Dissociating Target Error and Extrinsic Reward During Sensorimotor Adaptation

by

Jost Caspar Hausendorf

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The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the thesis entitled:

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Examining Committee:

Dr. Nicola J. Hodges, Professor, Kinesiology, UBC
Supervisor

Dr. Hyosub Kim, Assistant Professor, Kinesiology, UBC
Supervisory Committee Member

Dr. Romeo Chua, Professor, Kinesiology, UBC
Supervisory Committee Member

Abstract

Sensorimotor adaptation enables us to recalibrate movements to changes in body and environment, a process studied in visuomotor rotation tasks involving reaching movements with rotated cursor feedback. Adaptation is thought to arise primarily through sensory prediction errors but is also impacted by target errors and reinforcement mechanisms. A challenge for researchers has been to isolate how these processes impact adaptation. Learning from sensory prediction errors has been linked to cerebrocerebellar loops, encoding the discrepancy between predicted and actual sensory feedback. Cortical circuits have been associated with target errors, which represent the direction and magnitude of errors to a reaching target. Supplementing sensory feedback with reward aids motor performance via mesolimbic reward circuitry. A concern with attempts to distinguish across these 3 processes relates to how reward has been manipulated in these tasks. Some researchers have provided extrinsic rewards (e.g., money), whereas others relied on intrinsic rewards (i.e., target success). The latter combines the vectorial target error and a non-vectorial reward. For my thesis, we tested whether target error and reward make dissociable contributions to adaptation across two experimental studies.

In Experiment 1, we instructed participants to ignore a clamped feedback cursor that either hit (no target error) or missed (target error) one of four reaching targets. Some participants received performance-based rewards when they accurately reached to the intended target, thereby not adapting to the cursor. We predicted that adaptation, reflected by reaching errors opposing the clamp, should be lower in reward groups. Surprisingly, reaching errors increased when rewards were given. To further investigate

this surprising result, we modified the reaching task in Experiment 2, such that participants performed reaches to a single target and clamped and non-clamped trials were interleaved throughout adaptation trials. Rewards now attenuated compensatory reach adjustments, confirming our original prediction. A key finding of this work is that target error and rewards make dissociable contributions to adaptation. Further, depending on reward outcome at the previous trial, reward appears to modulate the solution the motor system computes to compensate for a sensory error.

Lay Summary

To successfully navigate through the world, we must continuously adapt our movements to changes in both body and environment. The brain solves this task effortlessly by evaluating sensory errors and rewards which together indicate whether a movement served its intended purpose. However, previous research did not distinguish sufficiently between sensory errors and rewards, making it difficult to determine how each signal contributes to our movements. Across two experimental studies, we showed that sensory errors and reward uniquely impact movement changes. We saw that sensory errors determine the direction of movement changes, which always occurred in the opposite direction of the observed error. In contrast, reward influenced how much participants adjusted their movements to the observed sensory error, with larger changes occurring when no reward was earned than when a reward was received. This work highlights the need for careful distinction between the variety of signals driving our movements.

Preface

The work presented in this thesis was written and conceptualized by Jost C. Hausendorf (JCH). Dr. Nicola J. Hodges (NH), Dr. Hyosub Kim (HK), and Dr. Romeo Chua (RC) read all chapters, contributed to the development and refinement of the research design, and provided comments that informed revisions to the submitted thesis document. Data collection was conducted in the Motor Skills Lab (Principal Investigator: Dr. Nicola J. Hodges) at the University of British Columbia and was approved by the University of British Columbia's Behavioural Research Ethics Board (certificate number: H25-01247).

JCH and NJH conceptualized the research questions and developed the experimental design for the studies outlined in Chapters 2-3. RC and HK refined the specifications of the testing paradigm and contributed to the experimental design more broadly. Custom Python scripts for the reaching tasks were created by Dusty Fox for the study in Chapter 2 and by JCH for the study reported in Chapter 3. JCH wrote all chapters and conducted the majority of data collection for both studies with Tianna Chang supporting with data collection for the study reported in Chapter 2. JCH pre-processed and analysed all data using custom R scripts.

Generative AI statement: Microsoft Copilot was used for efficient optimization of custom Python scripts used to program the reaching task. All writing and other code belong to JCH.

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Acknowledgements

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I also would like to sincerely thank Dr. Hyosub Kim and Dr. Romeo Chua, for their willingness to assist and collaborative spirit in providing feedback about my often-premature thoughts. You have taught me patience, the value of critically re-evaluating my own ideas, and the importance of careful attention to detail when formulating research questions and designing strategies to address them.

Finally, I want to thank my fellow colleagues, students, and friends from the Motor Skills Lab, the Perceptual Motor Dynamics Research Lab, and the Computation, Cognition, and Movement Lab who were always there to help and created an amazing environment for me to learn and appreciate the diverse worlds of motor learning and motor control.

1. General Introduction

The ability to learn and execute motor skills impacts both comfort and functionality of our daily lives. Yet, well-practiced movements require frequent recalibration to account for changes in both body and environment (e.g., Shadmehr et al., 2010). As an example, consider lifting a pot of coffee. If you are expecting the pot to be light in weight, you will apply little force when attempting to lift it. However, suppose it is unexpectedly heavy, resulting in a mismatch between your predicted and actual motor output. To lift the pot successfully, you need to account for the extra weight by adding force to your movement. This recalibration of your original movement plan is the result of both a voluntary and an involuntary response to the difference between predicted and actual motor output (e.g., Mazzoni & Krakauer, 2006). Researchers have termed this process sensorimotor adaptation and they have studied its importance in guiding our movements for over a century (Von Helmholtz, 1867; Krakauer et al., 2019). A popular method used to examine sensorimotor adaptation is the visuomotor rotation paradigm (e.g., Taylor & Ivry, 2011). Here, participants are often unable to see their hand as they are performing planar goal-directed reaches. Meanwhile, display of a digital cursor provides concurrent, visual feedback about reach trajectories. Rotating the visual feedback from the cursor causes participants to modify the direction of their reach to compensate for the discrepancy between predicted reach trajectories and visual display of the cursor (e.g., McDougle et al., 2015).

In past studies, researchers have used visuomotor rotation paradigms to distinguish between explicit and implicit learning mechanisms contributing to sensorimotor adaptation (e.g., Mazzoni & Krakauer, 2006; Huberdeau et al., 2015;

McDougle et al., 2016). Implicit contributions to sensorimotor adaptation have commonly been linked to subcortical error processing (Taylor et al., 2014), with cerebellar structures encoding the discrepancy between predicted motor outputs (e.g., successfully reaching to a target) and sensory feedback (e.g., perturbed cursor display) (Albus, 1971). This sensory prediction error serves as a signal to update the motor plan for subsequent movements and their predicted outcomes, collectively referred to as the forward model (e.g., Ito, 2006; Flanagan et al., 2013). In contrast, explicit learning is often classified as a voluntary process, predominantly associated with cortical structures (e.g., Seidler & Noll, 2008; Taylor & Ivry, 2014). Participants can consciously apply a strategy (e.g., reaching to a nearby target) to accommodate for any observed target error.

Target errors typically provide a vectorial error signal, indicating both the direction and magnitude of an error (e.g., Taylor et al., 2014), though also classified as a binary error (Morehead et al., preprint; Loew et al., 2018; Kim et al., 2019; Tsay et al., 2022), between movement goal (e.g., target) and movement outcome (e.g., final cursor position). Target errors have been related to activations in posterior parietal regions in human (Diedrichsen et al., 2005) and animal models (e.g., Inoue & Kitazawa, 2018) and can be quickly corrected using explicit strategies (e.g., Mazzoni & Krakauer, 2006). However, there is evidence that target errors also impact implicit adaptation (e.g., Cameron et al., 2010; Kim et al., 2019, Loew et al., 2018). Evidence for implicit learning in response to target errors has been shown in experiments where participants adapted their reach directions in response to ‘clamped’ feedback (Kim et al., 2019). In a clamped cursor feedback paradigm, a person is told to reach directly to a target, but the visible cursor trajectory shows a consistent bias away from the target (e.g., Morehead et al., 2017).

Despite instructions to ignore the perturbed cursor and aim for the target, participants adapt to the cursor error by involuntarily increasing the hand angle of their reaches away from the target to compensate for the visual error (Morehead et al., 2017).

In addition to sensory prediction- and target error processes at work during visuomotor adaptation, reinforcement mechanisms also impact adaptation (e.g., Izawa & Shadmehr, 2011). Reinforcement mechanisms work through intrinsic rewards evoked by task success (e.g., Holland et al., 2018, Kim et al., 2019) or extrinsic performance-based rewards (e.g., Galea et al., 2015; Nikoyaan & Ahmed, 2014). Such rewards can enhance the rate of adaptation (e.g., Nikoyaan & Ahmed, 2014) and its retention (e.g., Galea et al., 2015; Shmuelof et al., 2012). Supplementing sensory feedback with rewards is thought to aid adaptation by engaging dopaminergic reward circuitry that provides sensorimotor structures with an additional teaching signal based on previous action-outcome pairings (e.g., Taylor & Ivry, 2014). Even though the temporal and structural dynamics of reward signal integration within motor control loops remain poorly understood in humans (e.g., Codol et al., 2020), plausible mechanisms have been proposed based on observations in animal models (e.g., Ghanayim et al., 2024; Molina-Luna et al., 2009). For example, using two-photon calcium imaging in mice models, Ghanayim et al., (2024) showed that dopaminergic projections from the ventral tegmental area (VTA) to primary motor cortex (M1) drove plastic reorganization in M1 layers 2/3 as a function of motor learning in a reaching task. When the authors inhibited VTA-M1 projections, both behavioural learning and plastic changes in layer 2/3 networks came to a halt but returned to expected levels when the inhibition was lifted again. Thus, plastic reorganization in M1, driven by dopaminergic VTA-M1 projections, has been brought forward as a prominent mechanism of reward-based motor learning in human models (Zhao et al., 2024).

On a behavioural level, reward-based motor learning emerges from a non-directional reward signal related to the outcome of a task (e.g., Izawa & Shadmehr, 2011). Contrary to target- and sensory prediction errors, reward signals typically do not contain information about the direction or magnitude of a movement error. The learner only gains binary knowledge about whether their movement was successful and thus will either try and repeat a prior performance or explore a new movement strategy (e.g., Pekny et al., 2015; Izawa & Shadmehr, 2011). Once a learner identifies a strategy that maximizes reward, they repeat, thereby consolidating the corresponding movement. This reward-based learning process appears to be accompanied by a reward-dependent increase of movement efficiency and/or motor vigour (e.g., Summerside et al., 2018). In a study by Summerside et al. (2018), participants performed reaching movements with higher movement speed and reduced reaction times (RT) to targets where a performance-contingent reward signal was expected, compared to non-rewarded targets.

In the context of sensorimotor adaptation, several authors concluded that reward feedback contributes predominantly to explicit, strategic learning (Holland et al., 2018; Izawa & Shadmehr, 2011). For example, Holland et al. (2018) showed that participants successfully adapted to a gradually increasing visuomotor rotation based only on binary reward feedback (i.e., a green “tick-mark” for on-target reaches). When the authors interfered with explicit processing by introducing a secondary task, participants failed to adapt, indicating a strong explicit component in reward-based adaptation. Nevertheless, researchers have found evidence for neural correlates of reward processing during visuomotor tasks in human (Thoma et al., 2008) and animal (e.g., Sendhilnathan et al., 2020) cerebellar structures, thought to predominantly map implicit learning (Taylor & Ivry, 2014).

To test how reward functions in the context of target- and sensory prediction errors, these error signals have been manipulated concurrently (e.g., Izawa & Shadmehr, 2011; Kim et al., 2019; Tsay et al., 2022). Both reward signals and sensory prediction errors were sufficient to bring about adaptation to a cursor rotation, evidenced by an absence of difference in adapted reach directions between groups with different amounts of sensory feedback (Izawa & Shadmehr, 2011). However, proprioceptive adaptation (i.e., biases in hand estimates) was dependent on the quality of sensory feedback. The authors argued that there is an interactive process between reward signals and sensory prediction errors, where the presence and strength of one signal can up- or down regulate the processing of the other. Indeed, when sensory prediction error processes were put in conflict with reward signals concerning target success, implicit adaptation processes were modulated (Kim et al., 2019). In this study, the authors manipulated intrinsic reward by changing the size of a reaching target in the presence of clamped cursor feedback. The amount of adaptation was reduced when feedback from the clamp showed a 'successful' target hit due to a larger target, versus when it missed due to a smaller target. However, because there was a vectorized target error signal, the authors could not conclude that attenuation of implicit adaptation was a result of reward, rather than target error.

A concern with previous research on the role of reward during sensorimotor adaptation is how researchers defined and implemented reward signals. While some researchers used an extrinsic reward signal such as a point system (e.g., Nikoyaan &

Ahmed, 2015), others relied on an intrinsic reward signal induced via target success (e.g. Kim et al, 2019; Tsay et al., 2022). The latter conflates the contributions of two distinct signals in an adaptation paradigm: a vectorial error and a non-vectorial reward. Thus, to make inferences about the contribution of reward to the implicit sensorimotor adaptation process, these two signals need dissociating. The following experiments were motivated by the resolution of this issue. The overall aim of this thesis is to quantify and contrast the extent to which extrinsic reward impacts implicit adaptation processes driven by sensory prediction errors and target errors, thereby aiding the understanding of reward-related processes generally.

2. Experiment 1

2.1 Introduction

Our aim was to dissociate the effects of target error- and extrinsic reward on implicit adaptation in a between-participants design. Implicit sensorimotor adaptation and hence sensory prediction error were controlled through clamped cursor rotated feedback. Target error, but not reward feedback, was manipulated via target size, such that between groups, the clamped cursor either hit or missed the reached for target (Kim et al., 2019). Some participants also received an extrinsic, performance-based reward signal (i.e., monetary reward and target animations) on trials where they successfully directed their physical reaches into a pre-specified reward region (independent of displayed target size) around the original target. As such, the reward was given in response to not adapting to the clamped cursor. With this 2 x 2, orthogonal design of target error (target hit, target miss) and reward signal (reward, no reward), we evaluated the relationship between extrinsic reward, target error, and implicit adaptation.

Our pre-registered predictions were that implicit adaptation, evidenced by changes in reach direction opposing the clamp, should generally be attenuated when participants hit the target (i.e., target error is absent), replicating Kim et al. (2019), and when there are extrinsic rewards. Therefore, we are expecting main effects of target error and reward. Regarding potential Target Error-Reward interactions, we hypothesized that adaptation will be strongest when there is no reward and the clamped cursor misses the target (i.e., 'no reward + target miss'). In contrast, we expected implicit adaptation should be attenuated both when the clamped cursor hits the target (i.e., 'no reward + target hit') and when there is an extrinsic reward for physically reaching straight to target (i.e., 'reward +

target miss' and 'reward + target hit'). We thought the least amount of implicit adaptation should occur in the 'reward + target hit' condition, as the combination of extrinsic reward and absent target error should bias reach directions closest to the target. We also took measures of reaction time and movement speed, given prior research showing that rewarded trials are characterised by faster reaction and movement times (Summerside et al., 2018). However, reward could alternatively lead to longer RTs, as a result of making the participants aware of their error in physical reaching, leading to increased planning on the next trial (Georgopoulos & Massey, 1987). For participants in the reward groups, we also expected larger changes in hand angle following non-rewarded compared to rewarded trials, indicating increased movement exploration to maximize reward (Pekny et al., 2015).

2.2 Methods

2.2.1 Participants

We recruited 64 healthy participants (45 Females, 18 Males, 1 Non-Binary; M_{Age} = 25 ± 11 yr) with no known neurological conditions, normal or corrected to normal vision, and fluent in English. We excluded data from five participants. All five participants failed to adhere to the imposed movement time restriction (i.e., completing reaching movements in less than 300 ms) despite repeated instruction to speed up their movements. As we specified in our pre-registration, all trials with movement times >300ms were removed from statistical analyses. This resulted in the removal of >50% of trials for all five participants, which we had established as an exclusion criterion prior to data collection. We considered the remaining 59 participants for statistical analysis. We estimated the required sample size to detect the expected effect in an a priori power analysis using the

G*Power 3.1.9.6 “ANOVA: Repeated measures, within-between interaction” test with power (1 – beta) set at .9, type 1 error probability at .05, and 2 repeated measures. Two effect size estimates were identified from Kim et al. (2019), where there were differences in early adaptation rate ($f = 0.35$) and during late acquisition ($f = 0.45$) to a clamped cursor in a visuomotor rotation paradigm between groups with different target sizes. Based on these estimates, the recommended sample was N=64 (n = 16/gp) or N=24 (n = 6/gp) respectively. We opted for the more conservative estimate of n = 16 per group (N = 64) as our recruitment goal because we had also lowered the number of experimental trials to 400 (compared to the 640 trials, Kim et al. 2019). Handedness was verified for each participant with the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were recruited from the university via social media posts, online advertising, emails, and posters. Each participant received $15 for participating. Prior to participation in the study, participants gave written and verbal informed consent. The study was approved by the University of British Columbia’s ethics committee and all procedures were in accordance with the Declaration of Helsinki.

2.2.2 Apparatus

Participants sat at a modified desk setup and performed planar reaches by moving a digitized stylus (BAMBOO Ink Plus, Wacom Co., Japan) over a touch-screen surface sampling at 165 Hz (Summit A16 AI+ A3HMT, Micro-Star International Co., Taiwan). We created a gamified visuomotor paradigm using a custom-written Python script in PsychoPy (PsychoPy, Open Science Tools Ltd., United Kingdom; Pierce et al., 2019). Vision of the arms, stylus, and digitized surface were occluded by turning off the lights and requiring participants to wear visual restriction goggles (EVOVISION, GStrap, Switzerland). Visual feedback was therefore restricted to a fronto-parallel monitor facing the participant at eye-level.

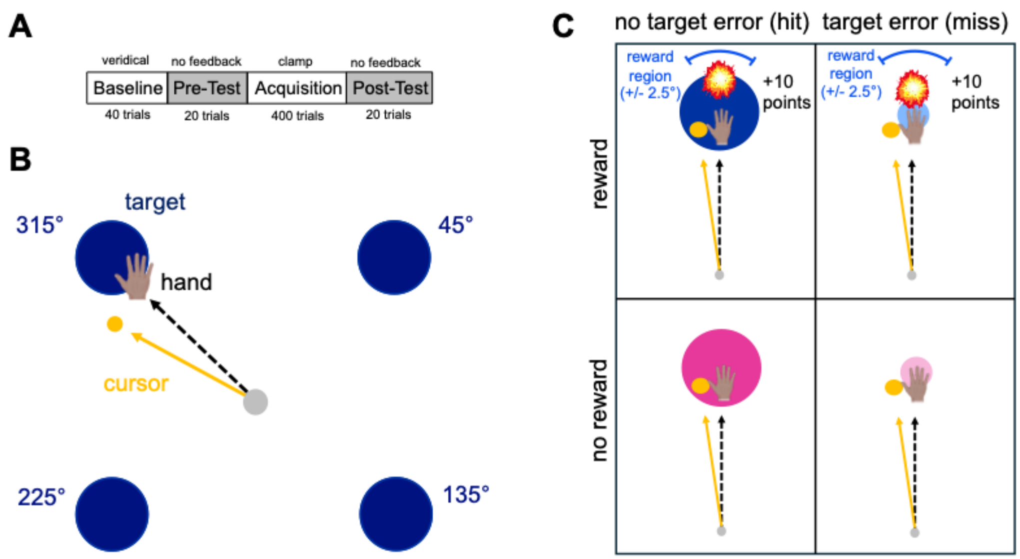

Figure 1. (A) Experimental procedure. (B) Task environment of reaching task. For each trial, a single target (blue circles) appeared at one of four locations surrounding the grey reference circle (i.e., 45°, 135°, 225°, and 315°). During acquisition, the yellow cursor followed a fixed trajectory relative to the target (i.e., 3.5° error clamp), but independent of the participants' reach directions. Vision of the hand was removed via occlusion goggles and dimmed room lighting. (C) Reaching conditions. In the 'no reward' groups, no extrinsic reward was provided. In the 'reward' groups, a target exploded and a display of points indicated a successful physical reach to the target zone. Clamped cursor feedback matched in magnitude and direction for all groups either 'hit' (no target error) or 'missed' the target (target error), through the provision of large and small targets respectively.

2.2.3 Reaching Task

The stimuli and groups were for the most part matched to the specifications of the clamped visuomotor paradigm implemented by Kim et al. (2019). Participants performed horizontal reaching movements (Figure 1B) from a centrally located reference circle (grey) with a 6 mm diameter. Four targets (blue) with a 6 mm (small) or 16 mm (large) diameter were located around the reference circle (8 cm radial distance to reference circle) at angles of 45°, 135°, 225°, and 315° (0° corresponds to straight reach). Between trials, participants kept the stylus, represented by a feedback cursor on the screen, within the reference circle. A trial began when one of the four targets appeared, signaling participants to swiftly and accurately swipe the stylus through its centre. Concurrent visual cursor feedback displayed the swipe trajectory from reference circle to target. Cursor feedback either showed the actual path of the stylus (veridical) or a cursor trajectory rotated by 3.5° relative to the target centre (clamped). We counterbalanced the direction of the clamped cursor within both experimental conditions.

Once a swipe exceeded the maximum radial amplitude between reference circle and target (i.e., 8 cm), visual feedback of the cursor's endpoint was shown for 500 ms. Thus, visual feedback of the final cursor position either represented the stylus's actual endpoint at the maximum radial distance (i.e., veridical) or the point where the clamped cursor trajectory hit or missed the target. Only participants in the reward groups received extrinsically rewarding feedback, whereby physical swipes into a reward region spanning around the target (i.e., within ±2.5°of target centre) were rewarded with 10 points per trial (Figure 1C). To increase reward salience, we told participants in the reward groups that they would receive additional monetary compensation based on the number of points they could accumulate during the experiment. Note that all participants, including both the reward and no-reward groups, received $15 for participating, independent of task performance. We debriefed participants accordingly after the experiment. The number of total points was visible in the top left corner of the feedback screen. Additionally, the reward signal was coupled with a target animation where the target exploded once a physical on-target swipe exceeded the radial boundary of 8 cm. The target explosion animation lasted 500 ms, with cursor endpoint feedback remaining on the screen for the same duration. However, no animation or points reward was presented when participants missed the target and only cursor endpoint feedback was shown. Participants that were not in the reward groups did not receive any extrinsic reward feedback. After endpoint feedback for all groups, the cursor disappeared until participants moved the stylus back into the reference circle. To encourage a planned rather than a corrected reach, we asked participants to make a fast, smooth swiping motion with the pen through the target. Through pilot testing, we determined that movement times would fall below 300 ms. As such, we constrained maximum movement times to 300 ms. That is, we excluded those trials from analysis where the time between swipe onset and target intersection exceeded 300 ms. Participants additionally saw a warning message on slow trials, reminding them to increase their movement speed on the subsequent trial.

2.2.4 Procedure

All testing took part on one day in the same room on the University campus. Participants were randomly assigned to one of four groups: reward + target miss, reward + target hit, no reward + target miss, no reward + target hit. They were correspondingly briefed about the experimental task and procedures in their group. All participants performed a set of 40 baseline trials (i.e.,10 per target) where they were told to swipe directly through the centre of the targets with veridical cursor feedback and no extrinsic rewards (Figure 1A). After, they completed 20 pre-test trials without cursor feedback. The experimenter then introduced the clamped cursor perturbation and let participants perform four demonstration trials to make sure they understood that the cursor rotation was fixed with respect to target locations rather than actual movement. We did not consider the demonstration trials for further analysis. Subsequently, we instructed all participants to ignore the visual cursor and continue to swipe directly through the specified targets. Acquisition thus consisted of 400 target swipes with clamped cursor feedback.

Once the acquisition phase was completed, all participants performed a final set of 20 post-test trials without any cursor- or reward feedback. Before onset of the post-test, participants received instructions about the feedback changes and a reminder to continue swiping directly through the targets. After completing the protocol, we conducted a semi-structured debrief to confirm that they tried to ignore the clamped cursor and did not develop any reaching strategy other than aiming straight to the target. In the debrief, we also asked whether reward feedback increased the participants' awareness of any unwanted change of reach direction in response to the clamped cursor. Finally, participants completed two short previously validated questionnaires regarding a) task motivation and engagement, using a modified version of the Intrinsic Motivation Inventory (IMI; Ryan, 1982), and b) reward sensitivity, via the Sensitivity to Reward and Sensitivity to Punishment Questionnaire (SPSRQ; Torrubia et al., 2001). We modified the IMI by only including items from the factors "Interest/Enjoyment" and "Effort/Importance". For the SPSRQ, we only considered the 24 items related to reward sensitivity.

2.2.5 Data Analysis

2.2.5.1 Measured Variables

Our main dependent variable was hand angle error from the centre of the target (°). This was calculated as the angle between the straight line connecting the reference circle to the target centre and the actual position of the stylus at the point of peak radial velocity during each swipe. For visualization purposes and the analysis of retention measures, we binned trials into movement cycles containing four consecutive reaches each (i.e., 4 trials/cycle). To provide a measure of reaching consistency, we also calculated variable error for 10 blocks of trials in acquisition (i.e., 40 trials/block). To obtain an unbiased estimate of variable error, we first removed any variation in hand angle error attributable to systematic change over time induced by the clamped cursor. To do so, we calculated mean hand angle error over a moving window of 8 trials during acquisition. We then removed this moving average from the trial-to-trial hand angle error data for every participant. Finally, we calculated variable error as the standard deviation of the transformed hand angle errors within each acquisition block.

The post-test, conducted without feedback or reward, provided an estimate of immediate retention. We calculated two measures of retention. First, we determined aftereffects in an analysis of participant-specific hand angle error during the first movement cycle (i.e., first four trials) of the post-test. Second, we calculated relative retention as the ratio of the mean hand angle error during the final movement cycle of acquisition (i.e., trials 461-465) to the mean hand angle error during the final movement cycle of the post-test (i.e., trials 481-484).

During acquisition, a number of secondary measures were collected about task performance. For the reward groups, we calculated the percentage of successful or rewarded trials within each of the 10 blocks (40 trials/block). We also measured change in hand angle (°) from trial t-1 to trial t following rewarded (success) and non-rewarded (no success) trials. In addition to looking at change in hand angle from trial t-1 to trial t, we also evaluated the success history of the last three trials (t-3, t-2, t-1) prior to trial t. That is, we categorized hand angle change at trial t based on all possible triplets of success outcomes (e.g., “0,0,1”, “1,1,0”, “0,0,0”, etc.) that could have occurred in the preceding three trials, thereby obtaining a more informative assessment of reward-based behavior. The analysis of success history was not featured in the OSF pre-registration.

To give some indication of movement processes during acquisition, especially with respect to reward, we calculated peak velocity and reaction time. We also assigned each participant a score for reward sensitivity from the “Sensitivity to Punishment and Sensitivity to Reward Questionnaire” (SPSRQ) and a score for task engagement from the “Intrinsic Motivation Inventory” (IMI).

2.2.5.2 Pre-Analysis Data Processing

Because we systematically counterbalanced the clamp direction during acquisition within groups, we adjusted the direction of hand angle measures, such that participants could be analyzed together. To do so, we multiplied hand angle measures by -1 when the cursor was clamped to a counterclockwise rotation from the target. We detected and removed outliers by using the stats:filter function in the statistical software R (version 4.41, http://www.r-project.org). A trial was removed when its corresponding hand angle exceeded 90°. To correct for individual target variation, we followed an approach used by Kim et al. (2019). We calculated each participant’s standard deviation in hand angle to each target during baseline trials 21-40 with veridical cursor feedback. This target-specific variation was then subtracted from all subsequent reaches (in pre-test, acquisition and post-test trials) to obtain corrected hand angle values.

2.2.5.3 Statistical Models

All data was analyzed using custom scripts in R. Linear Mixed Effect (LME) models were fit using restricted maximum likelihood to analyze hand angle error, change in hand angle error, peak velocity, variable error, and reaction time across groups, trials, and experimental phases. To evaluate model fit, we used the Akaike Information Criterion (AIC) (Akaike, 1974) and examined the random and fixed effects structure in the model output. We tested data assumptions including normality, linearity and equal variance, and used transformations as necessary. We report semi-partial R^2 (R^2_{sp}), the proportion of outcome variance uniquely explained by an individual predictor, as a measure of effect size. To provide context for the reported R^2_{sp} values, we also report marginal R^2 and conditional R^2, representing the model-specific proportion of total variance explained by the fixed effects alone and by the combined fixed and random effects, respectively (Edwards et al., 2008, Nakagawa & Schielzeth, 2013, Johnson, 2014). Marginal and conditional R^2 are reported in corresponding model summary tables (Appendix A-E). We chose an alpha of $p < .05$ to denote statistical significance.

For the main analysis, hand angle error served as our primary dependent variable and we accounted for individual differences by including participant as a cluster variable (i.e., random factor) for all models. Fixed factors in our analyses included reward (no reward, reward), target error (target hit, target miss) and their interactions as between-subjects variables. Depending on the analysis, we added trial number (continuous), acquisition block (1-10), and target (45°, 135°, 225°, 315°) as within-participant factors (in addition to their corresponding interactions). We included random slopes for trial, acquisition block, target, and their interactions, when model fit was improved and convergence allowed. We addressed convergence issues by carefully reducing the fixed and random effects structure of the model with respect to concerns of pseudoreplication (e.g., Scandola & Tidoni, 2020). Other fixed effects used in additional LME models included success (success, no success), task engagement (continuous; IMI score), and reward sensitivity (continuous; SPSRQ score). Measures of reward sensitivity (SPSRQ score) and task engagement (IMI score) were included as continuous fixed effects in our models if they improved model fit informed by the AIC.

We grand-mean centred and scaled reward and target error (i.e., factor levels were coded to -0.5 and 0.5), so that the model intercept represented the grand-mean and estimated slopes of corresponding main effects (i.e., their β-estimates) indicated group mean differences in an ANOVA-like model output (e.g., Schad et al., 2020). Tukey-corrected post hoc tests were used to examine interactions and any significant main effects with more than 2 levels (i.e., target, experimental block, and movement cycle).

Trial was scaled for all analyses by dividing each individual trial number by the total number of trials in the corresponding experimental phase (baseline, pre-test, acquisition, post-test). This transformation ensured that a unit increase of trial (i.e., its β-estimate) in the model output corresponded to the change occurring in the dependent variable (e.g., hand angle error) over the full range of trials within that phase (i.e., over 40 trials for baseline, 20 trials for pre-test, 400 trials for acquisition, or 20 trials for post-test). We then cluster-mean centered the scaled trial variable to evaluate hand angle error at the subject-specific average trial. We conducted the same transformation for other time-dependent variables, i.e., movement cycle and acquisition block, when they were included in the analysis. For all analyses, we used the stats:filter function in R to restrict the data to the corresponding set of trials; and modified the fixed effects structure and dependent variable accordingly.

We analyzed group-level differences in relative retention, IMI score, and SPSRQ score in 2 Reward x 2 Target Error between-participants ANOVAs as the corresponding data for these measures did not support the nested structure of our LME models.

2.3 Results

2.3.1 Baseline

As shown in Figure 2A, there were no group differences in hand angle error during baseline aiming with veridical cursor feedback (trials 1-40), for either reward, target error or their interaction. Baseline analyses are reported in Appendix A1-3. Neither peak velocity nor reaction time differentiated across the groups.

2.3.2 Pre-Test

During the pre-test (trials 41-60) without visual cursor feedback, there were no differences in reaching accuracy between groups that did or did not receive reward feedback (Figure 2A). We also did not observe an effect of target error and there was no Reward x Target Error interaction for reaching accuracy. Across groups, participants did show target-specific reach direction biases during the pre-test (β = -0.48, SE = 0.21, p = .02, R^2_{sp} = 0.007). Deviations in reaching accuracy were higher at the 45° target (M = 2.57°, SD = 5.76) and the 315° target (M = -2.93°, SD = 5.88) compared to the 225° target (M = 0.71°, SD = 3.64) and the 135° target (M = 0.06°, SD = 6.30) (all p's < .05). Hand angle errors were statistically different between the 45° and 315° targets (p < .01), but not between the 225° and 135° targets (Appendix B1). Pre-test movement speed and reaction time also did not distinguish across the main factors of reward and target error (Appendix B2-3).

2.3.3 Acquisition

2.3.3.1 Hand Angle Error

During clamped acquisition trials (65-464), as shown in Figure 2A, participants adapted to the clamped cursor as evidenced by increasing hand angle errors across trial (β = 7.88, SE = 0.91, *p* < .001, R^2_{sp} = 0.039). Importantly, there was a main effect of reward (β = 2.52, SE = 1.15, *p* = .03, R^2_{sp} = 0.013), where participants with reward feedback (M = 10.63°, SD = 12.06) surprisingly exhibited larger hand angle errors compared to participants without reward feedback (M = 7.29°, SD = 9.89; see Figure 2B). There was also a main effect of target error (β = -3.15, SE = 1.15, *p* = .008, R^2_{sp} = 0.024; see Figure 2C). As expected, participants in the 'miss' groups (M = 9.96°, SD = 11.98) adapted more than those in the 'hit' groups (M = 7.71°, SD = 9.95). There was no Reward x Target Error interaction (β = 3.61, SE = 2.29, *p* = .12, R^2_{sp} = 0.008).

The extent of adaptation during acquisition differed between the four targets (β = -1.29, SE = 0.44, *p* = .01, R^2_{sp} = 0.024). Compensation to the clamped cursor was lower at the 315° target (M = 3.58°, SD = 9.42) and the 135° target (M = 5.22°, SD = 10.13) compared to the 45° target (M = 14.64°, SD = 10.91) and the 225° target (M = 10.71°, SD = 10.13) (all *p*s < .01). Target-specific adaptation is illustrated in Figure C1 in Appendix C.

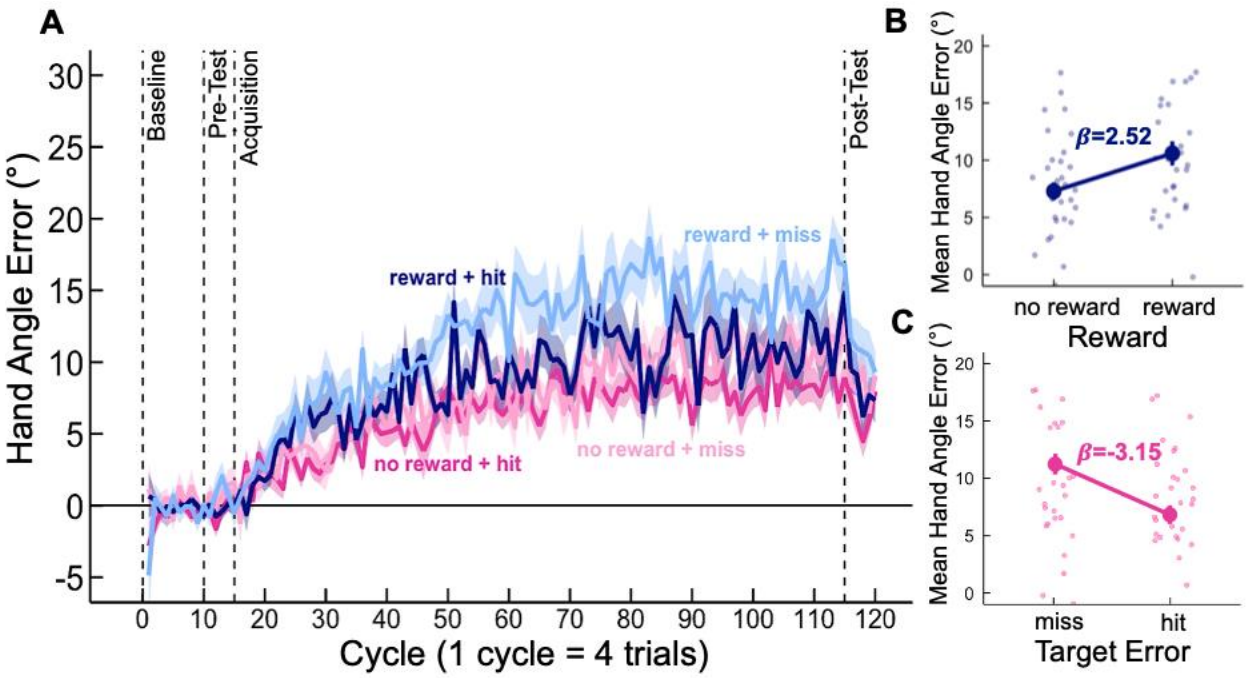

Figure 2. A) Averaged hand angle error (coloured lines) by group and over movement cycles containing four trials each for the full experiment. Shaded ribbons correspond to SEM. B) Mean difference in hand angle error between reward groups across acquisition trials. Large circles represent group means and small circles subject means. Error bars indicate SEM. C) Mean difference in hand angle error between target error groups across acquisition trials. Large circles correspond to group means and small circles to subject means. Error bars indicate SEM.

2.3.3.2 Peak Velocity and Reaction Time

Contrary to expectations, we did not find evidence for differences in movement speed between reward groups (β = -3.37, SE = 0.48, p = .49, R^2_{sp} = 0.002). Neither were there differences in velocity based on target error (β = 5.22, SE = 4.81, p = .28, R^2_{sp} = 0.004) or a Reward x Target error interaction (β = -11.08, SE = 9.63, p = .26, R^2_{sp} = 0.004). Movement speed did show differences between targets (β = -2.94, SE = 0.43, p < .001, R^2_{sp} = 0.006), with slower peak velocities for movements to the 45° target (M = 118.3 cm/s, SD = 45.5) and the 225° target (M = 120.0 cm/s, SD = 44.6) compared to movements to the 135° target (M = 103.8 cm/s, SD = 40.5) and the 315° target (M = 100.8 cm/s, SD =

26.7), all *p*'s < .0001. Reaction time was however sensitive to reward during acquisition (β = 76.12, SE = 17.30, p < .0001, R^2_{sp} = 0.040), where participants who received reward feedback (M = 460.0 ms, SD = 226.6) reacted slower than those who did not (M = 387.0 ms, SD = 139.1). There were no differences in reaction time between target error groups (β = 11.05, SE = 17.30, p = .53, R^2_{sp} = 0.001) and there was no interaction (β = -37.45, SE = 34.61, p = .28, R^2_{sp} = 0.003). LME output tables for movement speed and reaction time can be found in Appendix C2-3.

2.3.3.3 Variable Error

As a measure of consistency throughout acquisition, we measured variable error (VE) within 10 acquisition blocks (i.e., 40 trials/block) for every participant, as illustrated in Figure 3A. Reward significantly impacted VE (β = 1.82, SE = 0.88, *p* = .04, R^2_{sp} = 0.045), with higher VE in reward groups (M = 8.82°, SD = 5.05) compared to no-reward groups (M = 7.03°, SD = 3.29). There were no group-level differences in VE due to target error (β = 0.69, SE = 0.88, *p* = .43, R^2_{sp} = 0.007) and no Reward x Target Error interaction (β = -2.66, SE = 1.76, *p* = .13, R^2_{sp} = 0.024). Across groups, VE increased with time as evidenced by a significant positive slope of variable error over acquisition blocks (β = 3.49, SE = 0.56, *p* < .01, R^2_{sp} = 0.055) (Figure 3B). Model summary tables for the variable error analysis can be found in Appendix C4.

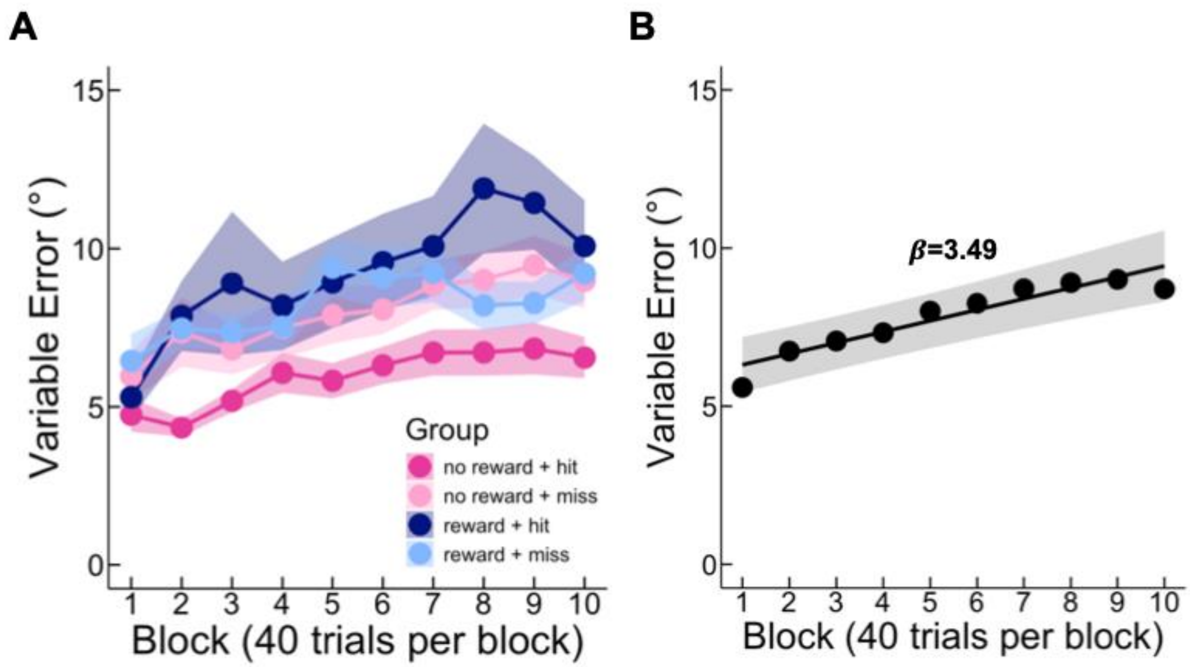

Figure 3. A) Mean variable error (VE) by group and over blocks containing 40 trials each during acquisition (400 trials). Coloured circles correspond to group-mean VE/block and shaded ribbons indicate SEM. B) Model-estimated slope of VE over acquisition blocks and averaged across groups (black line). Black circles correspond to mean VE/block across groups and grey shading represents 95% confidence interval.

2.3.3.4 Success

Surprisingly, participants had a low % of success across acquisition blocks and groups (M = 12.88%, SD = 13.9), as illustrated in Figures 4A-D. On average, success declined by ~13 % throughout acquisition (β = -13.07, SE = 3.67, p = .001, R^2_{sp} = 0.075). This pattern prevailed at the group (Figure 4A) and participant level (Figure 4D). We did not observe a significant main effect of target error (β = -6.79, SE = 3.76, p = .08, R^2_{sp} = 0.06), but visual inspection of group-mean success over acquisition blocks indicated that participants in the 'target hit' group (M = 16.14%, SD = 15.15) had a higher mean % success than participants in the 'target miss' group (M = 8.91%, SD = 11.28; Figure 4A). For a complete model summary of the success analysis, refer to Appendix C5.

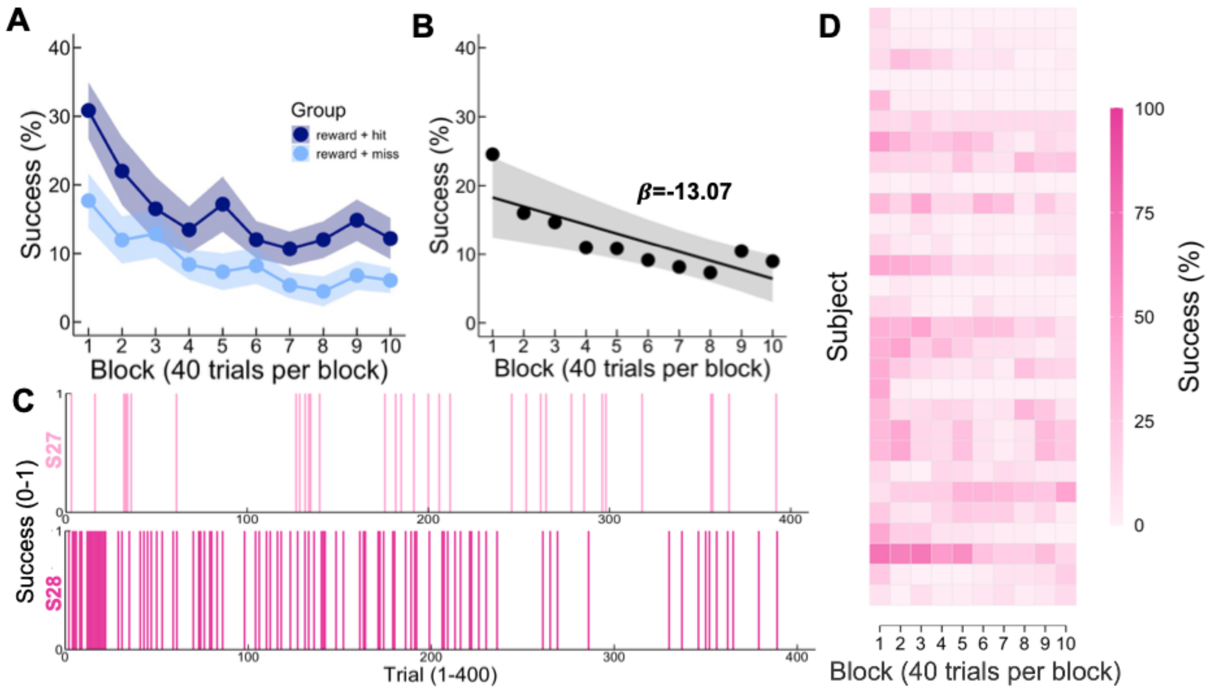

Figure 4. A) Group-mean success percentage per acquisition block between participants in the 'target hit' and 'target miss' groups. Coloured circles represent group means and shading indicates SEM. B) Model-estimated slope (black line) of success percentage over acquisition blocks and across groups. Black circles correspond to block mean success percentage across groups and grey shading illustrates 95% confidence interval. C) Individual success data from two representative participants (S27 & S28). Top row: S27 (target hit group), 8.25% average success. Bottom row: S28 (target miss group), 22.50% average success. Coloured bars indicate successful trials. D) Mean success at the subject-level by acquisition block. Every row on the y-axis corresponds to an individual participant. More successful blocks are highlighted with darker shading.

2.3.3.5 Hand Angle Change

To characterize how reward signals impacted adaptation on a trial-by-trial basis, we calculated the change in hand angle error (Δu_t) from trial t-1 to trial t after successful and non-successful trials for participants in the reward groups (i.e., 'reward + target hit', 'reward + target miss'):

$$\Delta u_t = u_t - u_{t-1}$$

where u_t corresponds to the hand angle error observed at trial t and u_{t-1} indicates the hand angle error at the previous trial t-1.

Success at trial t-1 significantly impacted reach direction at trial t (β = 8.88, SE = 1.17, $p < .001$, R^2_{sp} = 0.052), as illustrated in Figure 5A. Across trials, participants exhibited large changes in hand angle error compensating for the clamped cursor (i.e., reaching away from the reward region) after successful trials (M = 7.13°, SD = 11.71). In contrast, they adjusted their reaches in the opposite direction following non-successful trials (M = -1.46°, SD = 14.64). However, the direction of the observed effect must be interpreted with caution because we know that participants did not adapt consistently between reaching targets, thereby distorting the calculation of hand angle change.

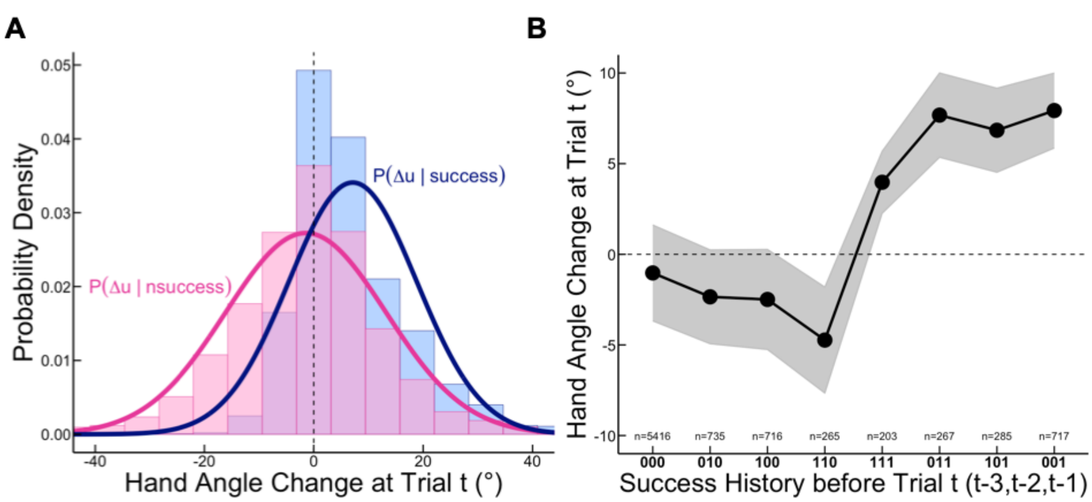

Figure 5. A) Probability density distributions for hand angle changes at trial t after successful (blue) and non-successful (pink) trials. For illustrative purposes only, we used the estimated mean and standard deviation obtained in our hand angle change data to generate smooth Gaussian curves and probability density values across the observed range of values (histograms). Generated values were only used for visualization of the distributions and not considered for statistical analysis. B) Mean hand angle change at trial t (black circles) as a function of success history on the preceding three trials (digit triplets in bold font by the x-axis). The number of observations available for analysis per success history is indicated in black text above the corresponding triplet. Grey shading indicates SEM.

To assess whether participants changed their reach directions in response to reward prediction errors, we assessed whether success history of the previous three trials (t-3, t-2, t-1) impacted hand angle change at trial t. That is, we predicted hand angle change from a factor ('success history') that contained a level for each triplet of possible success outcomes (i.e. 8 factor levels) during the three trials preceding trial t (Figure 5B).

Success history generally influenced hand angle changes (β = 1.31, SE = 0.17, p < .01, R^2_{sp} = 0.042). Consistent with our analysis of success outcome at the previous trial, success outcome triplets with success at trial t-1 (i.e., "1,1,1", "0,1,1", "1,0,1", "0,0,1") all resulted in large changes in hand angle error compensating for the clamped cursor, whereas triplets with no success trial t-1 (i.e., "0,0,0", "0,1,0", "1,1,0", "1,0,0") were followed by corrections in the opposite direction (all p's < .05). Hand angle changes did not differ statistically between triplets with the same success outcome at trial t-1. Summary tables for hand angle change model outputs can be found in Appendix C6-7.

Note that all hand angle change analyses are limited by an imbalance in the number of observations across conditions, with more non-successful than successful trials as highlighted in Figure 4D. This discrepancy reduces the reliability of estimates derived from successful observations and may affect comparisons with estimates from non-successful observations.

2.3.4 Post-Test (Immediate Retention)

As shown in Figure 2A, there were no statistical differences in aftereffects (i.e., first four trials of the post-test) due to reward (β = 1.80, SE = 1.67, p = .28, R^2_{sp} = 0.007) or target error (β = 1.88, SE = 1.67, p = .26, , R^2_{sp} = 0.007) and there was no Reward x Target

Error interaction (β = 1.71, SE = 3.33, p = .61, R^2_{sp}= 0.002). The corresponding LME model summary can be found in Appendix D1.

Similarly, in the analysis of relative retention (i.e., 2 Reward x 2 Target Error, between-participants ANOVA), we did not detect main effects of reward (F (1, 55) = 0.206, p = 0.65, partial η^2 = 0.00) or target error (F (1, 55) = 0.026, p = 0.87, partial η^2 = 0.00) and the Reward x Target Error interaction was not significant (F (1, 55) = 0.167, p = 0.68, partial η^2 = 0.00).

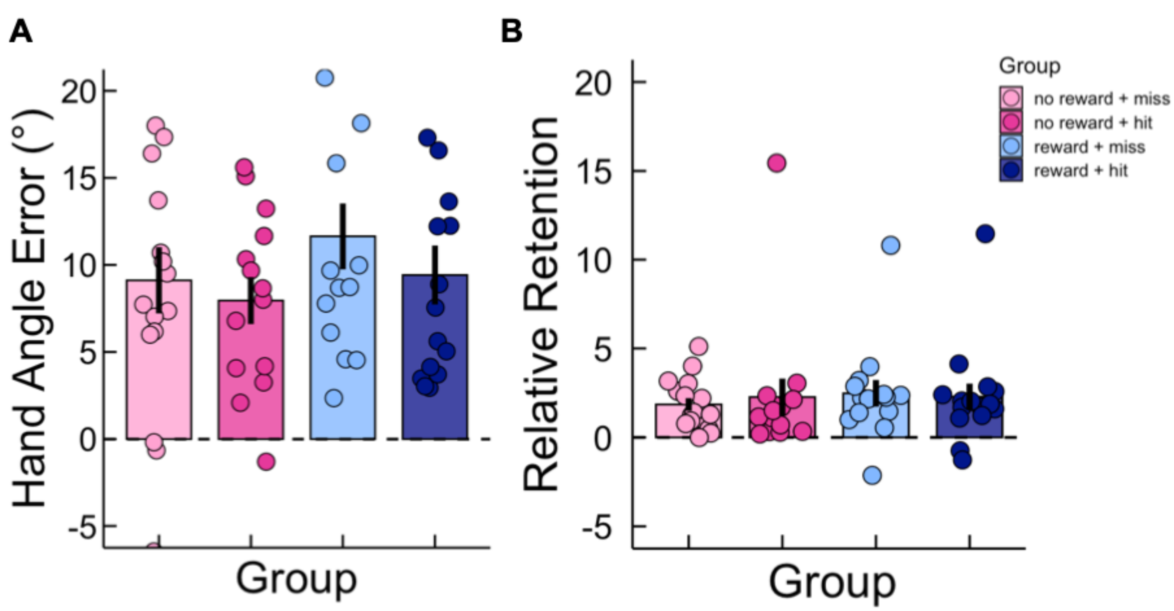

Figure 6. A) Aftereffects. Group-mean hand angle error (coloured bars) during the first four post-test trials (i.e., movement cycle 116). Black lines indicate SEM and coloured circles corresponding to participant means. B) Relative retention. Coloured bars indicate the group-mean ratio of the participant-specific mean hand angle error during the final movement cycle of acquisition (i.e., trials 461-465) to the mean hand angle error during the final movement cycle of the post-test (i.e., trials 481-484). Coloured circles represent participant means and black error bars indicate SEM.

2.3.5 Surveys

2.3.5.1 IMI

We accounted for task-related engagement by scoring and summing participants' responses to the "Interest/Enjoyment" and "Effort/Importance" subscales from the Intrinsic Motivation Inventory (IMI) into a single score. We first evaluated group-level differences in IMI score in a simplified analysis (2 Reward x 2 Target Error, between-subjects ANOVA). In a second step, we went back to our LME model for hand angle error during acquisition, and tested model fit with the grand-mean centered IMI score as a continuous predictor.

IMI scores were higher in the reward groups (M = 60.4 score, SD = 10.49) than no-reward groups (M = 49.6 score, SD = 11.38), $F(1, 56) = 14.3$, $p < .01$, partial $\eta^2 = 0.20$. These data are additionally illustrated in Figures 7A and B. There were no differences between target error groups ($F(1, 56) = 0.002$, $p = 0.97$, partial $\eta^2 = 0.00$) and no Reward x Target Error interaction ($F(1, 56) = 1.76$, $p = 0.19$, partial $\eta^2 = 0.03$).

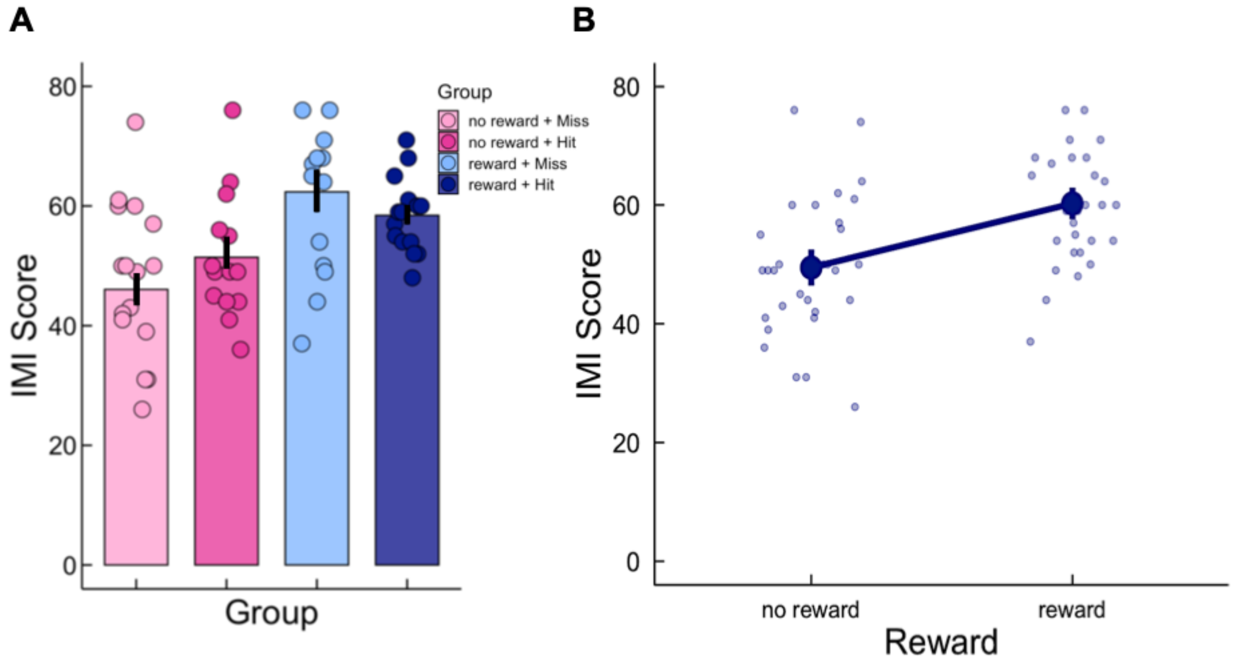

Figure 7. A) Group-mean IMI scores (coloured bars). Coloured circles represent subject means and black lines indicate SEM. B) Main effect of reward. Large circles correspond to group mean IMI scores by reward group and averaged across target error. Small circles represent corresponding subject means. Lines indicate SEM.

When we included IMI score as a predictor in the original model for hand angle error during acquisition, there was a reduction in the model-estimated slope of reward and the corresponding total variance explained for this factor (β = 1.86, SE = 1.24, *p* = .14, , R^2_{sp} = 0.006; Appendix E1), relative to the original model (β = 2.52, SE = 1.15, *p* = .03, , R^2_{sp} = 0.013; Appendix C1). However, IMI alone did not significantly impact hand angle error (β = 0.06, SE = 0.04, *p* = .16, , R^2_{sp} = 0.004) and model fit was not improved in comparison to the original model when we included IMI score as a fixed effect, as informed by the Akaike Information Criterion ($AIC_{original}$ = 131922.7 vs. AIC_{IMI} = 131927.2). Extending the original model by adding IMI, only impacted the model-estimated effect of reward and did not cause noteworthy changes to other predictors (Appendix E1).

2.3.5.2 SPSRQ

To assess group-level differences in sensitivity to reward, we ran a 2 Reward x 2 Target error, between subjects ANOVA. In a second step, we added grand-mean centered reward sensitivity score as continuous predictor to the original LME model for hand angle error during acquisition (Appendix E2).

We did not observe any group-level differences in reward sensitivity ($F(1, 56) = 0.75$, $p = .39$, partial $\eta^2 = 0.01$), target error ($F(1, 56) = 1.35$, $p = .25$, partial $\eta^2 = 0.02$), and no Reward x Target Error interaction ($F(1, 56) = 0.80$, $p = .37$, partial $\eta^2 = 0.01$). Including reward sensitivity as a predictor in the acquisition hand angle error model did not change the original pattern of results (Appendix E2).

2.4 Discussion

The overarching aim of Experiment 1 was to test whether extrinsic reward makes a distinguishable contribution to implicit sensorimotor adaptation during reaching movements. We investigated this issue by dissociating target error and extrinsic rewards as participants performed goal-directed reaches to a clamped cursor rotation. Specifically, the clamped cursor either hit or missed the target (i.e., target error groups) and we either rewarded or did not reward participants for directing their physical reaches into a reward region around the target with points and a target explosion (i.e., reward groups). In our pre-registered predictions, we argued that target error and extrinsic reward exert distinct effects, because these signals convey different information despite having been used interchangeably in previous work. In particular, we argued that implicit adaptation should be attenuated when target error is absent (Loew et al., 2018; Kim et al., 2019) and when extrinsic rewards are provided, as both signals indicate correct performance in this case.

We also thought that reward would impact reaction time and movement speed. That is, increased movement speed and decreased reaction time could hint at a reward-based modulation of motor vigour (Summerside et al., 2018). Yet, reaction time could also lengthen because reward may encourage extended planning of subsequent movements (Georgopoulos & Massey, 1987). We also expected inflated movement exploration in reward groups, evidenced by increased variable error relative to no-reward groups and larger trial-by-trial hand angle changes following non-rewarded versus rewarded trials (Pekny et al., 2015).

We replicated previously reported effects of target error on implicit adaptation (Loew et al., 2018; Kim et al., 2019). Across acquisition, hand angle errors were attenuated in groups where the clamped cursor hit a larger reaching target relative to groups where the cursor missed a smaller target. These findings align with previous notions that sensory prediction errors and target errors both contribute to adaptation in an interactive 'dual-error model' (Kim et al., 2019). In this model, implicit recalibration is primarily driven by sensory prediction error processing (Mazzoni & Krakauer, 2006) but also scales with target error under the premise that a sensory prediction error is present (Tsay et al., 2022).

All groups showed aftereffects of a magnitude of ~10 degrees. Contrary to previous work (Loew et al., 2018), however, hand angle errors during acquisition did not result in differences in immediate post-test measures of aftereffects or relative retention between target error groups. That is, even though target error impacted trial-wise adaptation, our results suggest that target error did not significantly influence how participants updated their internal reaching representations. A plausible reason for this might be that the authors in Loew et al. (2018) manipulated target error by displacing the reaching target during movement with a target jump, whereas we relied on two targets of different sizes. Even though researchers showed that target jumps can elicit neural responses indicative of target error processing and contribute to adaptation on a trial-by-trial basis (Diedrichsen et al., 2005), displacing reaching targets during movement can distract participants from processing of task-relevant sensory feedback (Tsay et al., 2022). Further, Loew et al. (2018) only reported absolute measures of retention despite large group-level differences in the extent of adaptation during acquisition. Thus, it is possible that a measure of relative retention could have moderated the effect of target error on implicit aftereffects reported by Loew et al., (2018). This would be consistent with the results observed in this study and those presented by Kim et al. (2019) who found that group-level differences in retention due to target error disappeared in a measure of relative retention. Unlike previously reported (e.g., Galea et al., 2015), we did not see any group-level differences in aftereffects or relative retention due to reward which aligns with the idea that learning from reward does not elicit remapping of sensory estimates (Izawa & Shadmehr, 2011).

Extrinsic rewards did have unique impacts on implicit adaptation during acquisition, but in a way that was contrary to our predictions. Reward groups compensated for the clamped cursor with augmented hand angle errors compared to no-reward groups. This was a counterintuitive result as we only rewarded accurate reaches to the target and explicitly instructed participants to ignore the clamped cursor (Morehead et al., 2017). Thus, at least conceptually, we incentivised participants to repeat performances for which they did not elicit an adaptive response. In doing so, we tested whether participants could 'overwrite' adaptation to the clamped cursor via reinforcement mechanisms. Yet, our results suggest the opposite. Simultaneous presentation of consistently rotated sensory feedback modulated the participants‘ ability to rely on reward signals to maintain their reaches on target and maximise monetary gain. This modulation was further evidenced by a decline in the percentage of successful trials over acquisition cycles in both reward groups.

It has previously been argued that the brain prioritizes sensory information over reward to update internal motor representations during adaptation when both signals are available (e.g., Izawa & Shadmehr, 2011). Even though computational architectures, such as the ‘optimal learner model’ (Izawa & Shadmehr, 2011), offer an explanation as to why participants were unable to overwrite or ignore the clamped feedback, they cannot account for the reward-based amplification of adaptation we observed. A limitation of the optimal learner model in this regard is the assumption that reward and sensory prediction error make additive contributions to the selection of new motor outputs. If this were the case, reward should have attenuated adaptation in our study, because reward signals and sensory prediction error were conceptualised to exert opposing influences on behavioural responses (i.e., SPE and rewards would encourage different behaviours). In an additive model, this directional conflict would have reduced the net error compensation composed of the summed contributions of both reward and sensory prediction error, resulting in reduced adaptation in reward groups. Instead, reward amplified error correction when presented concurrently with clamped sensory feedback.

Rather than additive effects of reward and SPE, our results hint at a process where reward augmented the solution computed by the motor system to compensate for the observed sensory error. A similar mechanism has been brought forward to explain how intrinsic reward (i.e., target error) impacts adaptation (e.g., Kim et al., 2019; Tsay et al., 2022). For example, Kim et al. (2019) proposed an ‘adaptation modulation model’, where reward does not make an additive contribution but rather acts as a gain controller of adaptation to an imposed sensory error. Importantly, the authors only tested the adaptation modulation model through manipulations to intrinsic reward (i.e., target error). However, because here we show that target error and extrinsic reward contribute to the adaptive process differently, it is possible that the observed effect of extrinsic reward could also be described by the adaptation modulation model. Congruent with this proposition, trials where participants in the reward groups successfully reached to the target, as indicated by an extrinsic reward, were followed by a large compensatory change in reach direction responding to the cursor-induced error on the next trial. In contrast, participants only made small adjustments to their reaches in the opposite direction after non-successful trials when no extrinsic reward was presented. We confirmed this pattern remained stable when considering not only success on the previous trial, but also the combination of success outcomes across the three trials leading up to a given action. The observation that compensatory behaviour increased after rewarded trials violates a fundamental assumption of reinforcement processes, namely that action policies leading to successful outcomes should be favoured and repeated on subsequent trials whereas non-successful outcomes should incentivize purposeful exploratory behaviour (Sutton & Barto, 2018; Pekny et al., 2015).

The assessment of reward-based effects at the single-trial level must be qualified. That is, hand angle change was calculated across reaching targets as participants switched between targets on almost every trial. Therefore, the direction of the observed effect must be treated with caution because we know that the extent of adaptation differed between reaching targets. For example, if a participant successfully reached to the 45°-target on trial t (within ±2.5° of target centre), but then on trial t+1 reached to the 315°-target, where they already developed a strong directional bias away from the target due to the clamp, Δu_t would be inflated, independent of the success outcome at trial t.

Despite the counterintuitive finding that changes in reach directions were seemingly greater after successful than non-successful reaches, our data generally support the widely accepted notion that reward-based learning increases movement variability or exploratory behaviour, as evidenced by greater variable error in groups that could earn rewards (e.g., Dam & Körding, 2009; Van Mastrigt et al., 2020; Wu et al., 2014; Izawa & Shadmehr, 2011; Pekny et al., 2015).

An alternative explanation as to why reward augmented adaptation could lie in our task design. In contrast to similar trial-by-trial analyses from previous work where the authors described reaching behaviour to a single target (e.g., Pekny et al., 2015; Holland et al., 2018), we used four targets (replicating Kim et al., 2019). When learners compensate for perturbations using reward feedback alone, success at one target could interfere with learning the same perturbation at another target, resulting in delayed or impaired adaptation. Similar between-target effects have been termed 'destructive interference' (Darshan et al., 2014). Even though participants received both clamped feedback cursor and reward in our task, they were explicitly informed that the visual clamp was performance-independent and thus not informative for achieving accuracy. Therefore, it is possible that the counterintuitive direction and magnitude of hand angle changes between trials observed in our study were the result of reward-based interference between targets.

We also looked at measures of speed (to respond and to act) to test ideas that reward modulates motor vigour (Summerside et al., 2018). Neither movement speed (i.e., peak velocity) nor reaction time became faster with reward. Instead, reaction times slowed down when rewards were given during acquisition. We suspected that the increase in reaction time was the result of increased movement preparation (Georgopoulos & Massey, 1987). This assumption aligns well with past research showing that reaction times slowed down when reward certainty declined (Opris et al., 2011), which could be a consequence of increased strategic processing after trials where no reward is obtained. Even though we did not manipulate reward certainty in our study, we know that participants generally struggled to obtain rewards. Thus, it is possible that a performance-based deterioration of reward certainty caused a delay in movement onset, potentially reflecting more elaborate computations required for selecting from a set of equally 'unattractive' motor actions in terms of maximizing reward.

Reward-related differences in adaptation could have been the result of increased task engagement due to an enriched environment (e.g., Lohse et al., 2016). That is, the addition of gamified features in the visuomotor task (i.e., display of points and target animations) may have incentivised participants in reward groups to perform the task more effortfully, with increased attention and motivation (Lewthwaite & Wulf, 2010). Indeed, we found that task engagement, inferred through measures of task enjoyment and interest from the Intrinsic Motivation Inventory (IMI), was higher in groups that received the enriched reward feedback. When we included IMI score as a predictor in the multilevel model analysis of hand angle error during acquisition, the effects of reward were attenuated, indicating overlap in the variance explained by reward and task engagement. Yet, unlike others (e.g., Lohse et al., 2016), higher levels of reward-driven engagement did not unambiguously benefit learning in our study, as evidenced by a lack of group-level differences in immediate retention measures. Given that we did not take any measures of delayed retention, we cannot determine with certainty how task engagement may have impacted learning in our study.

3. Experiment 2

3.1 Introduction

In Experiment 1, we replicated previous work showing that implicit adaptation was attenuated when target error was removed through a manipulation of target size. However, we also observed an unexpected contribution of extrinsic reward to implicit adaptation. Even though we rewarded some participants for accurately reaching to a target, they were unable to maintain their reaching in the direction that maximized reward. Contrary to predictions, the reward group showed a larger adaptive response to a clamped cursor rotation compared to the no-reward group.

The results from Experiment 1 provide evidence for my thesis that extrinsic reward and target error make dissociable contributions to implicit adaptation. However, Experiment 1 was designed to test an apriori hypothesis that extrinsic reward would attenuate adaptive responses to the clamped cursor feedback. Although we had good evidence that reward actually exacerbated implicit adaptation, there were some design features that could potentially explain the surprising nature of the reward-related effects, especially in view of prior predictions. Moreover, given the different pattern of results, replication of this effect was necessary.

One feature that may explain the pattern of data is related to the frequency of rewards. Because participants in reward groups exhibited strong implicit adaptation, thereby predominantly missing the reward region, their average success percentage (~13%) was below the range of success percentages that have previously been proposed to optimize reward-based motor learning (e.g., 50%, van der Kooij et al., 2026; 70%, Al-

Fawakhiri et al., preprint). Further, as evidenced by a decrease in success over time, the majority of rewarded observations available for data analysis occurred early in adaptation. This could have confounded the observed effect of reward with well-established properties of adaptation during early learning. That is, the large changes in hand angle error after rewarded trials could also be attributed to the generally increased rate of implicit learning at this stage. A second feature of the design that may have contributed to these data was the need to aim to four targets, with a switch to a new target on almost every trial. The observed changes in reach directions after successful and non-successful trials could have been confounded by interference between reinforcement mechanisms at several reaching targets. This concern was supported by the observation that the overall extent of adaptation differed between targets in our study.

Altogether, these considerations limit our ability to come to firm conclusions about how extrinsic reward impacted implicit adaptation. Therefore, we further tested these effects of reward in a second study, with modified task specifications and procedures designed to resolve concerns from Experiment 1. In a within-participants design, we restricted the task to a single target, to examine whether participants can maintain a reinforced reach direction. To help control for the possibility that reward-based changes in adaptive responses are time-dependent properties of adaptation to a clamped cursor (such as increased early learning rates or asymptotic behaviour; e.g., Morehead et al., 2017), clamped feedback was pseudo-randomly presented. The clamp varied in magnitude and direction, such that the mean error remained stable at 0°, thereby also controlling for comparable quantities of success between participants. We employed an interleaved schedule combining clamped feedback trials with veridical feedback and no-vision trials, such that each clamped trial was followed by a no-vision trial. This design provided a more stable assessment of trial-to-trial changes, as compensatory behaviour during no-vision trials only occurred in response to the clamped error experienced on the preceding trial. We maintained the extrinsic reward paradigm from Experiment 1, where participants were rewarded when they intersected the reward region around the target. In addition, we included clamped errors of different magnitudes to reveal the computational relationship between reward and observed sensory error. That is, if reward acts as a gain controller on the motor system's response to the previously observed sensory error, the scaling factor distinguishing rewarded from non-rewarded clamped trials should be similar across different error magnitudes.

Based on the results obtained in Experiment 1, our pre-registered predictions were that error compensation during no-vision trials will be elevated when the preceding clamped trial is paired with reward, compared to when it is not. However, we also entertained the possibility that reward would attenuate error compensation, because now participants only reach to a single target. Attenuation would indicate that the reward-based augmentation in Experiment 1 was due to interference from reaching to multiple targets and in particular, switching to a new target on almost every trial. It was also possible that differences in adaptation between reward and no-reward groups were due to task engagement. Hence, moving to a fully repeated-measures design, where all participants experienced the enriched task environment (i.e., reward stimuli), would now remove the effects of reward if due to increased task engagement.

3.2 Methods

3.2.1 Participants

We recruited a new sample of 30 right-handed participants (17 Females, 12 Males, 1 Non-Binary; M_{Age} = 23 ± 5 yr), with no known neurological conditions, normal or corrected to normal vision, and fluent in English. Handedness was verified for each participant with the Edinburgh Handedness Inventory (Oldfield, 1971). For recruitment, we relied on social media posts, online advertising, emails, and posters. Participants were compensated $20 for participation and gave written and verbal informed consent. The experimental procedures were approved by the University of British Columbia's ethics' committee and were in accordance with the Declaration of Helsinki.

We estimated the required sample size for a within-subjects design in an empirical a priori power analysis for multilevel regression models using the 'mlmpower' package (Enders et al., 2023) in R. The 'mlmpower' package requires partitioned R^2 effect sizes (Rights & Sterba, 2018), intraclass correlations (ICC), and variable weights as inputs for the power analysis (Enders et al., 2023). The primary comparison of interest in Experiment 2 was the effect of extrinsic reward on error compensation. Because we tested a similar effect in Experiment 1, we were able to extract (using the 'r2MLM' package, Rights & Sterba 2018), a partitioned effect size of $R^2 = 0.022$ from these data. Since we also investigated the effect of error clamp size in Experiment 2, we identified an effect size of $R^2 = 0.138$, from a study by Matsuda and Abe (2023), where the authors obtained a significant main effect of clamp error magnitude (i.e., 3°, 6°, 12°) on error compensation. Due to higher complexity in our model (i.e., Matsuda and Abe, 2023 only investigated the effect of clamp magnitude, whereas we also examined the effect of reward) and because we only obtained a small effect size for reward in our previous analysis, we chose the more conservative estimate of $R^2 = 0.022$ for the proportion of total variance explained by the within-subject predictors. Further, we distributed the weights of each predictor, such that reward accounted for a smaller proportion (reward = 0.4) relative to error magnitude (0.6) and set the ICC to 0.4 (based on the model for the reward R^2-estimate). We chose the remaining 'mlmpower' inputs based on recommendations of Enders et al. (2023). We ran 2000 Monte Carlo simulations for sample sizes of n = 24, 26 and 28 (i.e., 2000 simulations per sample size) to obtain power estimates, which represented the proportion of simulated datasets (out of 2000) that produced a significant p-value < .05 for each within-subjects predictor. For n=24 participants, we obtained power estimates of 72% and 96% for the effect of reward and error size respectively. At n=26, these estimates increased to 76% and 97%. For a sample size of n=28, the simulation indicated 80% for the effect of reward and 98% power for the effect of error size. To account for potential data loss, we aimed for a slightly higher recruitment goal of n=30 participants.

3.2.2 Apparatus

We did not make any changes to the desk setup and apparatus used in Experiment 1. However, we modified the original Python script in PsychoPy (PsychoPy, Open Science Tools Ltd., United Kingdom) (Pierce et al., 2019) to accommodate for changes in reaching task specifications and procedures as outlined below.

3.2.3 Reaching Task

To ensure consistency, we kept reaching task procedures similar between Experiment 1 and 2. Thus, we only report changes to stimuli and design in this section.

Participants now performed planar reaches to a single target (6mm diameter). The target was located at 225° on a circular perimeter (0° corresponds to centre-out straight reaches) surrounding the reference circle at a radial distance of 8 cm. We specifically chose the 225° target for Experiment 2 as it was most representative of the reaching behaviour observed in Experiment 1 (i.e., smallest target-specific deviation from the overall mean of adaptation when calculated across all four targets).

For clamped trials, the cursor followed a movement-independent trajectory resulting in deviations of 0°, ±3.5° and ±7.5° to the target, whereby the direction for each error magnitude was pseudo-randomized across trials between clockwise (positive) and counterclockwise (negative) rotations. For consistency, we maintained the 3.5° -clamp from Experiment 1. The additional error magnitude of 7.5° was based on previous work demonstrating reliable scaling of immediate adaptive responses with increasing error magnitude. For example, Matsuda and Abe (2023) observed greater error compensation in response to a 6°-clamp compared to a 3°-clamp. Notably, the error magnitude of 7.5° falls into a 'saturated' zone where immediate adaptive responses to a clamped cursor remain consistent with increasing error magnitude (Kim et al., 2018). This saturation effect has been estimated to occur for any clamped error with an error magnitude greater than 4.4°. In contrast, for clamped errors below 4.4° (i.e., proportional zone), error compensation is thought to scale reliably with increasing error magnitude. Thus, our manipulation included both an error magnitude within the saturated zone (i.e., 7.5°-clamp), and an error magnitude within the proportional' zone (i.e., 3.5°-clamp). All participants received the same extrinsic reward feedback, based on the same reward region, as in Experiment 1. Rewards were now given on veridical and clamped trials.

3.2.4 Procedure

All participants were tested in every phase of the experiment in a within-participants design as illustrated in Figure 8. At the start of the experiment, participants completed a practice phase consisting of 60 trials with veridical cursor feedback. The practice phase was followed by two baseline blocks consisting of 60 trials each. During Baseline I (i.e., trials 61-120) we familiarized participants with performing the task without cursor feedback (i.e., no-vision trials). Before Baseline II (i.e., trials 121-200), participants were briefed about the reward feedback and incentivized to accumulate as many points as possible. Both veridical cursor feedback and extrinsic reward were enabled for Baseline II. We decided to add this second baseline block in Experiment 2 to demonstrate, via the veridical cursor, when reaching performances resulted in a reward (i.e., when the physical reach intersected the target).

After completion of the baseline phase, using a pre-specified script, the experimenter introduced the clamp perturbation and instructed participants to reach directly to and through the target, thereby ignoring the clamped error. The experimenter further informed participants that, independent of their movement, the direction and magnitude of the clamped cursor would vary randomly between trials (see Matsuda & Abe, 2023). In addition, participants performed four demonstration trials with the clamped feedback enabled. During these demonstration trials, participants were directed to make reaching movements in four different directions (0°, 90°, 180°, and 270°), with the target always appearing at 225° and the clamped feedback being set to 3.5° degrees, consistently missing the target. These trials served to alert participants to the movement-independent nature of the clamped feedback and they were not included in any analyses.

Unlike in Experiment 1, to help participants identify clamped feedback trials, the cursor changed colour on movement initiation. This way we ensured that adaptive responses following clamped trials were not due to some failure to realize that the clamp was independent of movement, potentially causing an explicit compensatory strategy during subsequent no-vision trials.

We increased the number of trials relative to Experiment 1, where participants performed 100 reaches per target under clamped conditions (i.e., 400 clamped trials in total). The adaptation phase in Experiment 2 consisted of 800 trials despite participants only reaching to a single target. There were 400 veridical, 200 clamped, and 200 no-vision trials. The five clamped error magnitudes (i.e., 0°, ±3.5°, ±7.5°) were presented in a pseudo-randomized manner, such that each error magnitude was presented 40 times each to give 200 trials. This procedure was designed to ensure that the mean error remained at 0° over a 20-trial window. To obtain a clean estimate of implicit error compensation after clamped error trials, every clamped trial was directly followed by a no-vision trial. Clamped trials were always separated by a minimum of two other trial types (i.e., veridical or no-vision). Reward feedback was enabled during all veridical feedback trials. In contrast, reward feedback was interleaved on and off during clamped error trials, such that reward was omitted on half of these trials according to a pseudo-randomized schedule. That is, for every 10 clamped error trials, reward feedback was enabled on five randomly selected trials, to ensure balanced exposure throughout the experiment. Reward feedback was performance-contingent on both veridical and clamped trials (i.e., when physical reaches intersected the reward region around the target). Therefore, cursor and reward feedback were aligned during veridical trials but misaligned during clamped error trials, because the cursor always missed the target (with the exception of errors clamped at 0°). Reward feedback was not given on no-vision trials and participants were informed about this procedure.

After the adaptation phase, we confirmed, using a structured debrief, that participants understood and had attempted to comply with the task instructions (i.e., aimed directly toward the target throughout the experiment).

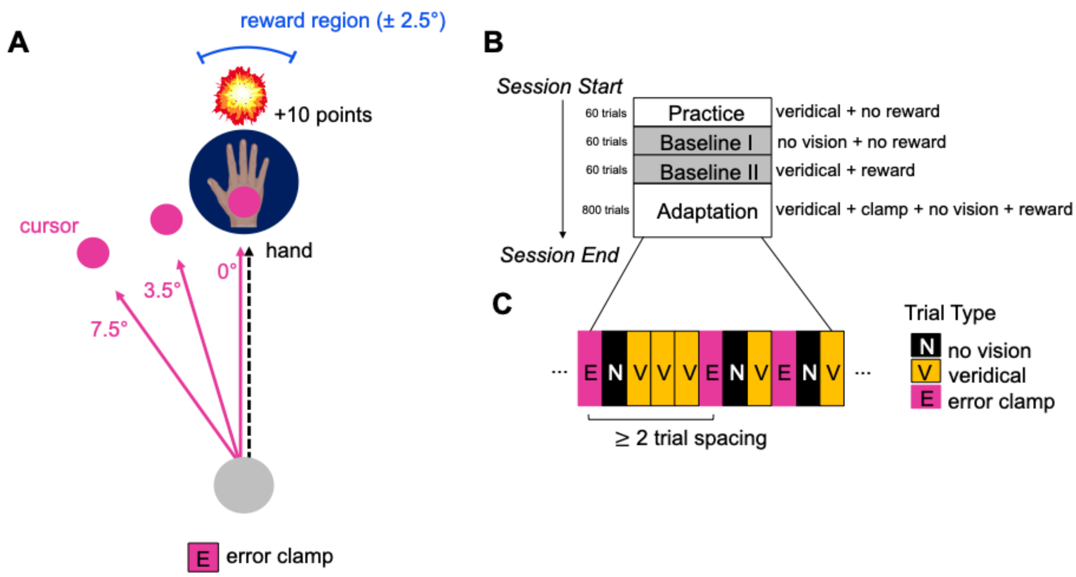

Figure 8. A) Feedback during clamped error trials. The clamped cursor will either hit the target (0°) or miss it by ±3.5° or ±7.5°. For visual clarity, we only included illustrations of clamped error feedback in the CCW (+) direction. B) Experimental procedure. C) Illustration of trial organization during adaptation phase. Clamped error trials are always followed by a no vision trial and spaced out by a minimum of two other trial types (i.e., no vision and veridical).

3.2.5 Data Analysis

3.2.5.1 Measured Variables

We measured hand angle error, reaction time, and peak velocity as previously defined (see 'Measured Variables', Experiment 1). However, the primary dependent variables in Experiment 2 were error compensation (EC_{te}) and hand angle change during no-vision trials. We defined EC_{te} as:

$$EC_{te} = NV_{te} - \mu NV_{0°}$$

where NV_{te} corresponds to the hand angle error observed in a no-vision trial *t* after a clamped error trial with an error size *e* (*e* = ±3.5°, ±7.5°), and $\mu NV_{0°}$ represents the participant-specific mean hand angle error during no-vision trials that followed clamped trials with a 0°-error. We calculated participant-specific error compensation in the adaptation phase for each error size *e* and also differentiated between error compensation following rewarded and non-rewarded performances. We further assessed whether error compensation patterns differed between directional values of *e* (e.g., -3.5° vs. +3.5°). We measured trial-to-trial hand angle change as a more direct measure of adaptation without subtracting the participant-specific mean response to the 0°-error. That is, this change score was defined as the difference between error in hand angle during a given clamped error trial (rewarded or non-rewarded) and the subsequent no-vision trial.

To capture trial-to-trial success when reward feedback was enabled (i.e., all veridical trials and 50% of clamped trials during the adaptation phase), we scored every trial where participants obtained a reward with “1” and every trial where participants failed to obtain a reward with “0”. As a measure of average success per participant, we calculated the percentage of rewarded trials across all veridical and clamped trials during Baseline II and the adaptation phase.

We took a baseline measure of movement variability, where we calculated variable error as the participant-specific standard deviation of hand angle error during no-vision trials in Baseline I (i.e., trials 61-120). In addition, we analyzed reward-based changes in movement variability by comparing variable error during no-vision trials after rewarded and non-rewarded reaches under clamped error feedback.

3.2.5.2 Pre-Analysis Data Processing

For statistical analysis, we adjusted the sign of error compensation and trial-to-trial hand angle change following clockwise (CW) and counter-clockwise (CCW) clamped errors. That is, observed compensatory responses in the opposite direction to the clamp were transformed into positive values. We accounted for potential differences between responses to either clamp direction by including a corresponding 2-level factor in our statistical analysis as outlined below. However, we also considered non-adjusted values for visualization purposes. Outliers were removed with the stats:filter function in R. Outliers were defined as hand angle errors beyond 90°. We removed trials where participants' movement time exceeded 300 ms.

3.2.5.3 Statistical Models

All statistical analyses were performed using a custom R script, where we fit linear mixed effect models using restricted maximum likelihood to analyze primary dependent variables (i.e., error compensation (EC_{te}), hand angle change), and secondary dependent variables (i.e., hand angle error, variable error, peak velocity, reaction time, trial success, success %) across trials, and experimental phases. Decisions about model fit were informed by the Akaike Information Criterion (AIC) and inspection of the random and fixed effects structure in the model output. To ensure comparable reports between Experiment

1 and 2, we report semi-partial R^2 as a measure of effect size. Once again, to indicate the relative size of the variance accounted for by individual predictors with the respect to the total variance captured by the models, we also report marginal and conditional R^2 in model summary tables in Appendices F-H (Edwards et al., 2008; Nakagawa & Schielzeth, 2013; Johnson, 2014). We employed adequate transformations when our data violated assumptions of normality, equal variance, or linearity. An alpha of $p < 0.05$ was considered statistically significant.

The primary dependent variables were error compensation (EC_{te}) and trial-to-trial hand angle change. Fixed factors included error magnitude (3.5°, 7.5°), clamp direction (CCW, CW), reward at the previous trial (reward, no reward), experimental phase (practice, Baseline II), and corresponding interactions. Where adequate, we added secondary predictor variables to the model, including baseline movement variability, defined as the variable error of hand angle errors during Baseline I (continuous), and trial (continuous). We set participant as our cluster variable (i.e., random factor) and allowed for random slopes for all within-subject predictor variables and their interactions (i.e., maximal model). When we faced convergence or singularity issues with the maximal model specification, we carefully broke down model complexity in the random and fixed effects without increasing the risk of pseudoreplication (e.g., Scandoli & Tidoni, 2024). Depending on the analysis of interest, we restricted our model to specific subsets of trials (e.g., the adaptation phase) using the stats:filter function in R.

We grand-mean centred and scaled error magnitude, clamp direction, reward, target success, and experimental phase (i.e., factor levels were coded to -0.5 and 0.5). This way, the model-estimated slopes of these variables (i.e., their β-estimates) represented the mean difference between their two factor levels in an ANOVA-like model output (e.g., Schad et al., 2020). When error compensation differed between CW and CCW rotations, clamp direction was included as an additional two-level (CW, CCW) in our model. Where applicable, we used Tukey HSD-corrected post hoc tests to break down significant interaction effects.

3.3 Results

3.3.1 Practice and Baseline

We ensured that hand angle errors were generally centred around the target during practice (M = 0.38°, SD = 3.01) and no-vision Baseline I (M = -0.03°, SD = 5.01). Low within-participant variable error (M = 3.19°, SD = 0.83) during Baseline I further indicated that participants were consistent in their reaching performances. For random-intercept-only model summary tables of primary and secondary dependent variables, refer to Appendix F1-3 for practice and G1-3 for Baseline I.

In Baseline II, where there was both reward and veridical cursor feedback, participants were generally successful at obtaining reward, with a mean reward percentage of ~87 % (SD = 9.01). To gauge how reward impacted performance under veridical cursor feedback, we statistically compared hand angle error, reaction time, peak velocity, and variable error between practice and Baseline II. Hand angle error was low in both phases, but biased in opposite directions (β = -0.64, SE = 0.16, p < .01, R^2_{sp} = 0.019; Appendix G7), with a small CCW bias during practice without reward (M = 0.39°, SD = 3.01) and a small CW bias during Baseline II with reward (M = -0.23°, SD = 3.17). Reaction times were also faster when reward feedback was available (M = 359.1 ms, SD = 230.2) compared to when only veridical feedback was provided in practice (M = 467.5

ms, SD = 434.3), β = -103.22, SE = 24.27, p < .01, R_{sp}^2 = 0.033 (Appendix G8). There were no differences between phases for peak velocity and variable error (Appendix G9-10).

3.3.2 Adaptation

3.3.2.1 Error Compensation

As shown in Figure 9A-B, error compensation increased with error magnitude, evidenced by a main effect of error magnitude (β = 0.61, SE = 0.12, p < .01, R_{sp}^2 = 0.009). Error compensation was larger for the 7.5°-clamp (M = 1.82°, SD = 2.93) compared to the 3.5°-clamp (M = 1.25°, SD = 3.11), across clamp directions. There was the predicted reward effect (β = -0.50, SE = 0.12, p < .01, R_{sp}^2 = 0.006), with attenuated error compensation following rewarded (M = 1.24°, SD = 2.62) relative to non-rewarded trials (M = 1.70°; SD = 3.20). However, the effect of reward impacted error compensation differently between CW and CCW clamp directions, as evidenced by a significant Reward x Clamp Direction interaction (β = 0.96, SE = 0.24, p < .01, R_{sp}^2 = 0.006). Tukey-corrected post hoc tests demonstrated that error compensation was lower after rewarded (M = 0.92°, SD = 2.75) compared to non-rewarded trials (M = 1.91°, SD = 3.42) following clamped errors in the CW direction (p < .01). There was no difference between rewarded (M = 1.50°, SD = 2.43) and non-rewarded trials (M = 1.50°, SD = 2.96) after clamped errors in the CCW direction. For the corresponding summary table refer to Appendix H1.

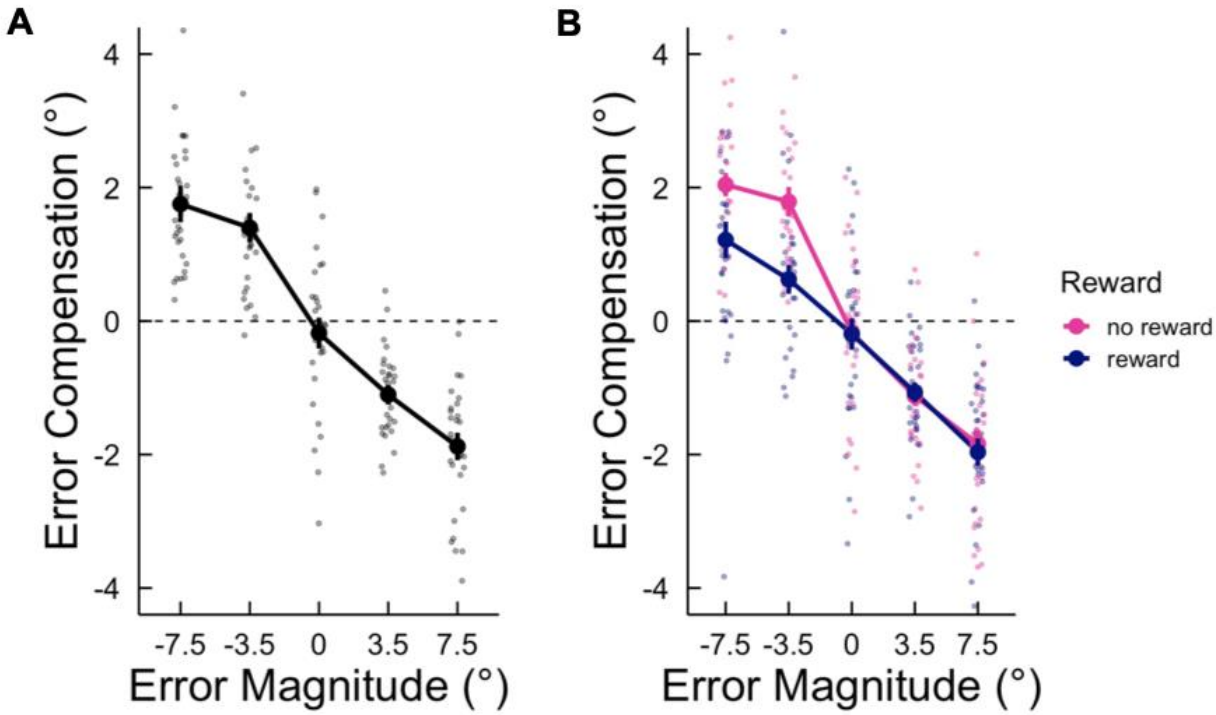

Figure 9. A) Mean error compensation across participants (solid black circles) and for individual participants (transparent black circles) plotted over error magnitude in CW (-) and CCW (+) clamp directions across reward levels. Error bars indicate SEM. B) Mean error compensation across participants and over error magnitude in CW and CCW clamp directions following rewarded (solid blue circles) and non-rewarded (solid pink circles) trials. Participant means are indicated via transparent circles. Errors bars represent SEM. Notably, error compensation over the ±3.5°- and ±7.5°-clamp was adjusted by subtracting each participant's mean response to the 0°-clamp. Values for error compensation to the 0°-clamp were not adjusted and thus reflect participants' mean response to the 0° clamp.

3.3.2.2 Hand Angle Change

In our analysis of hand angle change (i.e., the difference in hand angle error between a clamped error trial and a subsequent no-vision trial), there was a significant main effect of error magnitude (β = 0.74, SE = 0.17, p < .01, R^2_{sp} = 0.008). There were larger hand angle changes in response to the 7.5°-clamp (M = 2.10°, SD = 3.72) compared to the 3.5°-clamp (M = 1.40°, SD = 3.86), as illustrated in Figure 10A. Reward also significantly impacted hand angle change, which was lower after rewarded trials (M = 1.24°, SD = 2.85) relative to non-rewarded trials (M = 2.01°, SD = 4.18), β = -0.76, SE

= 0.17, p < .01, R^2_{sp} = 0.009. The absence of a Reward x Error Magnitude interaction (p = .37) showed that reward downscaled hand angle change consistently across error magnitudes. Even though hand angle change following CCW clamped errors (M = 2.01°, SD = 3.70) was higher than CW clamped errors (M = 1.50°, SD = 3.90), (β = 0.46, SE = 0.17, p < .01, R^2_{sp} = 0.003), Reward did not interact with Clamp Direction (Figure 10B). For the complete model summary, refer to Appendix H2.

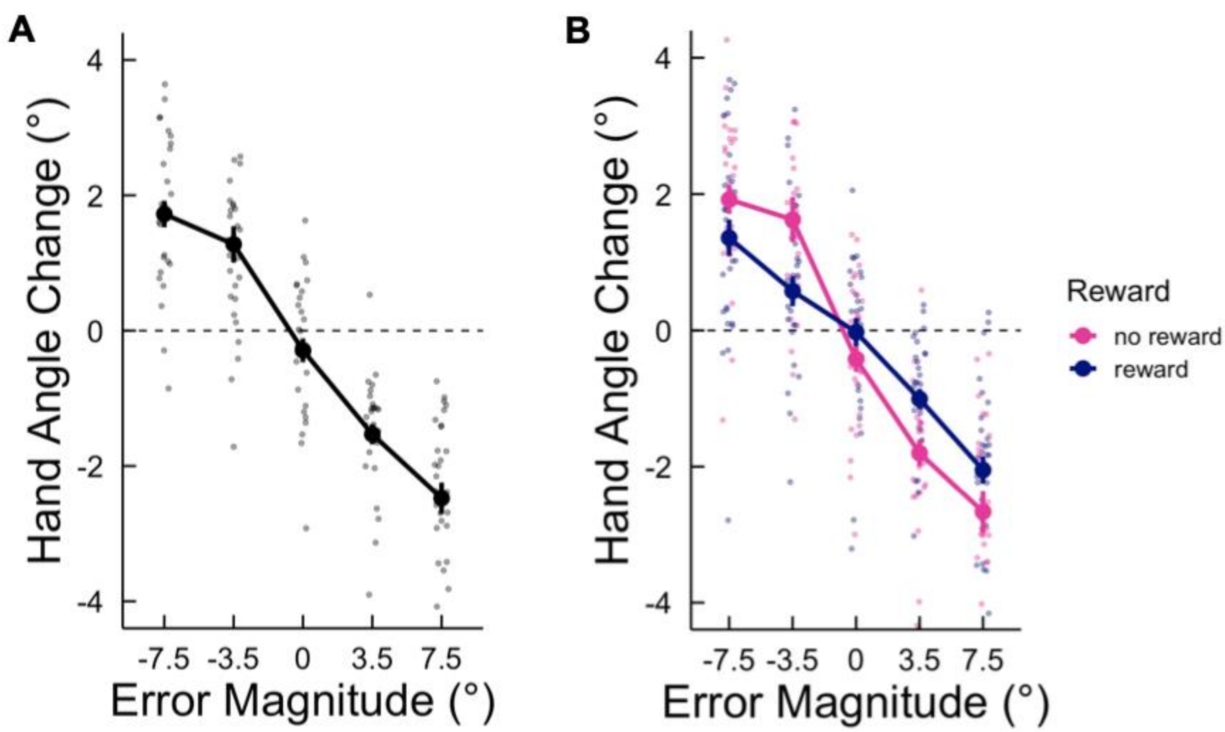

Figure 10. A) Mean hand angle change across participants (solid black circles) and for individual participants (transparent black circles) plotted over error magnitude in CW (-) and CCW (+) clamp directions across reward levels. Error bars indicate SEM. B) Mean hand angle change across participants and over error magnitude in CW and CCW clamp directions following rewarded (solid blue circles) and non-rewarded (solid pink circles) trials. Participant means are indicated via transparent circles. Errors bars represent SEM. Unlike error compensation (see Figure 9), hand angle change values were not adjusted, but rather reflect the 'true' change in hand angle error from an error clamped trial to the subsequent no-vision trial.

3.3.2.3 Peak Velocity & Reaction Time

For the analysis of peak velocity and reaction time (RT), we considered all trials (i.e., veridical, clamped, no-vision) in the adaptation phase (trials 185-984). We did not observe a relationship between RT and reward outcome at the previous trial (β = 3.12, SE = 4.79, p = .52, R_{sp}^2 = 0.000), with comparable RTs on trials following rewarded (M = 337.9 ms, SD = 241.6) and non-rewarded performances (M = 341.0 ms, SD = 252.7). Reward significantly impacted peak velocity (β = -2.40, SE = 0.87, p = .01, R_{sp}^2 = 0.002), but peak velocity was slower after rewarded trials (M = 103.46 cm/sec, SD = 35.52) than after non-rewarded trials (M = 107.33 cm/sec, SD = 36.58). For summary outputs see Appendix H3-4.

3.3.2.4 Variable Error

Variable error (VE) was calculated for the no-vision trials during adaptation. Participants exhibited greater VE following non-rewarded trials (M = 2.53°, SD = 1.97) compared to trials that followed a reward (M = 1.58°, SD = 0.56), (β = -0.95, SE = 0.32, p < .01, R_{sp}^2 = 0.098; see Appendix H5). When participant-specific baseline VE (i.e., from no-vision trials during Baseline I) was included as a predictor, it was significant (β = 0.58, SE = 0.24, p = .02, R_{sp}^2 = 0.115; see Appendix H6). Intuitively, greater VE during baseline predicted greater VE in adaptation (Figure 11A). As shown in Figure 11B, the baseline VE effect was isolated to observations that occurred after non-rewarded trials (β = 1.01, SE = 0.30), but not rewarded trials (β = 0.16, SE = 0.30), confirmed by a Reward x Baseline VE interaction (β = -0.85, SE = 0.36, p = .03, R_{sp}^2 = 0.064). Baseline movement variability was not a strong predictor of variability after rewarded trials.

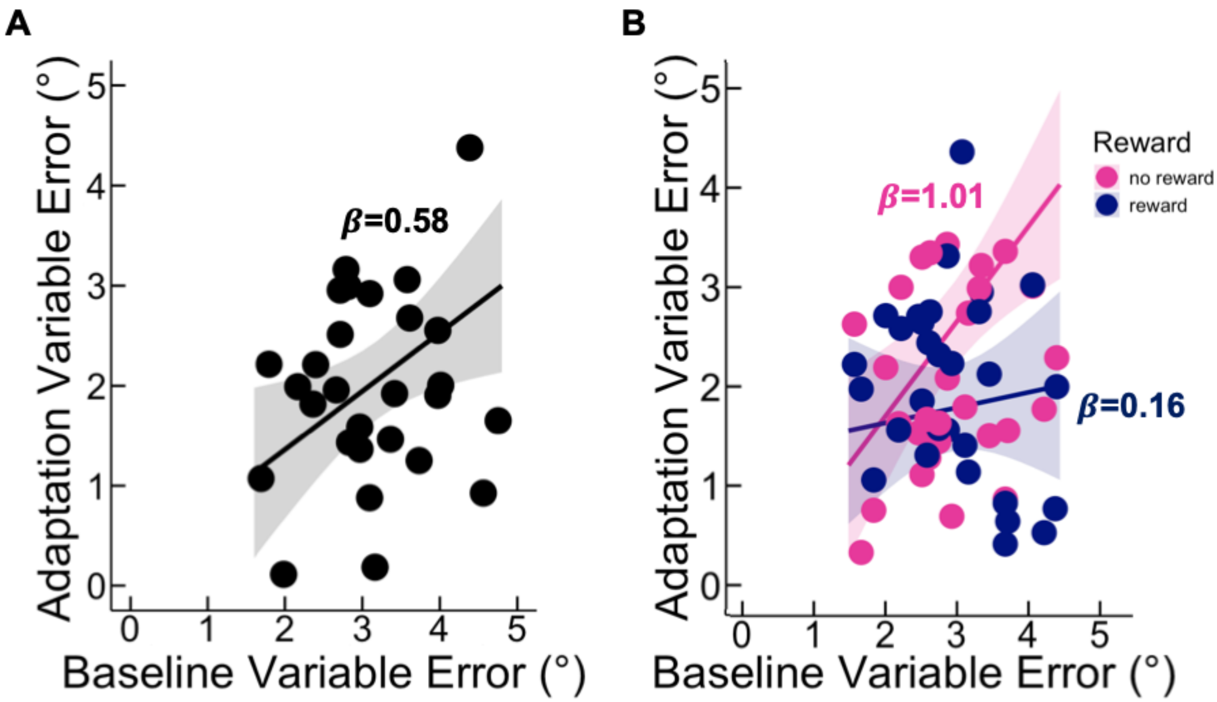

Figure 11. A) Model-estimated slope of adaptation variable error over baseline variable error (black line) across participants. Black circles correspond to participant-level data. Gray shading represents 95% confidence interval. B) Model-estimated slopes of adaptation variable error over baseline variable error (black line) plotted by reward (i.e., variable error was either calculated for trials after rewarded or non-rewarded performances). Coloured circles correspond to participant-level data by reward. Coloured shading represents 95% confidence intervals.

3.3.2.5 Success

As shown in Figure 12A, participants were generally successful during the adaptation phase with a mean success percentage of ~79.77% (SD = 8.69) across trials where reward feedback was enabled (i.e., all veridical trials and 50% of clamped error trials). Participants became more accurate in the task and thus were rewarded more frequently with time, as evidenced by a significant main effect of trial on trial-to-trial success (β = 0.07, SE = 0.01, p < .01, R^2_{sp} = 0.002; Appendix H7). We confirmed that this learning effect did not influence our primary analyses of error compensation and hand angle change, as including trial as a continuous predictor in the corresponding LME models did not yield a main effect of trial or a significant Reward x Trial interaction (see Appendix H8 & 9 respectively). Adding trial as a fixed effect also did not improve model fit, as indicated by higher AIC values for models including trial (error compensation model: AIC_{trial} = 17669.4; hand angle change model: AIC_{trial} = 19267.8) compared to models without it (error compensation model: $AIC_{original}$ = 17665.6; original hand angle change model: $AIC_{original}$ = 19266.2).

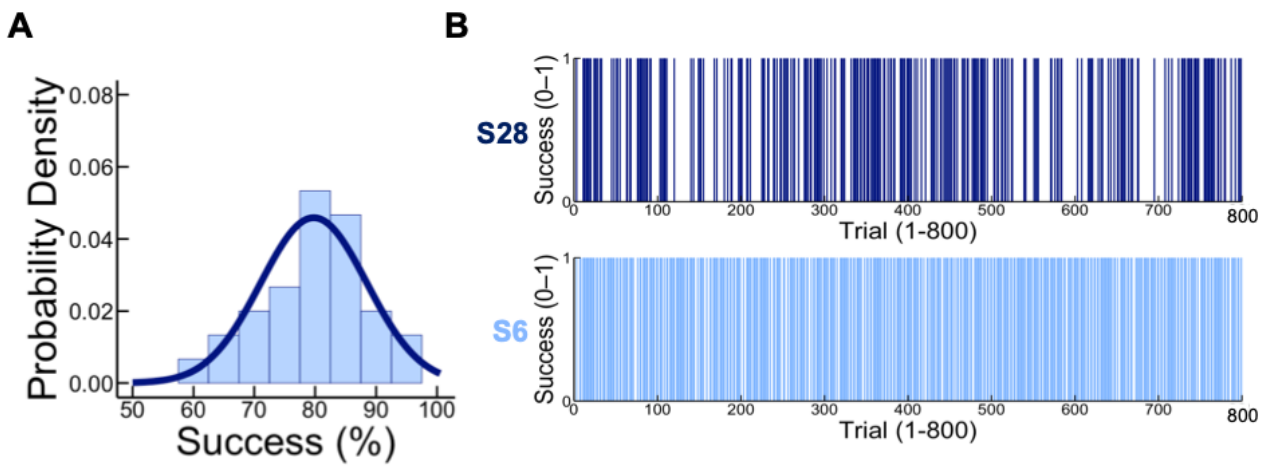

Figure 12. A) Probability density distribution (blue line) of success percentage across participants for trials with enabled reward feedback during adaptation phase. For illustrative purposes only, we generated a smooth Gaussian and probability density values based on the estimated mean and standard deviation obtained in our success percentage data across the observed range of values. Participant means were categorized into success % bins (histograms) with a 5-unit width. Generated values were only used for visualization. B) Individual success data from the participant with the lowest overall success percentage (S28, 58.85% average success) and a representative participant within one standard deviation of the overall mean success percentage (S6, 72.79% average success). Coloured bars indicate successful trials.

3.4 Discussion

In Experiment 2, we tested the general hypothesis that extrinsic rewards would have an independent effect on implicit adaptation to clamped cursor feedback. More specifically, we tested whether extrinsic reward augments implicit adaptation, as shown in Experiment 1, when participants aimed to multiple targets, or whether reward potentially attenuates implicit adaptation processes. Attenuation would be the result of the reinforcing properties of the reward signal, which are more likely to manifest when only a single target is present, allowing participants to “repeat” the same action. Experiment 2 was therefore designed to test the generalizability of results observed in Experiment 1 and to address three methodological concerns. First, to prevent between-target interference effects that could have impaired reinforcement mechanisms in Experiment 1, we reduced the number of targets from four to one. Second, we ensured that participants obtained more rewards by employing an interleaved feedback schedule, where veridical feedback was provided between clamped and no-vision trials. Moreover, because the clamp varied between CW and CCW directions, the moving average of participants’ hand angle error was centered over the reward region around the target. Third, we switched to a within-participants design to control for the possibility that between-group differences in task engagement drove the adaptation augmentation effect we saw in Experiment 1.

In our pre-registration, we predicted that reward should augment adaptation to the clamped error if reward directly amplifies the trial-to-trial error compensation calculated by the motor system. However, we also acknowledged the original hypothesis from Experiment 1, namely that reward would attenuate adaptation, if changing the task environment to a single target would enable reinforcement mechanisms to bias reaching directions toward the target. We anticipated that both measures of adaptation (hand angle change and error compensation), would scale with the magnitude of clamped errors

(Matsuda & Abe, 2023; Kim et al., 2018), but we did not predict a Reward x Error Magnitude interaction. We also expected that making participants more successful in Experiment 2 would affect movement process measures, including decreased reaction times and increased peak velocity. This result would support the previously established relationship between reward and motor vigour (Summerside et al., 2018), however, we failed to show vigour-related effects in Experiment 1. Finally, because all participants received reward feedback, we made a more precise prediction about movement variability than in Experiment 1, with variability expected to be greater following non-rewarded trials (Pekny et al., 2015).

Confirming the independent effects of reward observed in Experiment 1, we again showed that reward impacted on adaptation processes. However, in contrast to Experiment 1, reward now attenuated adaptation. For the measure of error compensation (defined as hand angle error during no-vision trials, adjusted by subtracting the participant-specific mean response to the 0°-clamp), this reward-based attenuation was predominantly driven by responses to errors clamped in the CW direction. However, when adaptation was assessed more directly through trial-to-trial hand angle change, reward reliably reduced adaptation in both clamp directions and across error magnitudes. These data support the hypothesis that extrinsic reward, obtained for adhering to an explicit reaching strategy, attenuates implicit adaptation to a clamped error that drives behaviour in a conflicting direction (e.g., Panthi & Mutha, preprint). Importantly, even though participants obtained a high overall reward percentage and became even more successful with time, the extent of reward-based attenuation of adaptation did not increase as participants accumulated more rewarded performances throughout the experiment. Therefore, attenuation was not the result of reinforcement mechanisms longitudinally enhancing the motor representation of accurate (i.e., to the target) reaching directions. Instead, reward-based attenuation operated at the single trial level, with 'trial-and-error' reinforcement processes modulating the extent of immediate adaptation based on reward outcome.

Reward attenuated but did not extinguish implicit adaptation. Although participants reached to the same target position hundreds of times, were repeatedly instructed to ignore the cued feedback cursor during clamped trials, and frequently received reward and veridical feedback to follow this instruction, some degree of implicit adaptation remained after rewarded trials. Therefore, even under highly controlled conditions, the motor system prioritized the compensation for the observed sensory error over the explicit strategy, despite the monetary incentive tied to the latter. This finding aligns well with the widely accepted notion that implicit adaptation overrides explicit strategies (e.g., Mazzoni & Krakauer, 2006) but extends this idea by demonstrating that a conflicting explicit strategy can slow down immediate implicit adaptation at the single trial level when paired with a salient reward.

Reward impacted movement variability. As previously reported, participants had greater variable error following non-rewarded compared to rewarded trials, suggesting that failure to obtain reward introduced exploratory variation in compensatory responses to the observed error clamp (e.g., Pekny et al., 2015; Holland et al., 2018). In contrast, less variable error in reaches after rewarded trials indicates that reward provided an explicit anchor, through which participants were able to reduce variation in their reaching movements. Reward at the previous trial caused comparable reductions in movement variability across participants independent of their baseline variability. This was surprising because we generally observed a strong positive relationship between variable error during Baseline I and the adaptation phase. Therefore, even participants who initially exhibited greater variability could attenuate fluctuations in their motor output following rewarded performances, thereby enabling exploitation of successful actions (Sutton & Barto, 2018).

We successfully replicated the effect of error magnitude on implicit trial-to-trial adaptation (Matsuda & Abe, 2023), as both error compensation and hand angle change increased with clamped error magnitude across reward conditions. Further, proportional reward-based attenuation of adaptation in our hand angle change data, evidenced by parallel main effects of reward and error magnitude, indicates that reward systematically contributed to the computation of compensatory motor outputs at the single trial level. This was likely achieved through the modulation of adaptation processes directly, as suggested in the adaptation modulation model (Kim et al., 2019). This model was also discussed in the context of Experiment 1, where the observed reward-based effect occurred in the opposite direction (i.e., augmentation rather than attenuation). Combining the findings from both studies suggests that, if reward indeed acts as a gain controller on adaptation as described in the adaptation modulation model, the setting of the corresponding gain parameters and thus the direction of the reward-based effect seem to depend on task constraints (e.g., the number of targets). We further address this idea in the General Discussion.

There was some evidence for a relationship between reward and motor vigour. When we compared movement process measures between practice and Baseline II, participants reduced their reaction time once we enabled the reward feedback. Yet, this reduction in reaction time during Baseline II could also be the result of increased familiarity with the task, given that participants already performed >120 reaches to the same target at this stage. In agreement with this alternative explanation, peak velocity was not different between practice and Baseline II, possibly because participants were unwilling to trade accuracy for speed (Schmidt & Lee, 1999; Nagengast et al., 2011). Because we employed a small reward region in our study (i.e., ±2.5°), compared to other work (e.g., ±50°; Summerside et al., 2018) where the authors examined the relationship between motor vigour and reward, this absence of a vigour effect is less surprising. Our results perhaps reflect more cautious behaviour aimed at maximizing monetary return. This conclusion is further supported by the slowing of peak velocity after rewarded trials in the adaptation phase, perhaps as a result of attempting to repeat the motor output that had been successful on the previous trial.

4. Concluding Chapter

4.1 General Discussion

In this thesis, I investigated the relationship between extrinsic reward and sensory errors during implicit sensorimotor adaptation across two experiments. The overarching goal was to determine whether reward makes a unique contribution to the motor system's computations of compensatory movement adjustments. There was evidence across both experiments supporting this claim.

In Experiment 1, reward and target error were dissociated in a reaching task. Participants reached under rotated clamped visual feedback to targets that could appear at one of four locations. We manipulated target error between groups by changing the size of the targets, such that the clamped cursor either hit or missed its goal. Half of our sample received performance-contingent monetary rewards when their physical reach accurately intersected the intended target. Thus, reward was given for not adapting to the cursor. Results confirmed our hypothesis that target error and reward impacted adaptation in a distinct fashion. When target error was removed (i.e., the cursor hit the target), participants adapted less, replicating previous work (Kim et al., 2019). Surprisingly, reward had the opposite effect. Instead of reducing adaptation by reinforcing accurate reaches to the target, reward augmented error compensation for the clamped cursor. We thus hypothesized that reward had a modulatory effect on adaptation, scaling the compensatory response for the observed sensory error. However, we also considered that the observed reward-based amplification of adaptation was an artefact of interference associated with switching between different targets and using rewards. This interference could have impacted reinforcement mechanisms, in that rewards could not be used to reenact the same motor plan, as the same target was not revisited from trial to trial and adaptation generally drove reaches away from the reward region. For the same reasons, the absence of a reward did not allow for unbiased exploration to “search” the reward region between different targets.

In Experiment 2, we interrogated the hypothesis that reward augments error compensation. To address methodological reasons for the effect from Experiment 1, we switched to a single-target paradigm and ran a fully-within design to test the effects of reward at the single-trial level. Success percentage was increased by combining veridical true hand position feedback, no-vision, and clamped error trials, in an interleaved feedback schedule, such that participants’ mean hand angle error was centred on the reward region around the target. Once again, there was a significant effect of reward. However, instead of augmenting compensation for the clamped error as observed in Experiment 1, rewards now attenuated adaptation. These results suggest that supplementing an explicit reaching strategy (i.e., reaching through the target) with extrinsic reward modulates adaptation, with the directionality of this effect dependent on task constraints. Notably, rewarding participants for adhering to the instructions to aim directly to the target did not abolish adaptation as participants continued to adapt to the clamped cursor (Mazzoni & Krakauer, 2006). Instead, there appeared to be a modulatory relationship between reward-based Markovian learning and error compensation for the observed sensory error (Kim et al., 2019).

At first glance, the results obtained in Experiment 1 and 2 appear contradictory. Why would reward attenuate adaptation in a single-target paradigm, but augment adaptation to multiple reaching targets? To answer this question, we must consider how reward impacted adaptation at the single-trial level. In Experiment 1, the interpretation of trial-to-trial hand angle changes did not provide a reliable estimate of reward-based effects, because the extent of adaptation differed considerably between reaching targets, thereby distorting hand angle change calculated across targets. A more precise estimate of trial-to-trial adaptation was obtained in Experiment 2, where participants only reached to a single target. Under these modified conditions, adaptation was attenuated after rewarded trials, which could also imply greater adaptation following non-rewarded trials.

To address the discrepancy in results from Experiment 1 and 2, it is helpful to consider reward as conditional gain controller (see Figure 13), modulating the adaptative response computed in response to the clamped sensory error (Kim et al., 2019). Based on the results of Experiment 2, I argue that the effect of this reward-based modulation on adaptation depends on the reward outcome at the previous trial, with down-regulation of adaptation after successful trials and up-regulation after non-successful trials. Notably, unlike previous work in which reward was presented without sensory feedback (e.g., Pekny et al., 2015; Holland et al., 2018), the clamped feedback introduced a directional bias, which systematically shifted compensatory responses in the direction opposing the clamp. Consequently, any reward-related changes in the compensatory response observed in our data can be interpreted as a direct modulation of the computations underlying adaptation to the observed sensory error.

If reward up-regulates adaptation after non-successful trials, as suggested, it is possible that low success in Experiment 1, caused by adaptation to the clamped cursor and between-target interference, induced greater adaptation in reward compared to no-reward groups. Indeed, on average, >80% of the trials were not rewarded in the reward groups. Thus, the hypothesis that reward processing acts as a conditional gain controller of adaptation provides a unifying explanation for the results of both Experiment 1 and 2. Specifically, in Experiment 1, this gain-controller framework would predict that participants in the reward groups would up-regulate, and as a result show greater adaptation to the clamped cursor whenever they failed to obtain reward. Because participants in these groups were rarely successful, adaptation would have been up-regulated on the majority of trials, promoting greater overall adaptation compared to no-reward groups. In Experiment 2, this gain-controller framework would predict what we actually showed, that there will be greater trial-to-trial adaptation (i.e., up-regulation) following non-successful compared to successful trials.

Additional research is necessary to confirm the hypothesis that reward modulates adaptation by acting as a conditional gain controller, up- or down-regulating adaptation depending on the reward outcome at the previous trial. A feasible approach in this regard would be to remove the reward feedback from the experimental protocol in Experiment 2 to test a new sample of participants in a third study (Experiment 3). This way, one could compare trial-to-trial adaptation in a between-groups analysis between samples from Experiment 2 and 3, whereby only non-rewarded trials would be considered for the participants from Experiment 2. Should trial-to-trial adaptation be greater in the old sample with reward feedback (Experiment 2) relative to the new sample without reward feedback (Experiment 3), this would pose strong evidence in favour of reward-based up-regulation of adaptation after non-rewarded trials. This result would then help explain the reward-based augmentation of adaptation observed in Experiment 1.

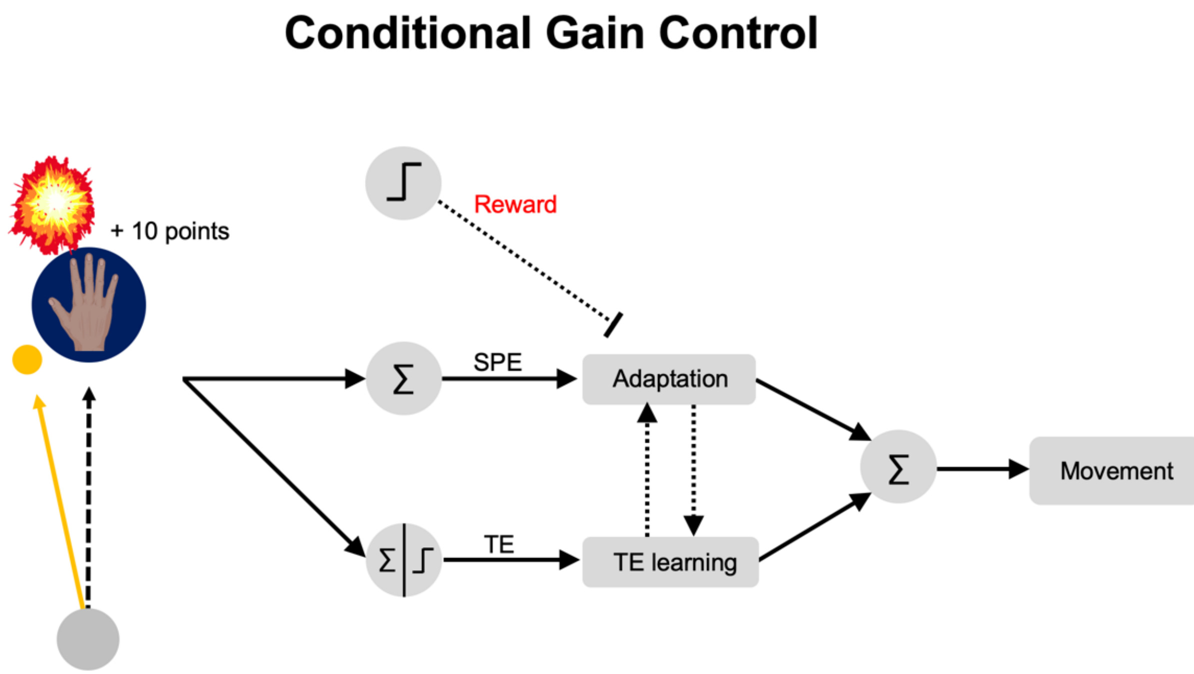

Figure 13. Conditional gain control hypothesis. Cursor feedback (yellow, non-dashed line) induces calculation of a compensatory response to the observed sensory prediction error (SPE) and target error (TE), as formulated in the 'Dual Error Model' by Kim et al. (2019). What has been added to this Dual Error Model is a modulatory relationship between Adaptation and TE learning (dashed arrows), as reported by Tsay et al. (2022). In this revised model, reward now directly modulates the adaptive process in a binary fashion. The corresponding step function illustrates the conditional effect of reward, which either up- or down-regulates compensatory reach directions (movement), depending on the reward outcome at the previous trial. Because reward modulates adaptation directly, movement always occurs in a direction compensating for the observed SPE and TE, with reward only changing the magnitude of the compensation.

4.2 Summary

Reward uniquely impacts sensorimotor adaptation. We demonstrated that reward and target error make dissociable contributions to the computation of adaptation. Target error affects adaptation according to the directional information it conveys. Therefore, adaptation to a clamped visuomotor rotation was greater when target error was present compared to when target error was removed. Meanwhile, reward appears to modulate compensatory motor actions, depending on reward outcome at the previous trial. Adaptation was reduced after receiving reward, whereas failure to obtain reward increased the compensatory response for the clamped cursor.

4.3 Future Implications

These results have important methodological implications for researchers in motor control and neuroscience who frequently incorporate and potentially dissociate rewards in their experiments. These data highlight the need for clear distinctions between extrinsic and intrinsic rewards or target errors in future work, which will hopefully lead to more consistent reports on the effects of these variables. This work also contributes to broader theoretical frameworks of reinforcement mechanisms during sensorimotor adaptation, with strong evidence showing that reward directly modulates adaptive processes. However, additional research is necessary to confirm this relationship and its neural implementation. Finally, this work could inspire clinical researchers and practitioners to conceptualize and test neurorehabilitation applications that supplement sensory feedback with reward signals to support the recovery of motor function in patients with motor impairments.

4.4 Limitations

There are potential limitations of this work and four primary limitations are considered. First, the calculation of trial-to-trial hand angle change in Experiment 1 was distorted by between-target differences in the extent of adaptation. Therefore, because participants switched between different reaching targets on almost every trial, the calculated trial-to-trial hand angle change was contaminated by differences in adaptation between targets, reducing the validity of this measure. We did get a more precise measure of the trial-to-trial impacts of rewards in Experiment 2. Second, the method of dissociating rewards and sensory errors, such that participants received reward for not adapting to the cursor, does not reflect how these signals naturally interact and conceptually differs from other experimental manipulations where researchers assessed the relationship of reward and motor learning. That is, rewards are usually provided as a supplementary signal to support gradual learning of a motor task, rather than as a reinforcer of a strategy to "aim normally" and over-ride the response to sensory errors brought about by an externally-driven feedback signal (i.e., error clamp). Thus, these results might not be directly comparable to studies where reward and sensory information are aligned.

The analysis of reward-based effects on motor vigour, specifically the absence of such effects, must be qualified by the fact that we chose a small reward region, compared to other work examining this relationship. As a result, participants likely prioritized accuracy over speed to maximize success, masking changes in measures indexing motor vigour. Further research would thus be needed where the reward region is increased to determine if the vigour effects generalize. Finally, given the need for careful control of sensory and reward feedback in our studies, we tested the effects of reward in a laboratory-based reaching task, thereby limiting the generalizability of our results to more applied motor skills, where movements are often more complex and subject to additional environmental constraints.

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Appendix A

Table A1

Baseline Hand Angle
hand angle ~ 1 + reward * target error + target + (1 + target | subject)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	-0.29	0.21	-0.69 – 0.12	0.169
target error	0.08	0.41	-0.71 – 0.88	0.838
reward	-0.03	0.41	-0.83 – 0.76	0.936
target	-0.18	0.18	-0.53 – 0.18	0.328
target error × reward	-1.25	0.81	-2.84 – 0.34	0.123
Random Effects				
σ^2	24.30			
$\tau_{00\ subject}$	1.66			
$\tau_{11\ subject.target}$	1.21			
$\rho_{01\ subject}$	0.30			
ICC	0.12			
$N_{subject}$	59			

Effect Sizes

Marginal R^2 / Conditional R^2: 0.005 / 0.121

Note. Significant p-values for predictors are highlighted in bold font.

Table A2

Baseline Peak Velocity peak velocity ~ 1 + reward * target error + target + trial + (1 + target + trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	109.22	3.20	102.95 – 115.50	**<0.001**
target error	8.34	6.30	-4.00 – 20.68	0.185
reward	4.13	6.30	-8.21 – 16.47	0.512
target	-2.03	6.30	-4.49 – 0.43	0.105
trial	4.39	1.25	-7.95 – 16.72	0.486
target error × reward	-6.18	12.59	-30.87 – 18.50	0.623
Random Effects				
σ^2	2312.07			
$\tau_{00\ subject}$	517.95			
$\tau_{11\ subject.trial}$	1257.45			
$\tau_{11\ subject.target}$	31.68			
$\rho_{01\ subject}$	-0.17			
	0.29			
ICC	0.22			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.010 / 0.228				

Note. Significant p-values for predictors are highlighted in bold font.

Table A3

Baseline Reaction Time reaction time ~ 1 + reward * target error + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	438.46	21.17	396.94 – 479.98	**<0.001**
target error	71.72	42.34	-11.31 – 154.76	0.090
reward	56.17	42.34	-26.86 – 139.21	0.185
target error × reward	90.40	84.68	-75.67 – 256.47	0.286
Random Effects				
σ^2	554047.58			
$\tau_{00\ subject}$	8144.94			
ICC	0.01			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.004 / 0.019				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix B

Table B1

Pre-Test Hand Angle
hand angle ~ 1 + reward * target error + target + (1 + target | subject)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	0.21	0.22	-0.22 – 0.64	0.339
target error	0.82	0.43	-0.02 – 1.65	0.055
reward	-0.18	0.43	-1.01 – 0.66	0.676
target	-0.48	0.21	-0.88 – -0.07	**0.021**
target error x reward	-0.31	0.85	-1.98 – 1.36	0.715

Random Effects

σ^2	30.99
$\tau_{00\ subject}$	0.90
$\tau_{11\ subject.target}$	1.00
$\rho_{01\ subject}$	0.51
ICC	0.07
$N_{subject}$	59

Effect Sizes

Marginal R^2 / Conditional R^2: 0.014 / 0.078

Note. Significant p-values for predictors are highlighted in bold font.

Table B2

Pre-Test Peak Velocity
peak velocity ~ 1 + reward * target error + (1 | subject)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	113.90	3.35	107.34 – 120.47	**<0.001**
target error	10.32	6.69	-2.81 – 23.45	0.123
reward	6.67	6.69	--6.46 – 19.80	0.319
target error × reward	-10.32	13.38	-36.58 – 15.94	0.441
Random Effects				
σ^2	1406.37			
$\tau_{00\ subject}$	570.07			
ICC	0.29			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2:	0.021 / 0.303			

0.021 / 0.3

Note. Significant p-values for predictors are highlighted in bold font.

Table B3

Pre-Test Reaction Time reaction time ~ 1 + reward * target error + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	407.60	10.13	387.72 – 427.49	**<0.001**
target error	7.37	20.26	-32.40 – 47.13	0.716
reward	33.17	20.26	-6.59 – 72.94	0.10
target error × reward	42.18	40.53	-37.34 – 121.71	0.298
Random Effects				
σ^2	58416.47			
$\tau_{00\ subject}$	2544.96			
ICC	0.04			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2:	0.006 / 0.048			

Note. Significant p-values for predictors are highlighted in bold font.

Appendix C

Table C1

Acquisition Hand Angle hand angle error ~ 1 + reward * target error * trial + target + (1 + target * trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	8.00	0.61	6.81 – 9.20	**<0.001**
target error	-3.15	1.14	0.90 – 5.39	**0.006**
reward	2.52	1.14	0.28 – 4.77	**0.028**
trial	7.88	0.91	6.08 – 9.67	**<0.001**
target	-1.29	0.44	-2.14 – -0.43	**0.003**
target error x reward	3.61	2.29	-0.88 – 8.10	0.115
target error x trial	2.70	1.82	-0.87 – 6.28	0.138
reward x trial	0.51	1.82	-3.07 – 4.08	0.781
target error x reward x trial	1.46	3.64	-5.69 – 8.60	0.689
Random Effects				
σ^2	71.78			
$\tau_{00\ subject}$	27.87			
$\tau_{11\ subject.trial}$	49.62			
$\tau_{11\ subject.target}$	14.70			
$\tau_{11\ subject.trial.target}$	11.48			
$\rho_{01\ subject}$	-0.00			
	0.54			
	-0.54			
ICC	0.41			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.089 / 0.465				

Note. Significant p-values for predictors are highlighted in bold font.

Figure C1

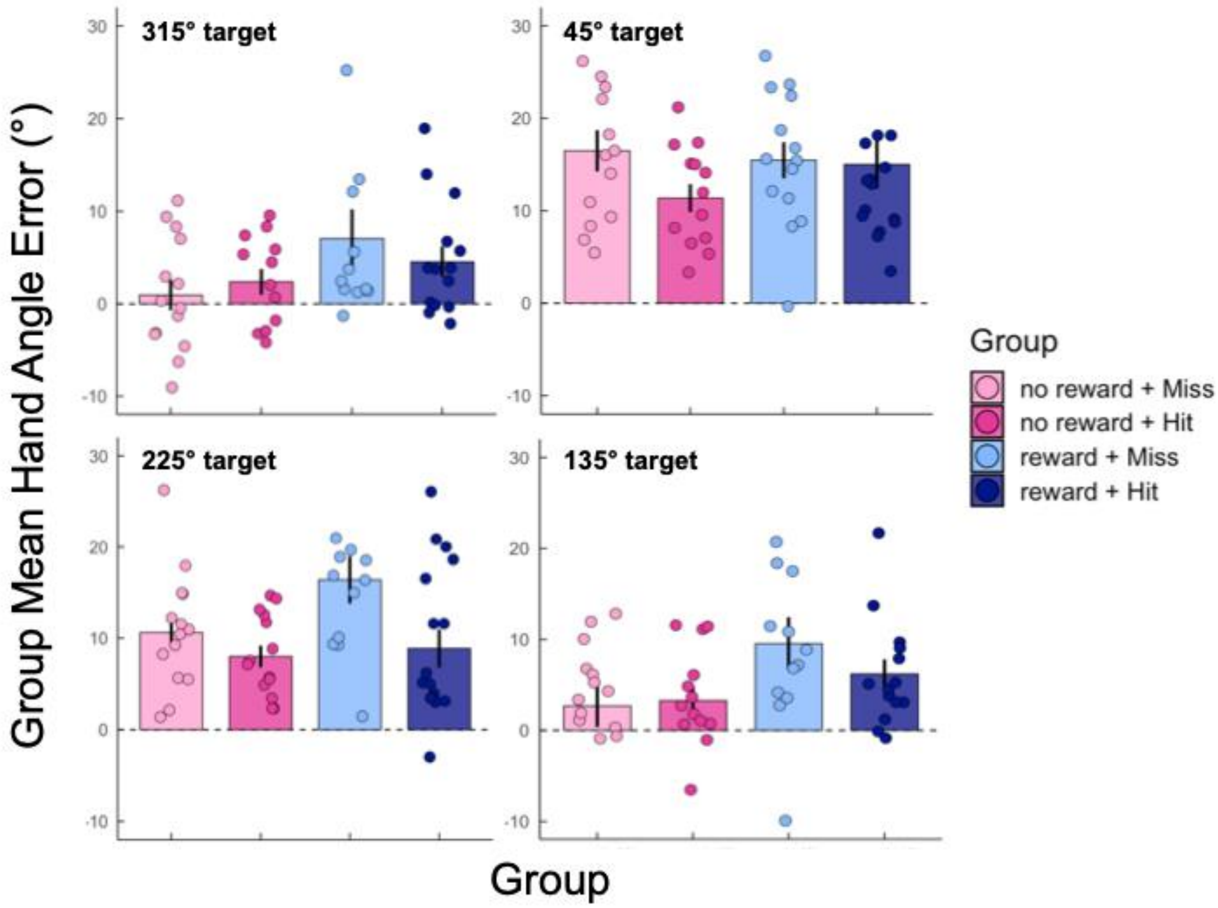

Figure C1. Group mean hand angle error at each reaching target averaged across groups and trials during acquisition. Bars represent group means and circles subject means. Black lines correspond to SEM.

Table C2

Acquisition Peak Velocity peak velocity ~ 1 + reward * target error * trial + target + (1 + target * trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	107.68	2.43	102.91 – 112.44	**<0.001**
target error	5.22	4.81	-4.21 – 14.66	0.278
reward	-3.37	4.81	-12.81 – 6.06	0.484
trial	4.24	2.67	-0.98 – 9.47	0.112
target	-2.94	0.43	-3.78 – -2.09	**<0.001**
target error x reward	-11.08	9.63	-29.96 – 7.79	0.250
target error x trial	-1.18	5.30	-11.58 – 9.22	0.824
reward x trial	1.83	5.30	-8.56 – 12.23	0.729
target error x reward x trial	4.93	10.61	--15.86 – 25.72	0.642
Random Effects				
σ^2	1337.64			
τ_{00} subject	350.18			
τ_{11} subject.trial	353.04			
τ_{11} subject.target	8.37			
τ_{11} subject.trial.target	84.87			
ρ_{01} subject	-0.22			
	0.16			
	0.17			
ICC	0.23			
N subject	59			
Effect Sizes				
Marginal R^2 / Conditional R^2:	0.018 / 0.239			

Note. Significant p-values for predictors are highlighted in bold font.

Table C3

Acquisition Reaction Time				
reaction time ~ 1 + reward * target error * trial + target + (1 + target * trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	424.84	9.04	407.12 – 442.56	**<0.001**
target error	11.04	17.30	-22.87 – 44.96	0.523
reward	76.12	17.30	42.21 – 110.04	**<0.001**
trial	28.24	17.23	-5.54 – 62.02	0.101
target	2.63	1.59	-0.49 – 5.75	0.099
target error x reward	-37.45	34.61	-105.28 – 30.38	0.279
target error x trial	-54.96	34.46	-122.50 – 12.57	0.111
reward x trial	57.16	34.46	-10.37 – 124.70	0.097
target error x reward x trial	-78.52	68.91	-213.60 – 56.55	0.255
Random Effects				
σ^2	28303.16			
$\tau_{00\ \text{subject}}$	4760.61			
$\tau_{11\ \text{subject.trial}}$	82.75			
$\tau_{11\ \text{subject.target}}$	16626.93			
$\tau_{11\ \text{subject.trial.target}}$	636.48			
$\rho_{01\ \text{subject}}$	0.34			
	0.28			
	0.17			
ICC	0.18			
N_{subject}	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.049 / 0.220				

Note. Significant p-values for predictors are highlighted in bold font.

Table C4

Acquisition Movement Variability
variable error ~ 1 + reward * target error * block + (1 + block | subject)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	7.71	0.44	6.85 – 8.58	**<0.001**
target error	0.69	0.88	-1.04 – 2.43	0.432
reward	1.82	0.88	0.09 – 3.56	**0.039**
block	3.49	0.56	2.39 – 4.59	**<0.001**
target error x reward	-2.66	1.76	-6.13 – 0.80	0.132
target error x block	-0.93	1.12	-3.13 – 1.27	0.407
reward x block	0.97	1.12	-1.23 – 3.17	0.385
target error x reward x block	-3.71	2.24	-8.11 – 0.69	0.099

Random Effects

σ^2	4.68
$\tau_{00\ subject}$	10.95
$\tau_{11\ subject.cycles\_s}$	12.62
$\rho_{01\ subject}$	0.32
ICC	0.73
$N_{subject}$	59

Effect Sizes

Marginal R^2 / Conditional R^2: 0.131 / 0.762

Note. Significant p-values for predictors are highlighted in bold font.

Table C5

Acquisition Success success % ~ 1 + target error * block + (1+ block | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	12.88	1.88	9.81 – 16.59	**<0.001**
target error	-6.79	3.76	-14.20 – 0.62	0.082
block	-13.07	3.67	-20.29 – -5.85	**0.001**
target error × block	3.00	7.34	-11.43 – 17.44	0.685
Random Effects				
σ^2	59.02			
$\tau_{00\ subject}$	98.76			
$\tau_{11\ subject.block}$	322.03			
$\rho_{01\ subject}$	-0.62			
ICC	0.66			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R2: 0.128 / 0.704				

Note. Significant p-values for predictors are highlighted in bold font.

Table C6

Acquisition Hand Angle Change hand angle change ~ 1 + success + (1 + success | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	2.74	0.34	2.09 – 3.40	**<0.001**
target error	8.88	1.17	6.58 – 11.19	**<0.001**
Random Effects				
σ^2	196.73			
τ_{00} subject	1.56			
τ_{11} subject.success	33.03			
ρ_{01} subject	0.74			
ICC	0.03			
N subject	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.050 / 0.070				

Note. Significant p-values for predictors are highlighted in bold font.

Table C7

Acquisition Hand Angle Change by Success History hand angle change ~ 1 + success history + (1 + success history || subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	1.89	0.28	1.34 – 2.44	**<0.001**
success history	1.31	0.17	0.98 – 1.64	**<0.001**
Random Effects				
σ^2	199.61			
τ_{00} subject	0.95			
τ_{11} subject.success history	0.67			
ICC	0.00			
N subject	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.043 / 0.047				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix D

Table D1

Aftereffect
hand angle error ~ 1 + target error * reward + (1 | subject)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	9.24	0.83	7.60 – 10.88	**<0.001**
target error	1.88	1.67	-1.41 – 5.16	0.261
reward	1.80	1.67	-1.49 – 5.08	0.282
target error × reward	1.71	3.33	-4.86 – 8.28	0.608
Random Effects				
σ^2	112.70			
$\tau_{00\ subject}$	9.46			
ICC	0.08			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.015 / 0.108				

Note. Significant p-values for predictors are highlighted in bold font.

Table D2

Relative Retention hand angle error ~ 1 + reward * target error * trial + (1 + trial || subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	9.52	0.78	8.00 – 11.05	**<0.001**
target error	2.88	1.55	-0.16 – 5.93	0.064
reward	2.01	1.55	-1.04 – 5.05	0.196
trial	-5.19	1.04	-7.23 – -3.16	**<0.001**
target error × reward	0.76	3.10	-5.33 – 6.85	0.806
target error × trial	-1.24	2.07	-5.31 – 2.83	0.551
reward × trial	-4.30	2.07	-8.37 – -0.23	**0.038**
target error × reward × trial	3.14	4.15	-5.00 – 11.28	0.449
Random Effects				
σ^2	95.12			
$\tau_{00\ subject}$	30.10			
$\tau_{11\ subject.trial}$	3.89			
ρ_{01}				
ρ_{01}				
ICC	0.24			
N $_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.043 / 0.273				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix E

Table E1

Acquisition Hand Angle (IMI) hand angle ~ 1 + reward * target error * trial + imi score + target + (1 + target * trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	8.04	0.61	6.85 – 9.23	**<0.001**
target error	3.12	1.15	0.87 – 5.37	**0.007**
reward	1.86	1.24	-0.57 – 4.30	0.134
trial	7.89	0.91	6.09 – 9.68	**<0.001**
imi score	0.06	0.04	-0.02 – 0.15	0.157
target	-1.29	0.44	-2.14 – -0.43	**0.003**
target error x reward	3.14	2.32	-1.40 – 7.68	0.175
target error x trial	2.72	1.82	-0.86 – 6.29	0.136
reward x trial	0.51	1.82	-3.07 – 4.08	0.781
target error x reward x trial	1.45	3.65	-5.70 – 8.59	0.692
Random Effects				
σ^2	71.79			
$\tau_{00\ subject}$	27.10			
$\tau_{11\ subject.trial}$	49.59			
$\tau_{11\ subject.target}$	14.66			
$\tau_{11\ subject.trial:target}$	11.45			
ρ_{01}	0.56			
	-0.00			
	-0.52			
ICC	0.41			
$N_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.093 / 0.463				

Note. Significant p-values for predictors are highlighted in bold font.

Table E2

Acquisition Hand Angle (SPSRQ) hand angle ~ 1 + reward * target error * trial + spsrq score + target + (1 + target * trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	8.03	0.61	6.82 – 9.24	**<0.001**
target error	3.32	1.17	1.03 – 5.61	**0.005**
reward	2.41	1.16	0.14 – 4.68	**0.038**
trial	7.88	0.91	6.09 – 9.67	**<0.001**
spsrq score	-0.14	0.13	-0.40 – 0.12	0.301
target	-1.28	0.44	-2.14 – -0.42	**0.003**
target error x reward	3.32	2.32	-1.22 – 7.87	0.152
target error x trial	2.70	1.82	-0.88 – 6.27	0.139
reward x trial	0.51	1.82	-3.07 – 4.08	0.782
target error x reward x trial	1.44	3.65	-5.71 – 8.59	0.692
Random Effects				
σ^2	71.78			
$\tau_{00\ subject}$	28.07			
$\tau_{11\ subject.trial}$	49.64			
$\tau_{11\ subject.target}$	14.71			
$\tau_{11\ subject.trial:target}$	11.50			
ρ_{01}	0.55			
	0.01			
	-0.53			
ICC	0.41			
N $_{subject}$	59			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.091 / 0.467				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix F

Table F1

Practice Hand Angle hand angle ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	0.42	0.18	0.06 – 0.78	**0.024**
Random Effects				
σ^2	8.20			
$\tau_{00\ subject}$	0.85			
ICC	0.09			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.094				

Note. Significant p-values for predictors are highlighted in bold font.

Table F2

Practice Reaction Time reaction time ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	461.21	29.51	404.49 – 517.93	**<0.001**
Random Effects				
σ^2	167388.89			
$\tau_{00\ subject}$	21321.50			
ICC	0.11			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.113				

Note. Significant p-values for predictors are highlighted in bold font.

Table F3

Practice Peak Velocity peak velocity ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	100.52	3.22	94.19 – 106.85	**<0.001**
Random Effects				
σ^2	582.61			
$\tau_{00\ subject}$	299.24			
ICC	0.34			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.339				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix G

Table G1

Baseline I Hand Angle hand angle ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	-0.09	0.70	-1.46 – 1.28	0.898
Random Effects				
σ^2	10.66			
$\tau_{00\ subject}$	14.41			
ICC	0.57			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.575				

Note. Significant p-values for predictors are highlighted in bold font.

Table G2

Baseline I Reaction Time reaction time ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	425.33	30.86	364.80 – 485.85	**<0.001**
Random Effects				
σ^2	41950.71			
$\tau_{00\ subject}$	27779.41			
ICC	0.40			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.398				

Note. Significant p-values for predictors are highlighted in bold font.

Table G3

Baseline I Peak Velocity peak velocity ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	117.92	5.31	107.50 – 128.35	**<0.001**
Random Effects				
σ^2	783.54			
$\tau_{00\ subject}$	832.39			
ICC	0.52			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.551				

Note. Significant p-values for predictors are highlighted in bold font.

Table G4

Baseline II Hand Angle hand angle~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	-0.22	0.17	-0.56 – 0.12	0.198
Random Effects				
σ^2	9.44			
$\tau_{00\ subject}$	0.69			
ICC	0.07			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.068				

Note. Significant p-values for predictors are highlighted in bold font.

Table G5

Baseline II Reaction Time reaction time~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	359.15	18.00	323.84 – 394.46	**<0.001**
Random Effects				
σ^2	45034.99			
$\tau_{00\ subject}$	8723.60			
ICC	0.16			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.162				

Note. Significant p-values for predictors are highlighted in bold font.

Table G6

Baseline II Peak Velocity peak velocity ~ 1 + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	99.49	4.65	90.37 – 108.62	**<0.001**
Random Effects				
σ^2	801.58			
$\tau_{00\ subject}$	631.41			
ICC	0.44			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.441				

Note. Significant p-values for predictors are highlighted in bold font.

Table G7

Practice vs. Baseline ii) Hand Angle hand angle ~ 1 + experimental phase + (1 + experimental phase | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	0.09	0.16	-0.22 – 0.41	0.553
experimental phase	-0.64	0.16	-0.95 – -0.32	**<0.001**
Random Effects				
σ^2	8.82			
$\tau_{00\ subject}$	0.67			
$\tau_{11\ subject.experimental\ phase}$	0.39			
$\rho_{01\ subject}$	-0.13			
ICC	0.08			
N $_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.010 / 0.090				

Note. Significant p-values for predictors are highlighted in bold font.

Table G8

Practice vs. Baseline II Reaction Time reaction time ~ 1 + experimental phase + (1+ experimental phase | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	409.55	20.61	369.13 – 449.97	**<0.001**
experimental phase	-103.22	24.27	-150.81 – -55.64	**<0.001**
Random Effects				
σ^2	106425.07			
$\tau_{00\ subject}$	11566.12			
$\tau_{11\ subject.experimental\ phase}$	12988.61			
$\rho_{01\ subject}$	-0.63			
ICC	0.12			
N $_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.022 / 0.141				

Note. Significant p-values for predictors are highlighted in bold font.

Table G9

Practice vs. Baseline II Peak Velocity peak velocity ~ 1 + experimental phase + (1+ experimental phase | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	99.99	3.46	93.21 – 106.78	**<0.001**
experimental phase	-1.06	4.04	-8.98 – 6.87	0.794
Random Effects				
σ^2	691.70			
$\tau_{00\ subject}$	351.01			
$\tau_{11\ subject.\ experimental\ phase}$	459.14			
$\rho_{01\ subject}$	0.42			
ICC	0.40			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.402				

Note. Significant p-values for predictors are highlighted in bold font.

Table G10

Practice vs. Baseline II Variable Error variable error ~ 1 + experimental phase + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	2.68	0.18	2.32 – 3.05	**<0.001**
experimental phase	-0.25	0.30	-0.85 – 0.34	0.402
Random Effects				
σ^2	1.33			
$\tau_{00\ subject}$	0.33			
ICC	0.20			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.010 / 0.206				

Note. Significant p-values for predictors are highlighted in bold font.

Appendix H

Table H1

Adaptation Error Compensation error compensation ~ 1 + error magnitude * reward * clamp direction + (1 | subject) + (1 | subject:error magnitude:reward:clamp direction)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	1.46	0.11	1.24 – 1.67	**<0.001**
error magnitude	0.61	0.12	0.37 – 0.84	**<0.001**
clamp direction	0.07	0.12	-0.16 – 0.31	0.550
reward	-0.50	0.12	-0.74 – -0.26	**<0.001**
error magnitude × clamp direction	0.42	0.24	-0.05 – 0.90	0.081
error magnitude × reward	0.20	0.24	-0.27 – 0.67	0.410
clamp direction × reward	0.96	0.24	0.48 – 1.43	**<0.001**
error magnitude × clamp direction × reward	-0.16	0.48	-1.11 – 0.79	0.744
Random Effects				
σ^2	8.53			
τ_{00} subject:error_magnitude:clamp_direction:reward	0.20			
τ_{00} subject	0.26			
ICC	0.05			
N subject	30			
N error_magnitude	2			
N clamp_direction	2			
N reward	2			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.022 / 0.072				

Note. Significant p-values for predictors are highlighted in bold font.

Table H2

Adaptation Hand Angle Change hand angle change ~ 1 + error magnitude * reward * clamp direction + (1 | subject) + (1 | subject:error magnitude:reward:clamp direction)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	1.64	0.11	1.42 – 1.86	**<0.001**
error magnitude	0.74	0.17	0.40 – 1.08	**<0.001**
clamp direction	0.46	0.17	0.12 – 0.80	**0.007**
reward	-0.76	0.17	-1.10 – -0.42	**<0.001**
error magnitude × clamp direction	0.46	0.35	-0.22 – 1.14	0.185
error magnitude × reward	0.31	0.35	-0.37 – 0.99	0.373
clamp direction × reward	-0.00	0.35	-0.68 – 0.68	0.996
error magnitude × clamp direction × reward	-0.26	0.69	-1.62 – 1.10	0.705
Random Effects				
σ^2	13.29			
τ_{00} subject:error_magnitude:clamp_direction:reward	0.73			
τ_{00} subject	0.16			
ICC	0.06			
N subject	30			
N error_magnitude	2			
N clamp_direction	2			
N reward	2			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.023 / 0.084				

Note. Significant p-values for predictors are highlighted in bold font.

Table H3

Adaptation Reaction Time reaction time ~ 1 + reward + (1+ reward | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	336.35	20.52	296.14 – 376.56	**<0.001**
reward	3.12	4.79	-6.27 – 12.52	0.515
Random Effects				
σ^2	48371.72			
$\tau_{00\ subject}$	12541.89			
$\tau_{11\ subject.\ reward}$	354.69			
$\rho_{01\ subject}$	0.37			
ICC	0.21			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.000 / 0.207				

Note. Significant p-values for predictors are highlighted in bold font.

Table H4

Adaptation Peak Velocity peak velocity ~ 1 + reward + (1+ reward | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	103.92	4.30	95.50 – 112.35	**<0.001**
reward	-2.40	0.87	-4.11 – -0.70	**0.006**
Random Effects				
σ^2	799.56			
$\tau_{00\ subject}$	553.11			
$\tau_{11\ subject.\ reward}$	17.09			
$\rho_{01\ subject}$	-0.40			
ICC	0.41			
$N_{subject}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.001 / 0.412				

Note. Significant p-values for predictors are highlighted in bold font.

Table H5

Adaptation Variable Error adaptation variable error ~ 1 + reward + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	2.06	0.21	1.63 – 2.48	**<0.001**
reward	-0.95	0.32	-1.58 – -0.31	**0.004**
Random Effects				
σ^2	1.49			
$\tau_{00\ \text{subject}}$	0.59			
ICC	0.28			
N $_{\text{subject}}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.098 / 0.355				

Note. Significant p-values for predictors are highlighted in bold font.

Table H6

Adaptation Variable Error (2) adaptation variable error ~ 1 + reward * baseline variable error + (1 | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	0.19	0.79	-1.38 – 1.77	0.808
baseline variable error	0.58	0.24	0.11 – 1.06	**0.018**
reward	1.75	1.18	-0.62 – 4.12	0.145
baseline variable error × reward	-0.85	0.36	-1.56 – -0.13	**0.022**
Random Effects				
σ^2	1.29			
$\tau_{00\ \text{subject}}$	0.50			
ICC	0.28			
N $_{\text{subject}}$	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.245 / 0.455				

Note. Significant p-values for predictors are highlighted in bold font.

Table H7

Adaptation Trial-to-Trial Success trial-to-trial success ~ 1 + trial + (1 + trial | subject)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	0.47	0.01	0.45 – 0.49	**<0.001**
trial	0.07	0.02	0.04 – 0.11	**<0.001**
Random Effects				
σ^2	0.25			
$\tau_{00\ \mathrm{subject}}$	0.00			
$\tau_{11\ \mathrm{subject.trial}}$	0.00			
$\rho_{01\ \mathrm{subject}}$	0.09			
ICC	0.01			
N_{subject}	30			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.002 / 0.012				

Note. Significant p-values for predictors are highlighted in bold font.

Table H8

Adaptation Error Compensation (2)
error compensation ~ 1 + error magnitude * clamp direction * reward + (reward * trial) + (1 + trial | subject) + (1 | subject:error magnitude:reward:clamp direction)

Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	1.47	0.12	1.24 – 1.70	**<0.001**
error magnitude	0.61	0.12	0.37 – 0.84	**<0.001**
clamp direction	0.07	0.12	-0.17 – 0.31	0.561
reward	-0.54	0.13	-0.79 – -0.30	**<0.001**
trial	-0.12	0.21	-0.53 – 0.29	0.565
error magnitude × clamp direction	0.43	0.24	-0.04 – 0.91	0.072
error magnitude × reward	0.20	0.24	-0.27 – 0.67	0.408
clamp direction × reward	0.95	0.24	0.48 – 1.43	**<0.001**
reward × trial	0.52	0.37	-0.20 – 1.23	0.158
error magnitude × clamp direction × reward	-0.17	0.48	-1.11 – 0.78	0.731
Random Effects				
σ^2	8.51			
τ_{00} subject:error_magnitude:clamp_direction:reward	0.20			
τ_{00} subject	0.28			
τ_{11} subject.trial	0.28			
ρ_{01} subject	-0.62			
ICC	0.05			
N subject	30			
N error_magnitude	2			
N clamp_direction	2			
N reward	2			

Effect Sizes

Marginal R^2 / Conditional R^2: 0.023 / 0.075

Note. Significant p-values for predictors are highlighted in bold font.

Table H9

Adaptation Hand Angle Change (2) hand angle change ~ 1 + error magnitude * clamp direction * reward + (reward * trial) + (1 | subject) + (1 | subject:error magnitude:reward:clamp direction)				
Predictors	*Estimates*	*std. Error*	*CI*	*p*
(Intercept)	1.64	0.11	1.42 – 1.87	**<0.001**
error magnitude	0.74	0.17	0.40 – 1.08	**<0.001**
clamp direction	0.46	0.17	0.12 – 0.80	**0.008**
reward	-0.83	0.18	-1.18 – -0.48	**<0.001**
trial	-0.04	0.23	-0.50 – 0.41	0.845
error magnitude × clamp direction	0.47	0.35	-0.21 – 1.15	0.175
error magnitude × reward	0.30	0.35	-0.37 – 0.98	0.380
clamp direction × reward	-0.00	0.35	-0.68 – 0.68	0.994
reward × trial	0.75	0.46	-0.15 – 1.65	0.102
error magnitude × clamp direction × reward	-0.27	0.69	-1.62 – 1.09	0.701
Random Effects				
σ^2	13.29			
τ_{00} subject:error_magnitude:clamp_direction:reward	0.73			
τ_{00} subject	0.16			
ICC	0.06			
N subject	30			
N error_magnitude	2			
N clamp_direction	2			
N reward	2			
Effect Sizes				
Marginal R^2 / Conditional R^2: 0.023 / 0.087				

Note. Significant p-values for predictors are highlighted in bold font.