10]	-79.22	-142.25 – -16.19	**0.014**
Group [KR-15] * Testing Phase [Adapt 2]	-43.04	-132.23 – 46.15	0.341
Group [KR+15] * Testing Phase [Adapt 2]	-35.38	-124.57 – 53.80	0.433
Group [KR-15] * Block [10]	49.99	-39.15 – 139.13	0.269
Group [KR+15] * Block [10]	26.91	-62.24 – 116.05	0.551
Testing Phase [Adapt 2] * Block [10]	-16.22	-100.33 – 67.90	0.703
Group [KR-15] * Testing Phase [Adapt 2] * Block [10]	44.62	-74.33 – 163.57	0.459
Group [KR+15] * Testing Phase [Adapt 2] * Block [10]	168.39	49.44 – 287.35	**0.006**
Random Effects			
σ^2	4497.68		
$\tau_{00\ \text{Block*Participant}}$	554.00		
$\tau_{00\ \text{Testing Phase*Participant}}$	559.22		
$\tau_{00\ \text{Participant}}$	7106.97		
ICC	0.65		
$N_{\text{Participant}}$	30		
$N_{\text{Testing Phase}}$	2		
N_{Block}	2		
Observations	120		

Marginal R^2 / Conditional R^2	0.254 / 0.736

Table 4: After-effects 1, Constant Error (CE): 3 Group X 2 Testing Phase (Pretest vs Post-test 1) X 2 Block (1 vs 2)

Regression model equation: CE ~ 1 + Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant) + (1|Block:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block and their interactions (see below);
Random effects = Participant, Participant*Testing Phase, Participant*Block

	After-Effects 1 – CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-1.99	-3.64 – -0.33	**0.019**
Group [KR-15]	0.79	-1.55 – 3.13	0.504
Group [KR+15]	-0.52	-2.86 – 1.82	0.658
Testing Phase [Post-test 1]	-15.07	-17.19 – -12.96	**<0.001**
Block [2]	-0.45	-2.25 – 1.34	0.616
Group [KR-15] * Testing Phase [Post-test 1]	1.73	-1.26 – 4.72	0.255
Group [KR+15] * Testing Phase [Post-test 1]	1.10	-1.89 – 4.09	0.468
Group [KR-15] * Block [2]	0.63	-1.91 – 3.17	0.626
Group [KR+15] * Block [2]	0.31	-2.23 – 2.84	0.812
Testing Phase [Post-Test 1] * Block [2]	4.77	2.37 – 7.17	**<0.001**
Group [KR-15] * Testing Phase [Post-test 1] * Block [2]	-3.73	-7.13 – -0.33	**0.032**
Group [KR+15] * Testing Phase [Post-test 1] * Block [2]	-1.05	-4.45 – 2.35	0.542

Random Effects

σ^2	3.67
$\tau_{00\ \mathrm{Block*Participant}}$	0.43
$\tau_{00\ \mathrm{Testing\ Phase*Participant}}$	2.02
$\tau_{00\ \mathrm{Participant}}$	0.83
ICC	0.47
$N_{\mathrm{Participant}}$	30
$N_{\mathrm{Testing\ Phase}}$	2
N_{Block}	2

Observations	120
Marginal R^2 / Conditional R^2	0.856 / 0.924

Table 5: After-effects 2, Constant Error (CE): 3 Group X 2 Testing Phase (Post-test 1 vs 2) X 2 Block (1 vs 2)

Regression model equation: CE ~ 1+ Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant) + (1|Block:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block and their interactions (see below);
Random effects = Participant, Participant*Testing Phase, Participant*Block

	After-Effects 2 - CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-17.06	-20.00 – -14.13	**<0.001**
Group [KR-15]	2.52	-1.63 – 6.67	0.232
Group [KR+15]	0.58	-3.58 – 4.73	0.784
Testing Phase [Post-test 2]	-1.98	-5.44 – 1.49	0.260
Block [2]	4.32	1.98 – 6.65	**<0.001**
Group [KR-15] * Testing Phase [Post-test 2]	-0.75	-5.65 – 4.15	0.762
Group [KR+15] * Testing Phase [Post-test 2]	-8.27	-13.17 – -3.37	**0.001**
Group [KR-15] * Block [2]	-3.11	-6.40 – 0.19	0.065
Group [KR+15] * Block [2]	-0.74	-4.04 – 2.56	0.656
Testing Phase [Post-test 2] * Block [2]	-0.14	-2.84 – 2.56	0.919
Group [KR-15] * Testing Phase [Post-test 2] * Block [2]	2.76	-1.06 – 6.57	0.155
Group [KR+15] * Testing Phase [Post-test 2] * Block [2]	3.31	-0.51 – 7.12	0.089

Random Effects

σ^2	4.63
$\tau_{00\ \text{Block*Participant}}$	2.29
$\tau_{00\ \text{Testing Phase*Participant}}$	10.64
$\tau_{00\ \text{Participant}}$	4.34
ICC	0.79
$N_{\text{Participant}}$	30
$N_{\text{Testing Phase}}$	2

N_{Block}	2
Observations	120
Marginal R^2 / Conditional R^2	0.405 / 0.874

Table 6: Explicit Awareness Assessment – Mean reported aiming angle (degrees)

Regression model equation: Aiming Angle ~ 1+ Group*Testing Phase + (1|Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, and their interactions (see below);
Random effect = Participant

	Aiming Angle		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.07	-5.93 – 5.79	0.981
Group [KR-15]	2.21	-6.07 – 10.49	0.601
Group [KR+15]	-0.86	-9.14 – 7.42	0.839
Testing Phase [Adapt 2]	-1.29	-7.34 – 4.76	0.676
Group [KR-15] * Testing Phase [Adapt 2]	0.81	-7.75 – 9.37	0.853
Group [KR+15] * Testing Phase [Adapt 2]	-4.34	-12.90 – 4.22	0.320
Random Effects			
σ^2	47.68		
$\tau_{00\ Participant}$	41.66		
ICC	0.47		
$N_{Participant}$	30		
Observations	60		
Marginal R^2 / Conditional R^2	0.085 / 0.511		

Table 7: Retention, Constant Error (CE): 3 Group X 2 Block (1 vs 2)

Regression model equation: CE ~ 1+ Group*Block + (1|Participant). lme4 notation used.
Fixed effects = Group, Block and their interactions (see below);
Random effect = Participant

	Retention – CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	9.83	6.21 – 13.44	**<0.001**
Group [KR-15]	3.94	-1.17 – 9.05	0.128
Group [KR+15]	-8.95	-14.06 – -3.84	**<0.001**
Block [2]	-3.57	-6.04 – -1.11	**0.005**
Group [KR-15] * Block [2]	-1.02	-4.50 – 2.47	0.558
Group [KR+15] * Block [2]	0.07	-3.41 – 3.55	0.968
Random Effects			
σ^2	7.54		
$\tau_{00\ \text{Participant}}$	24.89		
ICC	0.77		
$N_{\text{Participant}}$	30		
Observations	60		
Marginal R^2 / Conditional R^2	0.4920/0.882		

Table 8: Footnote 1, Adapt 2, Constant Error (CE): 2 Group (Correct KR vs No KR) X 2 Block (1 vs 10)

Regression model equation: CE ~ 1+ Group*Block + (1|Participant). lme4 notation used.
Fixed effects = Group, Block and their interaction (see below);
Random effect = Participant

	Adapt 2 - CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	13.26	10.99 – 15.53	**<0.001**
Group [No KR]	-1.58	-5.50 – 2.35	0.408
Block [10]	-8.56	-10.94 – -6.17	**<0.001**
Group [No KR] * Block [10]	2.02	-2.10 – 6.15	0.322
Random Effects			
σ^2	6.67		
$\tau_{00\ Participant}$	5.40		
ICC	0.45		
$N_{Participant}$	15		
Observations	30		
Marginal R^2 / Conditional R^2	0.576 / 0.765		

Table 9: Footnote 1, After-effects 2, Constant Error (CE): 2 Group (Correct KR vs No KR) X 2 Testing Phase (Post-test 1 vs 2) X 2 Block (1 vs 2)

Regression model equation: CE ~ 1+ Group*Testing Phase*Block + (1|Participant) + (1|Testing Phase:Participant) + (1|Block:Participant). lme4 notation used.
Fixed effects = Group, Testing Phase, Block;
Random effects = Participant, Participant*Testing Phase, Participant*Block

	After-effects 2 - CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-17.06	-19.77 – -14.35	**<0.001**
Group [No KR]	0.44	-4.25 – 5.12	0.852
Testing Phase [Post-test 2]	-1.98	-3.74 – -0.21	**0.029**
Block [2]	4.32	2.25 – 6.38	**<0.001**
Group [No KR] * Testing Phase [Post-test 2]	0.94	-2.12 – 3.99	0.540
Group [No KR] * Block [2]	-1.64	-5.21 – 1.94	0.362
Testing Phase [Post-test 2] * Block [2]	-0.14	-2.32 – 2.05	0.899
Group [No KR] * Testing Phase [Post-test 2] * Block [2]	1.17	-2.61 – 4.96	0.536
Random Effects			
σ^2	2.96		
τ_{00} Block*Participant	2.31		
τ_{00} Testing Phase*Participant	0.89		
τ_{00} Participant	11.96		
ICC	0.84		
$N_{Participant}$	15		
$N_{Testing Phase}$	2		
N_{Block}	2		
Observations	60		
Marginal R^2 / Conditional R^2	0.206 / 0.871		

Table 10: Footnote 1, Retention, Constant Error (CE): 2 Group (Correct KR vs No KR) X 2 Block (1 vs 2)

Regression model equation: CE ~ 1+ Group*Block + (1|Participant). lme4 notation used.
Fixed effects = Group, Block; Random effect = Participant

	Retention - CE		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	9.83	8.29 – 11.36	**<0.001**
Group [No KR]	-0.14	-2.80 – 2.51	0.911
Block [2]	-3.57	-5.10 – -2.05	**<0.001**
Group [No KR] * Block [2]	0.25	-2.39 – 2.88	0.848
Random Effects			
σ^2	2.72		
$\tau_{00\ \text{Participant}}$	2.79		
ICC	0.51		
$N_{\text{Participant}}$	15		
Observations	30		
Marginal R^2 / Conditional R^2	0.364 / 0.686		

Supplementary Table 1. Questionnaire of explicit awareness of rotation and erroneous KR provided in Adapt2. Adapted from Benson et al. (2011).

Question	Response
(1) Did you notice the task get harder at any point?	If **YES**, when? → Record Response: proceed to **(2)**. If **NO**, proceed to **(3)**.
(2) Do you know why it became harder?	**ROTATED**, proceed to **(4)**. **OTHER/NO**, proceed to **(5)**.
(3) Did the cursor move where you intended it to?	If **YES**, proceed to **(6)**. If **NO**, proceed to **(2)**.
(4) How many degrees was the cursor rotated?	Record Response:
(5) What did you do to correct for it?	**ROTATED FEEDBACK**, proceed to **(4)**. **OTHER**→Record Response:
(6) When you received error score during Adapt2, did this score accurately show your reaching error?	**YES** **NO,** proceed to **(7)**
(7) If you answered NO to (6), what was different about the FB with respect to your actual movement trajectory?	Record Response: