The effect of target jumps on implicit adaptation of reaching

by

Joie Tang

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Bachelor of Science in Exercise Science with Distinction

Spring 2020

The effect of target jumps on implicit adaptation of reaching

by

Joie Tang

Approved: ____

Hyosub Kim, PT, PhD
Professor in charge of thesis on behalf of the Advisory Committee

Approved: ____

Jared Medina, PhD
Committee member from the Department of Psych & Brain Sciences

Approved: ____

Elizabeth Orsega-Smith, PhD
Committee member from the Board of Senior Thesis Readers

Approved: ____

Michael Chajes, Ph.D.
Chair of the University Committee on Student and Faculty Honors

ACKNOWLEDGMENTS

I would like to thank the INBRE and ADaPT summer programs for providing me with the opportunity to venture into research. I was fortunate enough to meet so many different people who have shaped how I interpret information and how I can translate that knowledge to others. I appreciate all the researchers in the motor control and learning lab meetings for being so welcoming and willing to share their insight.

I would like to acknowledge Dr. Jared Medina and Dr. Elizabeth Orsega-Smith for serving on my committee and taking the time to provide their feedback. Additionally, this project would not have been possible without my advisor, Dr. Hyosub Kim, who introduced me to the world of coding and set aside time each week to talk through concepts and guide me throughout this process.

Lastly, I would like to thank my family and friends for their unwavering support as I concluded my senior year, particularly my roommate Jennifer Vorn as we tackled the senior thesis process side by side.

TABLE OF CONTENTS

LIST OF FIGURES

ABSTRACT

Sensorimotor adaptation is an implicit motor learning process that corrects and compensates for motor errors, contributing to the successful execution of everyday movements. Previous research into the control of reaching movements suggests that the implicit motor adaptation system is sensitive to two types of error signals - sensory prediction error (SPE), defined as the difference between where visual feedback of hand position is expected to appear and where it actually appears, and target error (TE), defined as the difference between the cursor position and final target position (Leow et al., 2018). Traditional adaptation experiments confound these two error signals, with the SPE and TE typically being the same. This prompted the introduction of shifting targets during reaching movements, a potential means of isolating TE and its effects. We have previously assumed that this method is able to induce a TE by having the target jump to a new location approximately one centimeter into the reach. However, it is unclear whether the motor system processes the target jump as a target error or if the jump introduces uncertainty regarding the SPE, as it is no longer anchored to the original target location. We refer to this latter perspective as a "low-level processing error". Here, we observed the effects of target jumps during three different conditions designed to assess adaptive responses to three combinations of SPE and TE conditions, "amplified", "consistent", and "opposite" in reference to whether the target jump amplified the TE, remained consistent throughout the trial, or elicited a TE in opposition to the SPE. This experiment aimed to determine whether target jumps elicit a TE, independent of SPE, or if they result in non-specific attenuation of adaptation due to low-level processing errors. Support for the former hypothesis would result in a graded amount of adaptation, with the most observed

during amplified trials and the least during opposite trials. In contrast, if target jumps result in low-level processing errors, then adaptation should be attenuated a similar amount during amplified and opposite trials, as the absolute target jump magnitudes were equivalent for these two trial types. Our results revealed a trend towards greater amounts of adaptation during the consistent condition, which had no target jump, compared with less adaptation in the amplified and opposite conditions. These results argue against the interpretation that target jumps elicit a "pure" TE, and suggest that they may have non-specific effects on adaptation from SPE, potentially due to a low-level processing error.

Chapter 1

1.1 Background

There is growing recognition within the field of motor learning that multiple processes contribute to our ability to successfully execute a wide array of skillful movements (Taylor & Ivry, 2014). Among these processes is the formation of explicit, or cognitive, strategies, which place high demands on cognitive resources, demonstrate great flexibility, and generalize broadly (Izawa & Shadmehr, 2011)(Therrien et al., 2016). A plethora of reaching studies have shown that cognitive strategies are largely driven by target error (TE), the difference between the movement goal and movement outcome. In contrast to cognitive strategies, implicit motor adaptation, or recalibration, occurs in an automatic manner, is relatively insensitive to task goals, and generalizes only locally (Shadmehr et al., 2010). A central focus of research into implicit adaptation has been on how this form of cerebellar-dependent, error-based learning, is driven by sensory prediction error (SPE), the difference between the predicted and actual sensory consequences of a given motor command.

Until recently, it has been methodologically difficult to disentangle learning from TE versus learning from SPE. Imagine a simple visuomotor rotation experiment, the traditional gold standard for studying implicit adaptation, in which you control a cursor and try to quickly land it on a target. Unbeknownst to you, a systematic rotation of 30 degrees is placed on the cursor, thus resulting in a large TE, since the cursor lands far from the goal. In addition to the TE, there is also a salient SPE, as your brain expected the visual feedback to follow a trajectory straight to the target, but the actual feedback was of the cursor following a trajectory 30 degrees away from the target. Furthermore, most participants become aware of the perturbation and thus, on subsequent trials, implement cognitive strategies, such as explicitly re-aiming in a direction opposite the rotation in order to get the cursor to land closer to the target. Simultaneously, though, the motor system implicitly recalibrates in response to the SPE. Therefore, absent any assay of where participants are aiming on a trial-to-trial basis, measurement of implicit adaptation is confounded by contributions of cognitive strategies.

The recent introduction of "task-irrelevant" clamped visual feedback, in which cursor feedback is clamped to a specific angular trajectory and participants are fully informed of the manipulation, has provided a means of studying learning from SPE, i.e., implicit recalibration, in isolation (Morehead et al., 2017). The invariant nature of the clamp, combined with the instructions to "ignore the cursor feedback and always aim directly to the target", effectively removes any potential confound of cognitive strategies (Morehead et al., 2017). Experiments using the clamp have revealed several constraints on implicit adaptation, including its automatic, obligatory nature, and relative lack of error-size dependence, except for within a very limited range (Kim et al., 2018; Morehead et al., 2017).

Results from the first studies using the clamp method suggested that the implicit recalibration system is impenetrable to information about target error, given the similar learning functions in response to clamps ranging from 5 degrees – 60 degrees (Kim et al., 2018; Morehead et al., 2017). However, more recent work has cast some doubt on this interpretation. Using a simple target size manipulation, we showed that for equal size clamps, learning was attenuated when the target was large enough for the clamp to hit the target on every trial (Kim et al., 2019). Two different computational accounts were presented in this work to explain this phenomenon. In the Adaptation Modulation model, hitting the target signals a reward which directly modulates the implicit recalibration system (Kim et al., 2019). In the Dual Error model, the implicit recalibration system learns from both SPE and TE in parallel (Kim et al., 2019). Both of these models could accurately account for our behavioral results, and both suggest a novel role for TE in implicit recalibration.

In order to clarify which of these models more accurately characterizes implicit learning from TE, we ran an experiment in which we maintained equal clamp sizes while manipulating TE with varied target jump sizes. Our results suggested that the Dual Error model is a more accurate representation of implicit recalibration from TE. A separate study showed that shifting the target during movement, interpreted as the TE, may modulate implicit recalibration from SPE, as in the Adaptation Modulation model (Leow et al., 2018). However, in these studies the size of the target jump and the size of the TE were not independently manipulated, assuming that a larger target jump would lead to a larger TE. It is unclear whether the observed results were an effect of the magnitude of the TE or of the target jump.

Here, we attempt to control for the confound of TE and target jump magnitude. By manipulating clamp and target jump magnitudes, we were able to examine the independent contributions of target jump versus TE on implicit adaptation. In this manner, we could assess the validity of our previous findings in support of the Dual Error model, where we expect magnitude and sign of the TE to affect overall adaptation. We could also determine to what degree our observation of a distinct TE-learning process was confounded by non TE-specific effects associated with target jumps. If the methods we use are confounded by these low-level processing effects, then we expect to see a generalized attenuation of adaptation, independent of the TE sign.

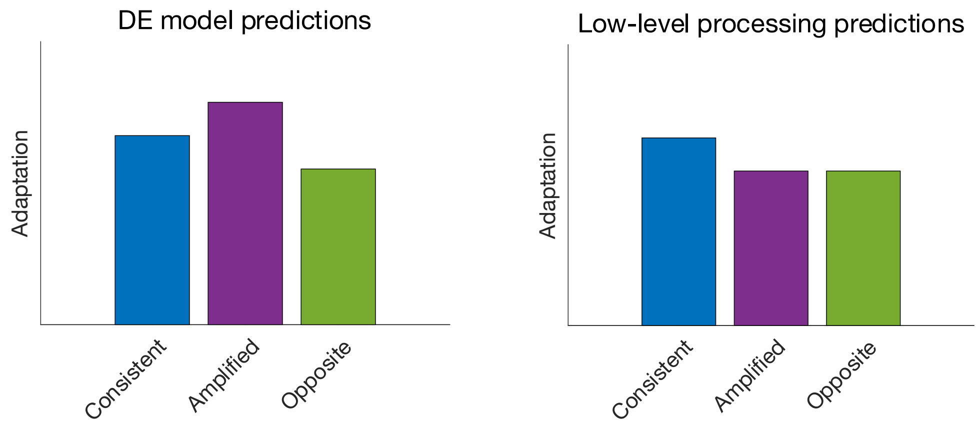

Figure 1. Predictions

Chapter 2

2.1 Methods

2.1.1 Subjects

For this experiment, we recruited a total of 20 healthy, young adults (11 females, age = 23 ± 4 years old [19-33 years old]) from the University of Delaware. We only tested right-handed subjects, confirmed with the Edinburgh Handedness Inventory. All participants provided written informed consent and received monetary compensation for participation in the study. This study was approved by the Institutional Review Board at the University of Delaware.

2.1.2 Experimental Setup

Participants completed the task seated in front of the Kinarm End-Point, a robotic manipulandum combined with a virtual reality environment (Fig. 2). Visual feedback was projected by a monitor placed directly above onto a mirror, which occluded vision of their hand during the experiment. The lights in the room were turned off prior to starting the experiment to improve vision of the screen and decrease vision of their arm. Participants held on to the Endpoint handle as they made reaching movements and were instructed to rest their hands on a disk at the bottom of the handle to minimize the effects of fatigue throughout the experiment. They were also instructed to keep their left hand in their lap or on the side of the table throughout the experiment, preventing interference with right hand movements.

Figure 2. Experimental Setup

2.1.3 Task Protocol

The starting position for every trial was indicated by a white circle. Once the subject reached the white circle, a white feedback cursor appeared representing the location of the handle. After subjects remained within the circle for 500 milliseconds, a blue target appeared 10 centimeters from the starting position. Subjects were instructed to make fast, straight shooting movements through the blue target as soon as the target appeared. Their reaction time was defined as the time from initial target presentation to the start of movement (defined as when the hand first exceeded 5 centimeters/second for at least 50 milliseconds). Their movement time was defined as the time between the start of movement and when the hand crossed the radial target distance of 10 centimeters. To ensure subjects were moving at the proper speed, we set the movement time parameters to 40-70 centimeters/second at peak hand velocity. If the subject's movement time at peak hand velocity was outside of those boundaries, a corresponding message would appear on the screen at the end of that trial, stating either “Too Slow” or “Too Fast”. Subjects received veridical feedback of their hand position only during the baseline trials. After they made their reach, subjects were instructed to relax their arm and shoulder and the robot moved their hand back to the starting position to minimize the effects of fatigue.

2.1.4 Task Structure

The experiment began with 100 baseline trials. This was followed by four perturbation blocks, consisting of 180 trials each. There were 9 different trial types throughout the experiment (Table 1). Each perturbation block was randomized, with a total of 20 trials of each trial type within each block. Each participant received a minimum of a two-minute break in between each block to minimize the effects of fatigue. Overall, participants took about an hour to complete the entire experiment.

For the trials involving a target jump, the target jumped once the participant reached one centimeter outside of the white start circle. All trials also involved the clamp method, where the cursor moves along a fixed path, based on the trial type, independent of the participant’s actual hand direction (Morehead et al., 2017).

Table 1. Trial Types

		Target Jump (degrees)		
		-8	0	8
SPE (degrees)	-4	Opp	Con	Amp
	0	Only tgt jump	No error	Only tgt jump
	4	Amp	Con	Opp

2.1.4.1 Conditions

Participants encountered three different conditions interleaved throughout the experiment (Fig. 3). We operationally defined target error as clamp size – endpoint target location. Assuming the target jumps induce target error, in the amplified condition the TE is larger than the SPE, but they have the same sign, where they are either both positive or both negative. For example, one amplified trial might involve a -4 degree SPE and a -12 degree target error (8 degree target jump). Here, the target error is larger than the sensory prediction error. In this case, the clamped cursor moves four degrees to the right, or clockwise, relative to the original target, independent of the participant's hand direction. Simultaneously, once the participant moves one centimeter out of the start position, the original target will disappear and immediately reappear 8 degrees to the left, or counterclockwise, to the original target location. This trial would lead to an overall -4 degree sensory prediction error and a -12 degree target error, with the TE amplified in relation to the SPE.

In the consistent condition, the TE and SPE are the same size and have the same sign. There is no target jump, but the cursor is either clamped to -4 or +4 degrees. With a +4 degree clamp and no target jump, there is simultaneously a +4 degree SPE and +4 degree TE, due to a misalignment between the target location and the cursor location. The motor system receives visual feedback of the cursor location inconsistent with the target location, creating a +4 degree TE. The +4 degree SPE results from a misalignment between where the participant predicts visual feedback of their hand to be located and where they receive visual feedback of the clamped cursor location, which is interpreted to represent their actual hand location.

In the opposite condition, both error signals are the same size but the signs are in opposition, with one positive and one negative. One trial might have a -4 degree clamp along with a -8 degree target jump. This leads to a -4 degree SPE, and a +4 degree target error, with the signs of the two errors opposing each other.

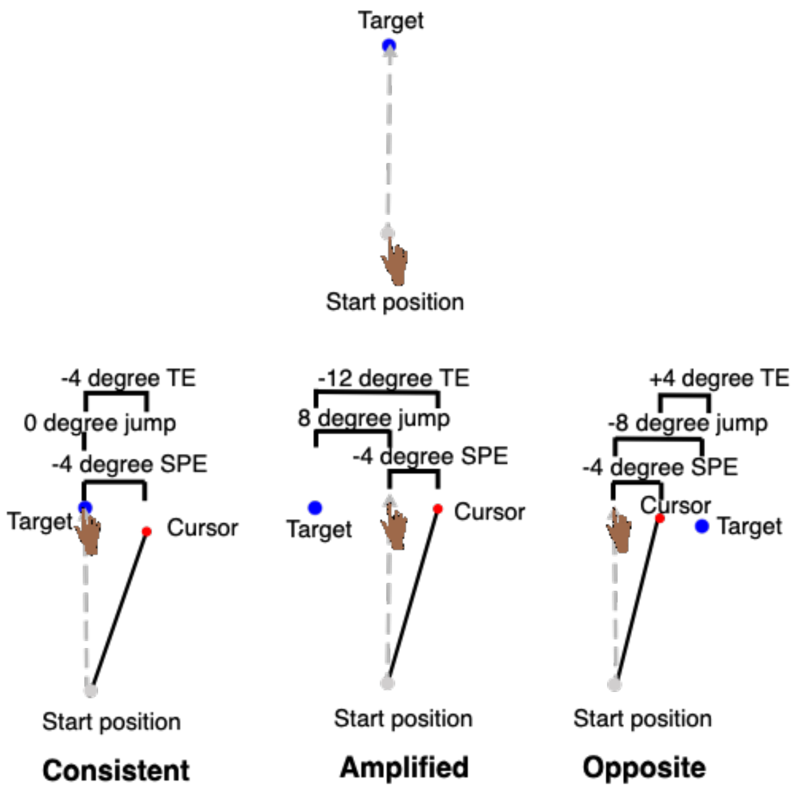

Figure 3. Conditions

2.1.5 Statistical Analysis

All statistical analyses were performed using MATLAB. The primary outcome variable for this study was a change in hand angle. We utilized a regression model to evaluate the relationship between the target jump conditions and the amount of error correction, and thus adaptation. We used the average change in hand angle across all subjects for each condition. The slope of a regression, the beta value, represents the percentage of error that the motor system corrects for. This beta value is multiplied by the perturbation size to predict the change in hand angle. If there is a 4 degree error, and the beta value equals .5, then the model predicts a 2 degree change in hand angle in response to the size of the clamp. To analyze reaction times and movement times, we used the group mean across each subject's median time for each condition. Outliers defined as movement times greater than 1500 milliseconds or reaction times less than 75 milliseconds were not included in the analyses. For all of the dependent variables analyzed (change in hand angle, reaction time, movement time) we also utilized repeated measures ANOVAs to assess differences across the 3 conditions. If the ANOVA was significant, post-hoc t-test comparisons were performed.

Chapter 3

3.1 Results

3.1.1 Responses to target jumps and clamp

When looking at an individual subject's hand trajectories in Figure 4, we can see that they made straight reaching movements during baseline and across the three conditions, indicating that they did not make changes mid-movement. We also see that introducing a perturbation, the target jump, led to a change in hand angle when compared with baseline reaches and trials with 0 degree error. A – 4 degree clamp led to an overall positive change in hand angle, while a +4 degree clamp led to an overall negative change in hand angle. Figure 5 shows an individual's change in hand angle across the three conditions - consistent, amplified, and opposite. Similar results can be seen when evaluating group averaged changes in hand angle for each condition (Fig. 6).

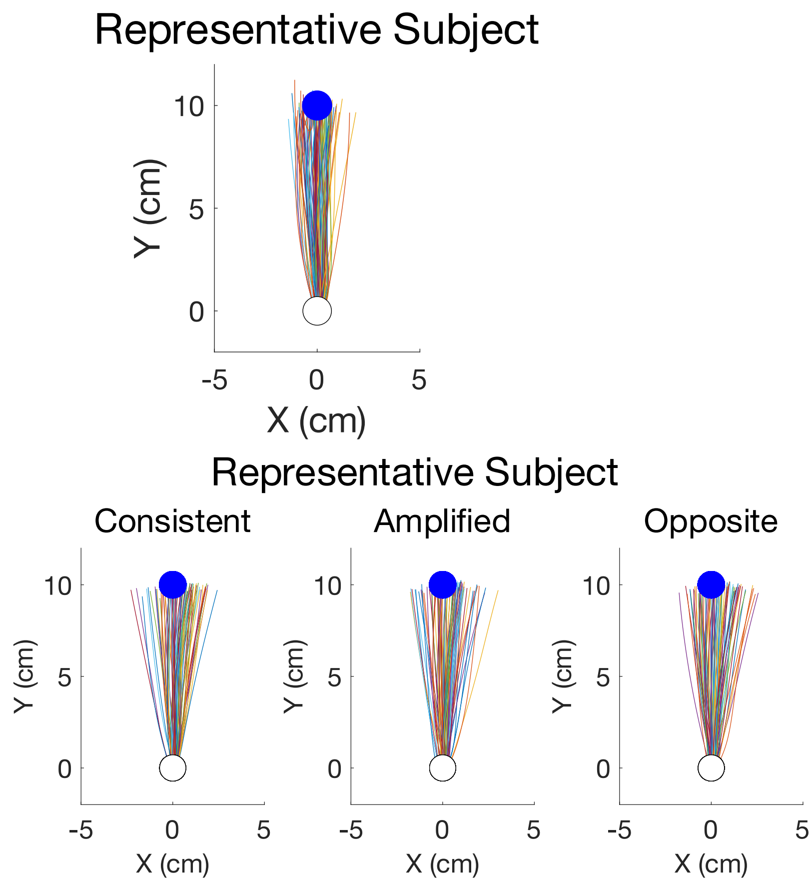

Figure 4. Hand trajectories during baseline and across conditions

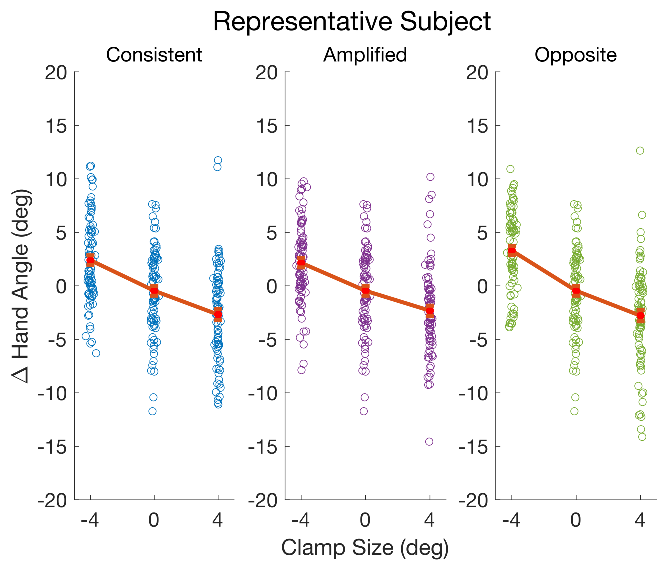

Figure 5. Individual change in hand angle across conditions

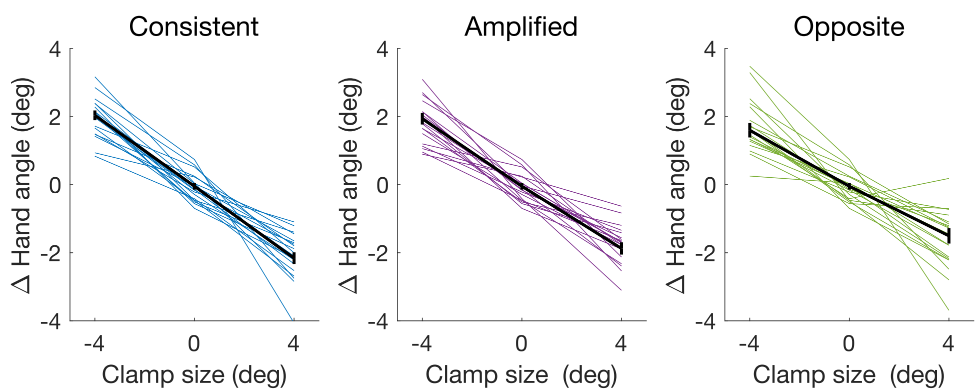

Figure 6. Group averaged change in hand angle across conditions

3.1.2 Error correction

The overall beta value of the regression model was around .5, which can be interpreted as the motor system correcting for about 50% of the error resulting from the clamp. Overall, the greatest amount of adaptation was seen in the consistent condition, y=.543 (Fig. 7). The least amount of adaptation was seen in the opposite condition, y=.362. In the amplified condition adaptation was y=.501. There was not a significant effect of the condition type on adaptation (F (2,38) = 3.07, p = .06).

However, there was some interindividual variability, with the amplified condition inducing the most adaptation, as opposed to the least, in some subjects across the three conditions.

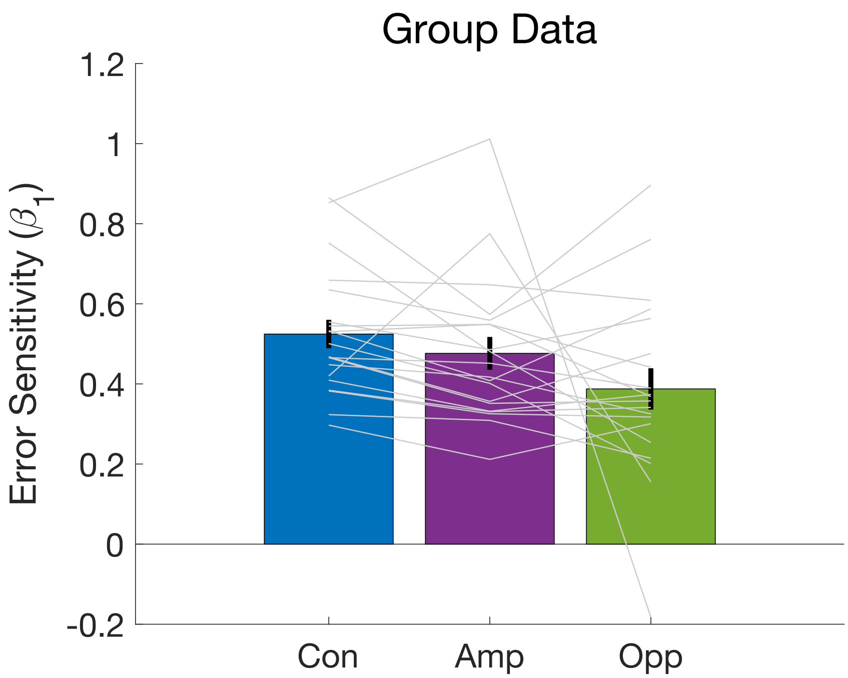

Figure 7. Error sensitivity across conditions

3.1.3 Reaction times

In order to determine whether motor planning may have differed across the conditions, we also analyzed reaction times, the time from initial target presentation to the start of movement (defined as when the hand first exceeded 5 centimeters/second for at least 50 milliseconds). The overall reaction time across participants was mean =

331.5 ± 13.5 milliseconds. There were similar reaction times within participants across conditions, as seen in the representative subject figure, indicating that there was similar motor planning in response to each combination of error (Fig. 8). Similar results are seen when looking at group averaged reaction times (Fig. 9). We did not find a significant effect of condition type on reaction time ($F(2, 38) = 1.77$, $p = .18$).

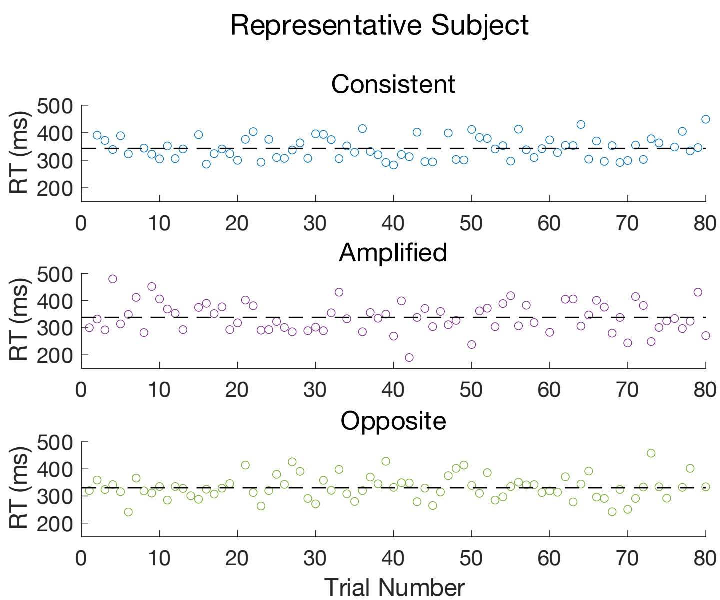

Figure 8. Individual reaction times across conditions

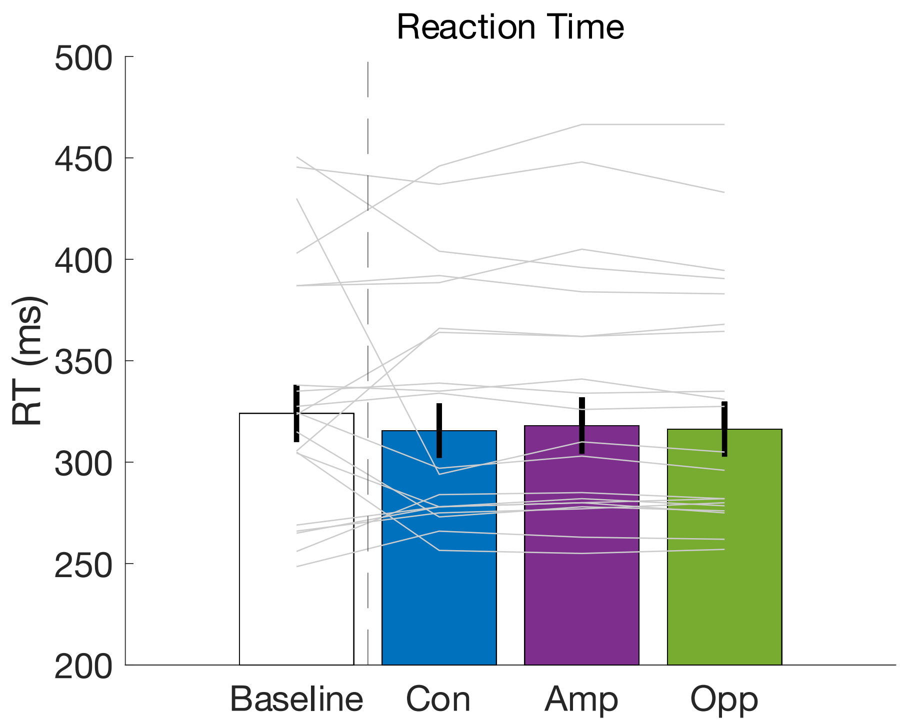

Figure 9. Individual and group averaged reaction times across baseline and conditions

3.1.4 Movement times

We looked at movement times (defined as the time between the start of movement and when the hand crossed the radial target distance of 10 centimeters) to ensure reaches were executed consistently within participants across the conditions. Looking at a representative subject's data, movement times were consistent across the three conditions (Fig. 10). When looking at the group averaged movement times, we did not see an effect of the conditions ($F(2,38) = 1.74$, $p=.19$) (Fig. 11). Note that while we include the baseline movement times in Figure 11, they are there as a point of comparison, but were not included in our analyses. We were primarily interested in how the three different conditions may have affected reaching behavior, and not how behavior changed from baseline to the start of the perturbation blocks.

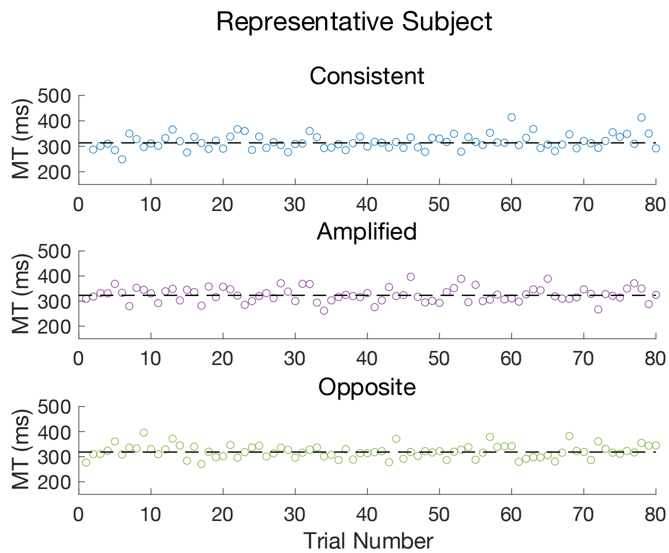

Figure 10. Individual movement times across conditions

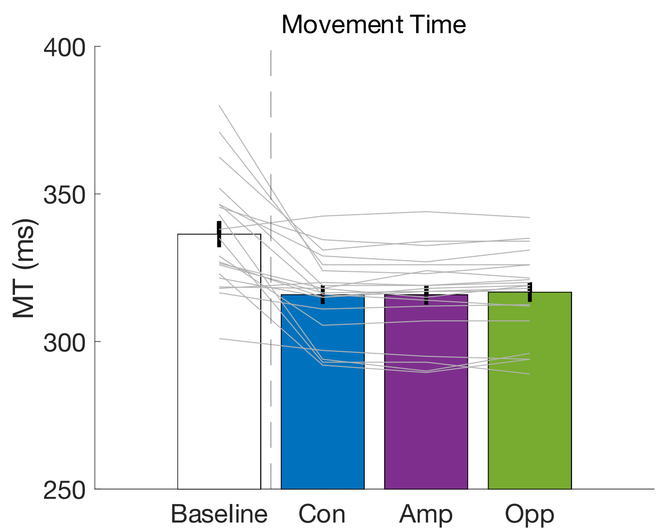

Figure 11. Individual and group averaged movement times across baseline and conditions

3.2 Discussion

Our goal was to assess the validity of our previous findings in support of the Dual Error model and determine to what degree our observation of a distinct TE learning process was confounded by non TE-specific effects associated with target jumps.

Participants were instructed to aim straight for the original target on every trial to counteract the use of cognitive strategies. During the perturbation blocks, they were presented with visual feedback that varied on each trial depending on the condition: consistent, where the TE and SPE had the same magnitude and sign, opposite, with equal magnitudes of TE and SPE but carrying different signs, and an amplified condition, where the two error signals have the same sign but the magnitude of TE is amplified in relation to SPE. We observed implicit recalibration across all of the trials, with the consistent condition showing the greatest amount of adaptation and the opposite condition showing the least. Because consistent clamp sizes of -4, 0, and 4 degrees were implemented across all three conditions, variations in overall adaptation can be attributed to varied TE or target jump magnitude and their role in implicit adaptation from SPE.

Our results are consistent with prior studies that reflect error processing with the perturbation of visual feedback of the target location (Cameron, Franks, Inglis, et al., 2010; Cameron, Franks, Timothy Inglis, et al., 2010; Magescas & Prablanc, 2006). Results from previous studies also suggest that TE may play a role in implicit recalibration (Leow et al., 2018). However, our results indicate that target jumps may not be interpreted by the motor system purely as a TE, suggesting that observed differences in adaptation across conditions may also be due to non-specific attenuation associated with the absolute magnitude of the target jump.

Our previous findings suggested that the Dual Error model was a more accurate representation of implicit recalibration, identifying two individual processes driven by their individual errors, TE and SPE. If target jumps were representative of pure TE, as in the Dual Error model, we would expect to see the greatest amount of adaptation in the amplified condition, which elicits the greatest TE. The consistent condition would produce an intermediate TE, and the opposite condition is predicted to result in the least amount of adaptation, as a result of the SPE and TE opposing each other. Our results show that the consistent and amplified conditions elicit more adaptation than the opposite condition, potentially indicating a TE driven process. However, when evaluating further, we see a greater change in hand angle in the consistent rather than the amplified condition. We interpret this to indicate that the implicit recalibration of the motor system cannot be solely attributed to TE size. Although the amplified trials elicit a larger TE than the consistent trials, the amplified trials also implemented greater target jump magnitudes. The magnitude of the target jump appears to attenuate adaptation, regardless of its sign. This finding contradicts the sign-dependent learning predicted by the DE model.

Overall, the sign-independent attenuation of adaptation we observed suggests that attenuation of adaptation may be due, in part, to target jump magnitude, rather than error processing of TE alone. There is a possibility that target jumps instead attenuate implicit adaptation from SPE. The target jumps may induce a low-level processing error, rather than pure TE, modulating adaptation from SPE. By this view, it is solely the visual feedback of the target moving that attenuates adaptation, rather than the interpretation of target jumps as TE. SPE is defined as the difference between predicted and actual feedback. Typically, the motor system is able to use information from the environment to make a prediction about the feedback that will result from the next motor command. With target jumps, when the target shifts from its original location, we suggest that the variability impacts the motor system's ability to make an effective prediction of where the visual feedback will appear. This is a similar interpretation as suggested by Taylor and Ivry in a study that explored the relationship between strategic and implicit changes during visuomotor adaptation (Taylor & Ivry, 2011). They proposed that due to the uncertainty presented by a shifting target, participants depend on external cues to generate a prediction. As this uncertainty increases, the ability to make an accurate prediction is impacted, leading to attenuated adaptation. We would then expect to see similar adaptation in the amplified and opposite conditions, which both contain the same target jump magnitude. If attenuation of adaptation is an effect of the size of the target movement, the same target jump sizes should be processed similarly as low level processing errors and induce the same amount of noise, therefore weakening the SPE the same amount.

However, our results do not directly support the predictions for either the Dual Error model or a low-level visual processing error. We did not observe significant results between the amplified and opposite conditions, suggesting that modulation of adaptation from target jumps is not a purely TE-driven effect. Another potential interpretation is that the motor system interprets target jumps as a combination of both TE and a low-level processing error.

Additionally, target jumps appear to induce variable adaptation across individuals. Taylor and Ivry also found considerable variability among individuals, suggesting that it may be attributed to multiple sources of noise (Taylor & Ivry, 2011). Although overall, the amplified condition reflects an intermediate amount of adaptation when compared with the other two conditions, in about half of the participants the greatest amount of learning is seen in the amplified condition, while in the other half of participants the amplified trials result in the least amount of learning. There could be subgroups throughout the general population who respond to target jumps differently, which should be evaluated further in future research.

Chapter 4

4.1 Conclusion

Our results have provided insight into the potential effects of target jumps on implicit recalibration. This work shows that target jumps cannot be interpreted as an unconfounded means of eliciting TE. However, these results do not rule out the possibility of Dual Error processing by the adaptation system, only that target jumps may not be the most effective means of eliciting TE. This information is of consequence to the motor learning field, as many have adopted target jumps as a proxy measure of TE. This work also contributes to the existing foundational knowledge of error signals that influence how the motor system successfully executes movements. Ultimately, these findings contribute to a greater understanding of how people learn and process different forms of movement-associated errors.

REFERENCES

Cameron, B. D., Franks, I. M., Inglis, J. T., & Chua, R. (2010). Implicit motor learning from target error during explicit reach control. *Experimental Brain Research*, *206*(1), 99–104. https://doi.org/10.1007/s00221-010-2402-4

Cameron, B. D., Franks, I. M., Timothy Inglis, J., & Chua, R. (2010). Reach adaptation to explicit vs. Implicit target error. *Experimental Brain Research*, *203*(2), 367–380. https://doi.org/10.1007/s00221-010-2239-x

Izawa, J., & Shadmehr, R. (2011). Learning from sensory and reward prediction errors during motor adaptation. *PLoS Computational Biology*, *7*(3), e1002012. https://doi.org/10.1371/journal.pcbi.1002012

Kim, H. E., Morehead, J. R., Parvin, D. E., Moazzezi, R., & Ivry, R. B. (2018). Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Communications Biology*, *1*(1), 19. https://doi.org/10.1038/s42003-018-0021-y

Kim, H. E., Parvin, D. E., & Ivry, R. B. (2019). The influence of task outcome on implicit motor learning. *ELife*, *8*. https://doi.org/10.7554/eLife.39882

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

Magescas, F., & Prablanc, C. (2006). Automatic Drive of Limb Motor Plasticity. *Journal of Cognitive Neuroscience*, *18*(1), 75–83. https://doi.org/10.1162/089892906775250058

Morehead, J. R., Taylor, J. A., Parvin, D. E., & Ivry, R. B. (2017). Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience*, *29*(6), 1061–1074. https://doi.org/10.1162/jocn_a_01108

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience*, *33*, 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135

Taylor, J. A., & Ivry, R. B. (2011). Flexible Cognitive Strategies during Motor Learning. *PLoS Computational Biology*, *7*(3), e1001096. https://doi.org/10.1371/journal.pcbi.1001096

Taylor, J. A., & Ivry, R. B. (2014). Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Progress in Brain Research*, *210*, 217–253. https://doi.org/10.1016/B978-0-444-63356-9.00009-1

Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2016). Effective reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. *Brain: A Journal of Neurology*, *139*(Pt 1), 101–114. https://doi.org/10.1093/brain/awv329