Movement-Based Cues Aid the Formation and Retrieval of Multiple Motor Memories

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Abstract

The ability to switch between different visuomotor mapping accurately and efficiently is an invaluable feature to a flexible and adaptive human motor system. This can be examined in dual adaptation paradigms where the motor system is challenged to perform under randomly switching, opposing perturbations. Typically, dual adaptation doesn't proceed unless each mapping is trained in association with a predictive contextual cue. To investigate this, in Experiment 1 I explored whether dual adaptation occurs if cued by distinct movement types (ballistic or pursuit/tracking reaches), and how adaptation to a perturbation while tracking an object generalize to ballistic reaches. Next, motivated by Experiment 1 findings that support the idea that "intrinsic" or motor-based cues (i.e., pertaining to a distinct goal) is key to dual adaptation along with recent work that shows the critical role of motor planning in dual adaptation, in Experiment 2 I looked at whether movement skew as elicited by distinct visual obstacles can facilitate dual adaptation. Next, in Experiment 3 I look at whether intrinsic cues need to be actively produced to elicit dual adaptation. Additionally, to better understand the underlying components of dual learning, I implement a Process Dissociation Procedure borrowed from cognitive sciences literature to understand the underlying explicit and implicit processes contributing to dual adaptation. In Experiment 4 I give participants an explicit strategy to drive learning where it otherwise would not occur due to an insufficient extrinsic visual cue. Finally, to understand dual adaptation in the most ecologically valid manner, in Experiment 5 I implemented the conventional virtual reality paradigm in Head-mounted VR, while also answering how the brain attributes error in this novel setup. Together, these findings provide further insight as to how the motor

system plans movements and learns to adapt to an ever-changing environment, and the underlying mechanisms that drive it.

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Chapter One: General introduction

Humans are perpetually faced with the task of maintaining motor performance in an ever-changing environment, whether those changes are external such as manipulating a new tool or moving underwater, or internal such as adapting to an injury or fatigue of a limb. This process is called motor adaptation, and it refers to a behavioural change that involves adjusting a well-practiced action to maintain performance in a fluctuating environment (Krakauer et al., 2019). The rise of modern technologies has nevertheless exacerbated the demand on the motor system to adapt and switch between different recalibrated or learned mappings of vision and movement, also referred to as visuomotor mappings (Wise et al., 1996). Indeed, the practical relevance of studying motor adaptation is well appreciated, given its applications to sports, rehabilitation, animal training, and musical practice to name a few.

Motor adaptation has been studied as far back as the nineteenth century by von Helmholtz, using prism goggles to induce changes in the environment (von Helmholtz, 1866). Modern paradigms utilize non-standard mappings in virtual reality paradigms, where visual feedback and movement of the hand can be decoupled, allowing for greater precision and flexibility in manipulating feedback and context (Gorbet & Sergio, 2009; Wise et al., 1996). These widely used modern methods, such as inducing a perturbed visual feedback of a hand-cursor representing the unobserved hand, has allowed for the detailed characterization of the mechanisms behind motor adaptation (e.g., Figure 2.1 C). For instance, we know that removing visual feedback of the hand following motor adaptation to a visuomotor perturbation leads to reach aftereffects—a compensatory adaptive response in the absence of the perturbation. Additionally,

movement aftereffects following visuomotor adaptation are local to the trained direction and thus, shows a narrow generalization pattern that drops off as a function of the angular distance away from that trained direction (Donchin et al., 2003; Krakauer et al., 2000; Thoroughman & Shadmehr, 2000). Although simplified, these methods of studying motor adaptation in the laboratory provide foundational insights into the components of learning motor skills in real life, while maintaining experimental rigour at a relatively short period of time.

A perplexing phenomenon in motor adaptation is the way in which humans display seamless transition between different tasks accurately and efficiently. In daily life, we frequently use different tools, correct for errors while using them, and then anticipate the consequences of switching to a completely different tool or environment. Although we may start with large errors when first learning to move under a novel circumstance, our motor systems adapt quickly, such that eventually we produce smooth, accurate movements despite behavioural or environmental constraints. What affords the motor system this remarkable flexibility?

1.1 Dual adaptation or anterograde interference

Motor adaptation is thought to arise through the updating of an internal model of body dynamics (Hollerbach & Flash, 1982). In the experimental setting, we typically probe the ability of the Central Nervous System (CNS) to maintain and recall multiple internal models, sometimes referred to as motor memories, simultaneously by introducing variants of the same environment serially (i.e., ABA paradigm) or concurrently (i.e., dual adaptation paradigm). While ABA designs typically investigate whether the learning of one internal model will be affected by the subsequent learning of

another (e.g., Tong & Flanagan, 2003), dual adaptation designs allow us to see simultaneous learning, acquisition, and switching between internal models. A typical dual adaptation paradigm involves training with opposing visuomotor perturbations (e.g., visuomotor rotations, force fields) and performance can be measured as in conventional visuomotor learning paradigms, where a reduction in movement errors across training, and following training the presence of systematic deviations in the absence of visual feedback of the movement (i.e., reach aftereffects) for both perturbations implicates dual learning.

Adaptation to one perturbation (A) can impede the ability to adapt to a second perturbation (B), a phenomenon known as interference. More specifically, anterograde interference refers to interference of learning the second perturbation B in the future, after adapting to the initial perturbation A. Retrograde interference then refers to the adaptation to B interfering with the retrieval of A. Typically, interference is the greatest when adaptation to B immediately occurs following A, and gradually reduces as the time elapsed between perturbation exposures increases. This was thought to reflect the consolidation of a motor memory—an offline learning process whereby recently learned memories are transformed into long term (Brashers-Krug et al., 1996), although interference has been documented to occur even when time between perturbation exposures was spaced out up to 24 hours (Caithness et al., 2004).

As expected, dual adaptation to both visuomotor variants does not proceed when there is a lack of predictability of the impending perturbation from trial to trial, even with ostensibly salient visual cues that prompt a change in the necessary visuomotor mapping (e.g., Baldeo & Henriques, 2013). Indeed, interference has been found in

several studies that examine the successive adaptation to two or more perturbations (Brashers-Krug et al., 1996; Caithness et al., 2004; Karniel & Mussa-Ivaldi, 2002; Krakauer et al., 1999). A key question further complicates the phenomenon of anterograde interference: i.e., what cues prevent it and why are they successful at doing so?

1.2 Contextual dependence in dual learning

Simply observing how humans interact with their physical environments suggests that the efficacy of a contextual cue might not be as arbitrary as it seems. A cue can be any contextual signal orthogonal to the sensorimotor transformation necessary for adaptation itself, such as the sensation of wearing eyeglasses that signals the use of a distinct gain of the vestibulo-ocular reflex (Krakauer et al., 2019; Wolpert & Kawato, 1998). For instance, certain visual features of an object, such as its colour, might not convey useful information to the CNS for motor planning. Indeed, extrinsic cues such as visual features of the target tend not to provide any additional predictive information for the motor system (Baldeo & Henriques, 2013; Woolley et al., 2007). Dual adaptation as facilitated by extrinsic cues has been found to occur (Krouchev & Kalaska, 2003; Osu et al., 2004), or not occur (Baldeo & Henriques, 2013; Gupta & Ashe, 2007; Hegele & Heuer, 2010; Hinder et al., 2008; Hirashima & Nozaki, 2012; Woolley et al., 2007). For example, one study by Woolley and colleagues used background colour as a predictive cue and found no evidence for dual adaptation while training with opposing visuomotor rotations (Hinder et al., 2008; Woolley et al., 2007). Likewise, Baldeo & Henriques (2013) found similar results after integrating target and cursor colour as predictive visual cues. Interestingly, using a more explicit approach with colour cues to facilitate dual

adaptation, Osu and colleagues (2004) found that participants were able to dual adapt to opposing force-field perturbations after distributed training over two consecutive days, although these results may have been influenced by large practice breaks which may have led to facilitated learning through enhanced consolidation of the motor memories (Brashers-Krug et al., 1996), and a rather contextually rich environment. Interestingly, visual cues that indicate the orientation or the specific control point of the object being manipulated can facilitate dual adaptation (Heald et al., 2018; McGarity-Shipley et al., 2020; Proud et al., 2019). Together, these mixed findings cast doubt on the general efficacy of extrinsic cues, and when they do elicit dual adaptation, it remains unclear what qualities differentiate them from those which are ineffective.

On the other hand, humans frequently interact with certain features of our environments by using a different end-effector or recruiting distinct muscle patterns. Unlike extrinsic cues, intrinsic (or “motor-based”) cues have been shown to be more promising in enabling dual adaptation (Ayala et al., 2015; Ayala & Henriques, 2018; Baldeo & Henriques, 2013; Galea & Miall, 2006; Gandolfo et al., 1996; Wang & Musseler, 2014; Woolley et al., 2011). This is likely because generalization of motor learning depends on context, which is determined based on the history of the prior movement of that end-effector (Baraduc & Wolpert, 2002; Krakauer et al., 2006). In fact, using different target set (distinct hand trajectories) and end effectors (left and right hands), humans can even adapt to four perturbations (Thomas & Bock, 2012). Indeed, Krakauer and colleagues demonstrated that when adapting to visuomotor rotations, the extent by which this adaptation generalizes depends on the proximity of the novel target direction compared to the trained direction (Krakauer et al., 2000). Baraduc and Wolpert

(2002) further showed that even when the target or hand path direction is identical, reach aftereffects and thus, generalization, become smaller when reaches are made with increasingly different arm postures than the one used during training with a visuomotor rotation (i.e., the upper arm becomes more adducted relative to the arm posture used during training). Ayala, ‘t Hart, & Henriques (2015) were able to elicit dual adaptation to opposing visuomotor rotations by simply changing hand and body postures (and thus, the joint angles) associated with each perturbation. Interestingly, even an illusory grasp (or a lack thereof) of the end-effector can facilitate dual adaptation (Cothros et al., 2009), a finding which starts to hint at what type of information the motor system values when adapting and retrieving multiple motor memories.

Dual adaptation is further impeded when hand trajectories overlap, slowing the learning rate compared to adaptation to a single perturbation. This is evidenced by a shallower learning curve for adaptation to reaches towards overlapping targets compared to that of separated targets (Baldeo & Henriques, 2013; Wang & Musseler, 2014; Woolley et al., 2011). While reaching with distinct hand trajectories requires distinct motor programming, planning movements with identical or overlapping trajectories is more ambiguous to the motor system and thus, require context to dissociate between internal models. Indeed, Schween et al. (2018) showed that opposing rotations can be learned simultaneously for physically identical movements if each is associated with a distinct workspace (left visual workspace vs. right visual workspace). Furthermore, we have shown that enhanced association between the cues and the visuomotor variants through extended training does not lead to further

reductions in reaching error or larger reach aftereffects, suggesting that cue-dependent dual adaptation saturates over time (Ayala et al., 2015).

A recent pivotal study by Sheahan and colleagues used distinct follow-through movements as contextual cues and dissociated the contributions of motor planning and execution by manipulating the timing of the presentation of the follow-through targets (Sheahan et al., 2016). To isolate the planning component, participants saw both initial (perturbed) and follow-through targets as they initiated their reach, but the follow-through target was extinguished to signal to participants that a follow-through motion is not required. Their main finding, that compensation occurs even in the absence of the execution of the follow-through, suggests that the key component in representing motor adaptation lies in action planning, and not in the act of executing a physically different limb state. Thus, it has then been suggested that interference during dual adaptation is not simply a low-level mistake by the motor system, but a high-level cognitive mistake, with extrinsic cues showing inefficacy since they simply do not differentiate a distinctive goal (Krakauer et al., 2019; Sheahan et al., 2016).

1.3 Explicit and implicit components of dual adaptation

How much of motor adaptation relies on overt cognitive processes? While this topic is beyond the scope of this review, there is now consensus that motor learning is not simply driven by a single mechanism. This line of research was spurred by the fundamental finding that providing participants the cognitive or explicit component of learning via an aiming strategy during adaptation drives a sensory prediction error, due to a mismatch between the intended direction of the unobserved hand and the observed direction of the cursor, leading to drift or a worsening of task performance (Krakauer et

al., 2019; Mazzoni & Krakauer, 2006). Accordingly, recent research looking at the role of instruction show that adaptation can be characterized by at least two qualitatively different learning mechanisms: (1) an explicit process which arises due to the implementation of conscious aiming strategies (Heuer & Hegele, 2008; Taylor et al., 2014), and (2) an implicit process which is thought to operate outside of awareness, reflect adaptation of internal models in the cerebellum, and largely produce reach aftereffects (Heuer & Hegele, 2008; Taylor et al., 2010).

In one of their dual adaptation experiments, Schween and colleagues (2018) show that overlapping strategies lead to interference, but when provided with compensatory strategies, participants show overall learning and reach aftereffects (Schween et al., 2018). However, they implemented large alternate training blocks (of 8 trials) during dual training and large rotations which may more easily lend itself for strategy implementation. Thus, it remains unknown to what extent explicit and implicit processes contribute to dual learning in most of this literature, and whether explicitly mediated dual adaptation engages the implicit system.

1.4 Computational models of dual adaptation

While the mechanism behind dual learning remains unclear, it has been theorized that it arises due to the formation of distinct, separate motor memories (i.e., internal models). One popular model is the Modular Selection and Identification for Control (MOSAIC) theory, which suggests that a contextual switching mechanism must exist in order to change between internal models of specific motor commands and sensory states (Haruno et al., 2001). Thus, for dual adaptation to proceed, a specific contextual cue must be associated to each of the visuomotor variants experienced. This

predictive cue provides information about the impending sensorimotor mapping via responsibility predictors which add greater weighting on the probability of encountering one of the perturbed environments over the others (Haruno et al., 2001; Kawato, 1999). This view has been challenged recently, where it was argued that dual adaptation might not require the formation of separate visuomotor mappings. Using a generalization paradigm, Schween & colleagues (2018) had participants adapt to large opposing perturbations and had them reach to targets in novel directions after dual adaptation training. They found that not only can their participants explicitly judge the direction of the two perturbations, but they also generalized their learning around these movement plans. Critically, the generalization pattern for these two perturbations were indistinguishable from each other, suggesting that only a single mapping is utilized, and that dual learning arises as a single Gaussian with localized dents around the movement plan or trajectory (Schween et al., 2018). While these models provide us with a mechanism for understanding how humans can dually adapt, they do not inform us on what qualifies for an effective contextual cue or the actual cues themselves.

In sum, in the currently limited number of studies across a wide variety of paradigms investigating what kinds of contexts are useful to the motor system, it is evident that motor-based cues tend to be more successful at facilitating learning, yet not all are adequate sources of contextual information. Especially so, when hand trajectories overlap in cases where reach targets are similar or identical, contextual cues and strategies need to be employed to prevent interference and enable learning. Although recent work shed light on a critical component characterizing effective

contextual cues (i.e., the role of motor planning), there remains a need to reveal what aspects of a cue enable learning and what mechanisms allow it to proceed.

1.5 Overview of the project

In this series of experiments, I further explore what contextual features aids the human motor system in adapting and preserving what it has learned despite constraints in time and movement workspaces. I examined a variety of contexts that may aid in dual learning, both in the ubiquitous 2D paradigm, and in an enriched 3D virtual reality environment, parcelling out what components may lead to a successful cue. Additionally, I examined the role of explicit processes in dual learning by providing verbal instruction and compensatory strategies. To answer these questions, I used the dual adaptation paradigm where participants experienced randomly presented opposing perturbations to the visual feedback of their movement. Specifically, across all conditions, participants reached towards visual targets using a visual hand-cursor controlled by their unseen right hand. All experiments included two control groups ("SINGLE" conditions), each learning only a single visuomotor perturbation (i.e., a clockwise (CW) *or* a counterclockwise (CCW) rotation, relative to the starting position), and thus, a single context (e.g., a visual cue flanking left of the target). In the critical "DUAL" groups, the visuomotor perturbation experienced (CW or CCW) changed from trial-to-trial, with each predicted by a distinct contextual cue.

In the first series of experiments (Chapter 2), I implemented the dual adaptation paradigm to determine whether different movement types (such as tracking and reaching) can facilitate dual learning. I further examined the extent to which tracking movements generalize to reaching movements (Ayala & Henriques, 2018). I

hypothesized that adaptation of perturbed tracking movements generalize to that of reaching movements. Given this prediction, there should be significant reach aftereffects in both expected directions after training with rotated reaching and oppositely-rotated tracking movements. In other words, I hypothesize that what was learned during tracking trials will transfer to reaching trials (in the form of reach aftereffects). Additionally, I hypothesize that participants will be able to concurrently adapt to two opposing visuomotor rotations given the intrinsic contextual cue in the form of movement types (tracking vs. reaching). This was expected to manifest in a significant reduction in reaching errors across rotations over time.

Motivated by findings from Experiment 1 and recent work that shows the critical role of motor planning in dual adaptation, in the second series of experiments (Chapter 3), I used distinct visual obstacles as contextual cues to determine whether path obstructions that elicit differently skewed movements can facilitate dual learning. I hypothesized that participants in the DUAL obstacle group will be able to dual adapt given the intrinsic contextual cues in the form of movement skew. If participants were able to dual adapt, there will be a reduction in reaching errors for both rotations. Given unexpected behaviour from participants because of the visual obstruction, I also looked at whether performance differs between obstructed and unobstructed targets, to understand where learning generalized across differently obstructed targets. I hypothesized a faster rate of learning for unobstructed targets compared to obstructed targets. This would be evident in smaller reaching errors by block 2 of training for unobstructed targets.

For the third series of experiments (Chapter 4), my objective was to better understand what information the motor system is using when for distinctly planned motor-based cues (Ayala & Henriques, 2020, under review). I looked at whether motor cues need to be actively produced, or if merely passively viewing the movement sequences can sufficiently facilitate dual learning. In the second experiment of this chapter, I investigated the role of instruction using the second part of the previous set of experiments as the control group. Unlike the first part of Chapter 4 experiments, here participants were given detailed instructions on how to counter the dual perturbations, and the relationship of those perturbations to the visual cues. I hypothesized that groups who received active sequence cues will show a significant simultaneous reduction in reaching errors (i.e., dual adaptation) and reach aftereffects. If this is true, this will suggest that movement sequences facilitate dual adaptation. Next, I hypothesized that those who only observe a passive (or visual) movement sequence will not show significant dual adaptation or reach aftereffects. This will imply that active, not passive movement sequences facilitate dual learning. Finally, I hypothesized that there will be no significant dual learning or reach aftereffects in the control group that will receive only a static visual cue to distinguish the opposing rotations.

In the final experiment (Chapter 5), I wanted to approach the problem with a more ecologically valid lens, while validating some key questions to characterize motor learning in a novel 3D setting (Head-mounted VR environment). I adapted the dual adaptation paradigm to HMD-VR to determine whether a contextually richer and thus, more motivating environment will elicit dual learning when it has not been shown to be effective before in the 2D tablet environment. Because HMD-VR is still relatively new to

motor learning research, I used the control conditions to additionally ask how the motor system assigns error in this novel environment by looking at patterns of transfer of learning between trained and untrained limbs, and novel and trained objects. For this experiment, I chose stimuli pairs that have a clear relationship to further engage and enrich the training session, and to maintain a clear task goal for each context. I hypothesized that in this immersive 3D paradigm, dual adaptation can be elicited by visual cues (object identity), manifesting in reduced reaching errors and significant reach aftereffects for both opposing rotations. If this is true, then it will suggest that dual adaptation to extrinsic cues is possible if the task is engaging enough, reconciling previous work. Additionally, I hypothesized that there will be significant transfer of learning between trained and untrained limbs, although reduced in the untrained limbs based on literature on bimanual transfer. Consequently, I predicted no significant transfer of learning between distinct objects, which would suggest that some error would be attributed to the trained object.

In the final chapter (6), I summarize the findings of my research. What cues facilitate dual adaptation and what characteristics make a sufficient contextual cue? How are underlying mechanisms of adaptation differently engaged in dual adaptation? Can a highly immersive and engaging HMD-VR paradigm adequately elicit dual adaptation to task-relevant extrinsic cues? My research shows that our ability to concurrently adapt and retrieve multiple visuomotor mappings can take advantage of explicit mechanisms of learning when implicit mechanisms are not engaged and depends on whether the cue is extrinsic or intrinsic to the motor system, in either

conventional VR or HMD-VR settings.

Chapter Two: Context-dependent concurrent adaptation to static and moving targets

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2.1 Abstract

Is the neural control of movements towards moving targets independent to that of static targets? In the following experiments, we used a visuomotor rotation adaptation paradigm to examine the extent to which adapting arm movements to static targets generalize to that of moving targets (i.e., pursuit or tracking). In the first and second experiment, we showed that adaptation to perturbed tracking movements generalizes to reaching movements; reach aftereffects following perturbed tracking were about half the size (≈9°) of those produced following reach training (≈ 19°). Given these findings, in the final experiment we associated opposing perturbations (-30° and +30°) with either reaching or tracking movements and presented them within the same experimental block to determine whether these contexts allow for dual adaptation. We found that the group that experienced opposing perturbations was able to reduce both reaching and tracking errors, as well as produce reach aftereffects following dual training of ≈7°, which were substantially smaller than those produced when reach training was not concurrent with track training. This reduction in reach aftereffects is consistent with the extent of the interference from track training as measured by the reach aftereffects produced when only that condition was performed. These results suggest partial, but not complete, overlap in the learning processes involved in the acquisition of tracking and reaching movements.

2.2 Introduction

To adapt and acquire new motor skills, the motor system must learn novel relationships between motor commands and their subsequent sensory consequences. The formation of these novel relationships (or “mappings”) allows us to maintain accurate movements despite having to switch from one behavioral or environmental context to another. To determine what affords the motor system this flexibility, we can associate specific contexts with distinct mappings and observe how this affects motor learning. When no context is provided, it is extremely difficult to adapt to opposing visuomotor mappings (Brashers-Krug et al., 1996; Shadmehr & Brashers-Krug, 1997). However, when suitable contextual cues are associated with two or more distinct mappings, “dual adaptation” has been found to occur across different types of sensorimotor transformations including lateral prism shifts (e.g., Galea & Miall, 2006), force-fields (e.g., Gandolfo et al., 1996; Howard et al., 2013a), and visuomotor rotations (e.g., Baldeo & Henriques, 2013; Wang & Musseler, 2014). While a range of contextual cues have been examined, it remains unknown whether distinct types of movement can facilitate dual learning. Here, we explore the extent to which tracking movements (towards moving targets) generalize to reaching movements (towards static targets), and whether the motor system is able to distinguish and retrieve opposing visuomotor mappings using these distinct movement types as contextual cues.

The current literature suggests that contextual cues related to the state of the end-effector best facilitate dual adaptation. In force-field adaptation tasks, it appears that visual cues unrelated the state of the arm such as target, cursor colour, or background colour yield no changes in compensatory forces (Gandolfo et al., 1996;

Howard et al., 2013b), while other cues relying more on proprioceptive feedback such as workspace locations (i.e., reach directions) seem to be more effective (Green & Labelle, 2015; Howard et al., 2013a; Hwang et al., 2003; Klintsova et al., 2004; Woolley et al., 2011). In visuomotor adaptation tasks, dual adaptation has been shown to occur by associating different starting locations which elicited distinct arm postures, different hands, as well distinct postures of the hand or the body, to opposing visuomotor rotations, to name a few (Ayala et al., 2015; Bock et al., 2005; Wang & Musseler, 2014). Altogether, these findings from both force field and visuomotor adaptation paradigms suggest that sensory information related to the arm provide the most useful information for allowing for concurrent motor learning. Here, we investigate another possible parameter related to the state of the arm that may facilitate dual learning: movement type.

Current models which explain the role of context in motor control suggest that distinct neural populations may be involved depending on the context variant (Nozaki et al., 2006; Nozaki & Scott, 2009). Indeed, in recent theories of limb control, neural activity in the cortex is thought to reflect a dynamical system in which a preparatory state has a mechanistic role for the upcoming movement generation activity (Ames et al., 2014; Churchland et al., 2012). This has been supported by neurophysiological findings by Ames and colleagues (2014) in a movement delay and target switch task. They found that when there is no movement delay during a target switch condition (i.e., an action requiring a new motor plan), a new preparatory state is achieved that takes a parallel and separate path through the neural state space (Ames et al., 2014). These findings could potentially explain the role of context and movement planning in

concurrent learning, where different motor plans are required given a specific context. Indeed, after discovering the role of follow-through movements in adapting to opposing force-field perturbations, Howard and colleagues postulated the idea that different contexts might engage separate neural populations or perhaps simply alter the preparatory state (Howard et al., 2015). More recently, Sheahan and colleagues (2016) showed that the planning of movements is a fundamental component in concurrent learning of opposing force-field perturbations. In their experiments, the planning component was isolated by having participants adapt to opposing force-field perturbations that were each predicted by a secondary target that either appears (i.e., execute secondary movement) or disappears mid-movement (i.e., do not execute secondary movement). They found that planning a secondary movement even without its execution allows for concurrent adaptation of opposing force-fields, even to the same extent as having always executed the planned movement (Sheahan et al., 2016). These findings emphasize the importance of motor planning and the relevant movement parameters in dual adaptation.

While our aim is to investigate the cues necessary for concurrent adaptation within the same training block, interference studies that look specifically at task-dependent learning may also offer some insight as to what possible cues allow for dual adaptation. A key finding is that task dissimilarity seems to reduce interference experienced when learning opposing perturbations in a series of interference tasks (Tong & Flanagan, 2003). In one experiment by Tong and Flanagan (Tong & Flanagan, 2003), participants reached to a clockwise (CW) rotation, followed by exposure to an opposing counter-clockwise (CCW) rotation when doing either the same reaching task

or a different arm movement task (figure-eight drawing or continuous random tracking). Firstly, participants were able to adapt serially to the successive CW and CCW rotations, regardless of the task type. However, on retest of the reaching task, those who adapted to opposing rotations for the same task experienced the most interference while those who experienced opposing rotations for different tasks performed similarly as controls (Tong & Flanagan, 2003). Their findings show that two different tasks can be learned in close succession with very little interference. Similarly, a set of recent ABA studies by Morehead and colleagues (Morehead et al., 2014) looked specifically at transfer across different tasks and found the greatest amount of generalization when the training and test context were most congruent. Due to the constraints of the serial ABA interference paradigm, we are unable to infer how different tasks may affect each other (i.e., how tracking adaptation affects reaching adaptation), and ultimately, how both can be learned concurrently. These provide the insight that it is possible to learn a series of related tasks performed on separate blocks of training (i.e., ABA paradigm), but do not necessarily reflect whether they can be learned within the same block. To this end, we implement a concurrent learning paradigm in the present experiments to challenge the motor system to form and interchangeably use two distinct visuomotor mappings.

In addition, while both Tong & Flanagan (Tong & Flanagan, 2003) and Morehead et al. (Morehead et al., 2014) suggest that the environmental context is conducive to reducing interference, they do not allow us to infer specifically which aspects of the environment allow for this. This is because different tasks may also require different movement parameters that may have unique and independent contributions in facilitating dual adaptation. For instance, Tong & Flanagan (2003) found no interference

when a different task was associated with the opposing interfering task that required movements in different directions, velocities, and task endpoints suggesting that subjects were planning movements for a completely different workspace as point-to-point reaching. Thus, these differences suggest that each task required a different movement type as well as an entirely distinct movement path (i.e., radial reaching movements vs. tracking movements in pursuit of an erratically moving target). On the other hand, in their series of serial ABA experiments, Morehead et al. used a gradually-introduced rotation under different training tasks including point-to-point reaching and random pursuit movements amongst others (Morehead et al., 2014). The reach aftereffects produced following center-out and target-to-target reach training were the largest, presumably due to the similarity of the training and test learning contexts, while the least amount of transfer occurred for random movements. Using a laterally displaced cursor, Simani et al. found that track training of randomly moving targets led to reach aftereffects and track aftereffects of similar magnitude (Simani et al., 2007). The cause of the positive transfer in Morehead et al. (2014) and Simani et al. (2007) and the lack of interference in Tong & Flanagan (2003) are not clear, however, since certain movement types may require different movement directions which, on its own, have been shown to be successful at facilitating dual adaptation (Baldeo & Henriques, 2013; Woolley et al., 2011). In a similar experiment, gradual introduction of the perturbation may also exert some effect as it has been shown that dual adaptation can occur when both rotations are gradually introduced (Hirashima & Nozaki, 2012). Thus, to eliminate these possibilities and isolate the role of different movement types, we introduced the perturbations abruptly while holding movement and task endpoints

(targets) constant across perturbations. As a result, both reaching and tracking tasks require very similar outward movements with only the type of movement serving as the uniquely contributing contextual cue.

The key objective of the following experiments was to determine whether adaptation to a perturbation with distinct movements generalize to other movement types, specifically whether tracking movements towards moving targets generalize to reaching movements towards static targets, and further, to see if these distinct movement types can facilitate dual adaptation. First, we examined whether adaptation to a rotated tracking task produces significant learning and reach aftereffects. One group of participants made out-and-back reaches to static targets with a 30^{o} CW-rotated cursor while a different group tracked a moving target with a 30^{o} CCW-rotated cursor. If adapted tracking movements do not entirely generalize to reaching movements (seen via reach aftereffects following adaptation to a perturbed tracking task), it is possible that distinct reaching movement types can facilitate adaptation to two opposing visuomotor rotations (i.e., dual adaptation). To this end, we completed another experiment in which we used a concurrent (dual adaptation) interference paradigm to investigate the efficacy of different movement types in facilitating the acquisition of opposing visuomotor mappings. In this third group of participants, both reaching (associated with a 30^{o} CW-rotated cursor) and tracking (associated with a 30^{o} CCW-rotated cursor) trials were interleaved within the same experimental block. This task is distinct from the typical interference task such that adaptation to both visuomotor rotations can be analyzed as they are acquired simultaneously.

2.3 Methods

2.3.1 Participants

Fifty-four participants (eighteen males and thirty-six females, 19.97 ± 2.44 years old, mean ± SD) were recruited and assigned to participate in the following experiments and were granted a bonus credit for an undergraduate psychology course. All participants were right-handed, had normal or corrected vision, and were naïve to the purpose of the experiment. All participants provided written, informed consent. Procedures were approved by York University's Human Participant Review Committee and were in accordance with the declaration of Helsinki. Due to arm discomfort, two participants chose to discontinue and were excluded from the experiments.

2.3.2 Apparatus

Participants sat on an adjustable chair facing a digitizing tablet (Wacom Intuos3, 12" x 12" surface, resolution of 5080 lines/inch, sampled at 50 Hz) and screen. The tablet was placed at waist level so that hand movements were made along the horizontal plane (See Figure 2.1 for detail). An Epson 3LCD projector rear-projected an image onto the screen located approximately 60 cm from the tablet workspace. To prevent participants from observing their arm movements, an opaque shield was placed above the tablet work surface (Baldeo & Henriques, 2013; Balitsky Thompson & Henriques, 2010; Dionne & Henriques, 2008). All tasks involved five radially spaced targets located at 60°, 75°, 90°, 105°, and 120°. All targets began at a common starting point located 12 cm away from the home position (during the reaching trials) or beginning at the home position and landing at the same final positions (during tracking trials). Participants acquired the targets (1.5 cm in diameter) using a hand-held stylus

that they moved across the surface of the tablet, moving a cursor (1 cm in diameter) on the screen (Figure 2.1B). The relationship between hand and cursor was similar to using a desktop computer; movements were made with a 1:1 ratio.

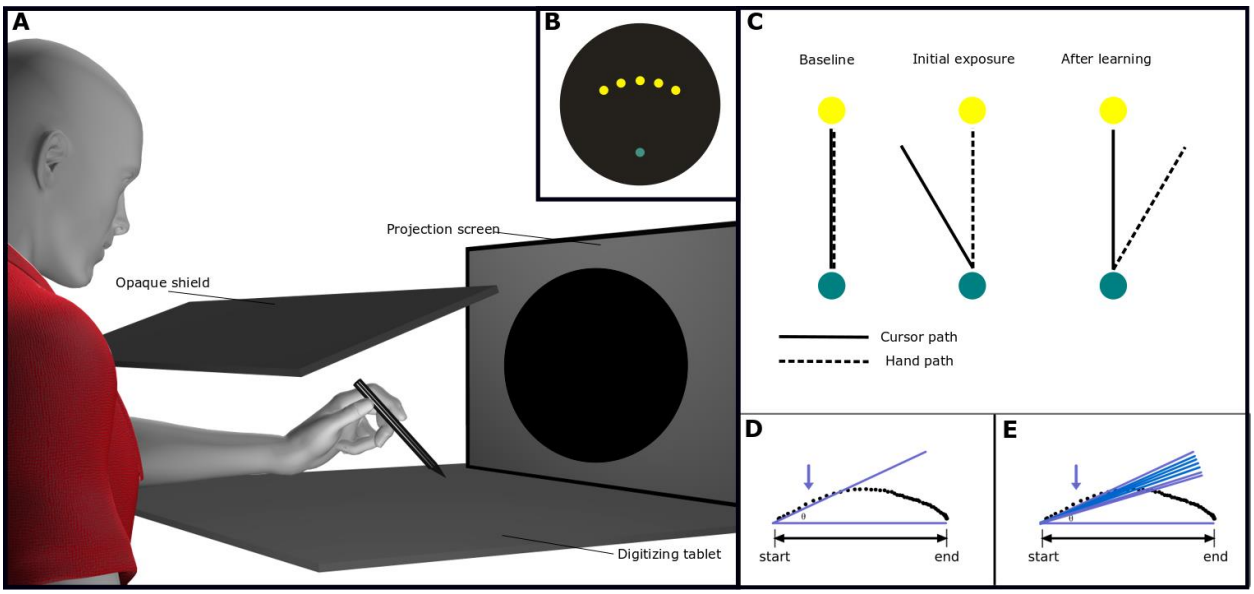

Figure 2.1. Experimental apparatus and display of target. Stimuli were projected (using a projector) on a vertically positioned screen approximately 60 cm away from the tablet. Participants reached or tracked targets on a digitizing tablet (A) using a handheld stylus on the horizontal plane while observing a projected image of the targets and cursor on a circular-edged vertical screen. The light blue circle represents the home position (B). The five yellow circles represent the five possible locations for the target (60°, 75°, 90°, 105°, 120°) which were the same across reaching and tracking trials. (A) is depicted as mirror image. C. Typical visuomotor rotation paradigm with an exposure to a 30° CCW rotation. Dashed lines represent the unseen hand path while solid lines represent the cursor path. Key measures of reaching error. D. Key measures of reaching error (1) Angular error at maximum velocity is the angular difference of the target and cursor at the maximum velocity of hand movement. Black dots represent reaching movement samples and θ represents the angular error at maximum velocity. E. (2) Root-mean-square-error reflects the mean absolute error of every movement sample relative to the straight path to the end target. The blue lines represent a sample from all angular errors that are considered when calculating the RMSE.

2.3.3 General Procedure

In the first experiment (henceforth referred to as the “SINGLE reaching experiment”), we examined adaptation to a single visuomotor rotation while reaching to

static targets (Figure 2.2A). This experiment served as a control group for the following two experiments. In the second experiment (henceforth referred to as the “SINGLE tracking experiment”), we examined adaptive tracking movements to a semi-predictable target trajectory when presented with a visuomotor rotation (Figure 2.2B). Additionally, we examined whether this adaptation to a rotated tracking task influences reach adaptation by looking at any present reach aftereffects following rotated tracking training. Reach aftereffects from the SINGLE reaching experiment served as the control for that of the SINGLE tracking experiment. Given the results of the SINGLE tracking experiment, we conducted another experiment (henceforth referred to as the “DUAL adaptation experiment”) where we investigated whether dual adaptation to tracking and reaching movements occurs when each type of movement was associated with distinct and opposing visuomotor rotations (Figure 2.2 C). Tracking adaptation results from the SINGLE tracking experiment served as the control group for the tracking trials in the DUAL adaptation experiment. Reach adaptation results from the SINGLE reaching experiment served as the control group for the reaching trials in the DUAL adaptation

experiment.

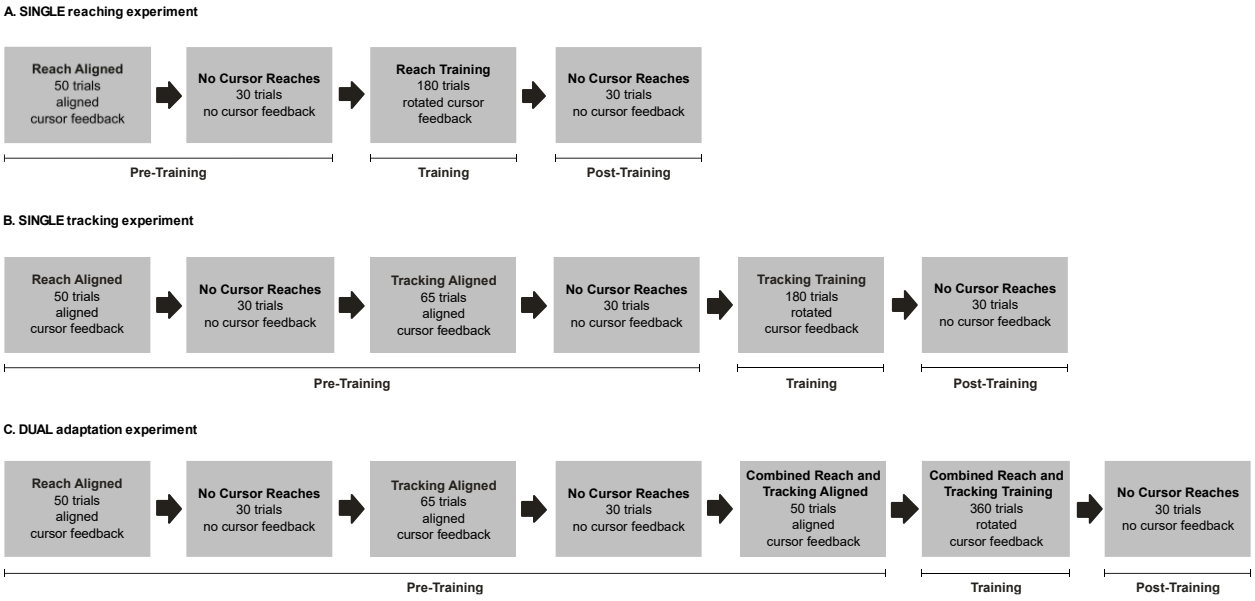

Figure 2.2. Session sequence. Session sequence for the SINGLE reaching experiment (A), the SINGLE tracking experiment (B), and the DUAL adaptation experiment (C). For the SINGLE experiments, only one distortion was experienced throughout training: counter-clockwise (CCW) for the SINGLE tracking experiment, and clockwise (CW) for the SINGLE reaching experiment. The DUAL adaptation experimental group experienced both reaching and tracking trials, which were associated with CW and CCW rotations (i.e., with the same association as in SINGLE reaching and tracking experiments), respectively. Critically, no-cursor trials were identical across all conditions – there was no visual feedback of the cursor and thus were all open-loop reaches.

Depending on the trial type (TRACK or REACH trial), participants either tracked a moving target or reached toward a static target. TRACK and REACH trials were preceded by “T” and “R” across all experiments, respectively. Targets appeared 12 cm away from home position (REACH trials) or moved 12 cm from home position (TRACK trials) but all reached the same 5 possible final target locations of either 60 °, 75°, 90°, 105° or 120°. All participants started at the same home position and were told to either make smooth and direct reaches to the target (REACH trials) or follow the target as closely and accurately as possible (TRACK trials). For TRACK trials, the moving targets took 1500 ms to cover the 12 cm distance (8 cm per second) for all but the initial 15

baseline trials. This incremental change in overall movement time ensured that participants were initially accustomed to pursuing the target, and were able to adjust to a faster speed as the condition progressed. During baseline aligned (veridical) tracking trials in both the SINGLE tracking and DUAL adaptation experiments, the overall movement time of the target started off at 1800 ms at trial 1, and decreased by increments of 20 ms during each trial until it reached 1500 ms. By trial 16, the target movement time was always 1500 ms, including trial 1 of the rotated tracking conditions.

To aid and motivate the participants during TRACK trials, the colour of the target changed depending on the distance of the cursor from the target. The target appeared green when the cursor successfully overlapped with the target, yellow when it was 1 to 4 cm away, orange when it was 4 to 8 cm away and red when it was more than 8 cm away from the target. The home position appeared as a light blue circle on the screen (1.6 cm), and the cursor appeared as a smaller white circle (1 cm). Each target appeared individually in a pseudo-randomized order.

For trials involving visual feedback of the hand-cursor (also referred to as “closed-loop trials”), participants pursued a moving target, or reached towards a static target in order to complete the trial. For trials involving no visual cursor feedback (also referred to as “open-loop trials”), participants reached towards the target with their unseen cursor, and remained stationary for 500 ms until the home position appeared. Visual feedback of the hand-cursor appeared when participants were within a 2 cm radius of the home position. In order to facilitate returning to the home position and proceed to the next trial during open-loop trials, a smiley-face represented the home position that changed in orientation depending on the position of the pen. We also

placed a physical, solid edge located just below the home position to help guide movement back to home position. Prior to no-cursor trials, participant were merely told that the cursor would not be visible. We did not include any specific instruction (i.e., to implement a strategy as in Taylor et al., 2014) since recent work by Werner and colleagues (Werner et al., 2015) and results from our lab suggest that for small rotations, instruction for the no-cursor tasks does not affect the size of the reach aftereffect.

We did not measure tracking aftereffects due to the assumption that smooth tracking (i.e., maintaining the same speed as that produced during training) would require a visible cursor. Instead, we exclusively captured reach aftereffects for all three groups. This allowed us to test for whether adaptation of tracking movements could transfer to reaching movements and whether concurrent training of tracking and reaching movements while each was associate with an opposing perturbation would interfere (i.e., reduced reach aftereffect in the DUAL group).

For each experiment, participants completed pre-training, training, and post-training sessions. In both the SINGLE tracking experiment and the SINGLE reaching experiment, participants completed the task in approximately one hour. In the DUAL adaptation experiment, participants completed the task in approximately two hours. Participants were not informed regarding the presence or nature of the rotation at any point in the experiments. After the experiment, participants answered a series of questions to assess their awareness of the rotation and the experimental objectives.

2.3.4 Experiment 1: SINGLE reaching experiment

Nineteen participants completed the SINGLE reaching experiment, which served as the control group for the reaching trials in the DUAL adaptation experiment. During training, these participants experienced a 30º CW rotation of the cursor (Figure 2.2 A, box 3); this was congruent with the associated rotation and movement type in the DUAL adaptation experiment (Figure 2.2 C, box 6).

Aligned training (baseline measures). The aim of the pre-training session was to obtain baseline performance and familiarize participants with the task. Participants reached for static targets 50 times with visual feedback of the aligned cursor, followed by 30 reaches with no visual feedback of the cursor (i.e., no-cursor) in order to record baseline open-loop reach errors (Figure 2.2 A, boxes 1 & 2).

Rotated Reach Training (adaptation) and post-training (reach aftereffects). The aim of training was to expose participants to a single visuomotor rotation in order to assess the learning rate and reach aftereffects to compare to the reaching conditions in the DUAL adaptation experiment. Participants reached 180 times with a 30º CW rotated cursor, followed by 30 no-cursor reaches (Figure 2.2 A, boxes 3 & 4).

2.3.5 Experiment 2: SINGLE tracking experiment

Aligned training (baseline measures). Seventeen participants completed the SINGLE tracking condition. During pre-training sessions, participants reached towards static targets (REACH trials), and tracked moving targets (TRACK trials), both with an aligned cursor (Figure 2.2 B, boxes 1 & 3). The aim of the pre-training session was to familiarize participants with the tasks and capture baseline performance. During the aligned REACH training session, participants reached 50 times to static targets,

followed by 30 no-cursor reaches to record baseline reach aftereffects. During the aligned tracking pre-training session, participants tracked moving targets 65 times, followed by 30 no-cursor reaches. The extra 15 trials for baseline tracking was to familiarize participants with the task; again, the target-movement duration began at 1800 ms but gradually reduced to 1500 ms duration for the remaining trials and for all the rotated tracking trials.

Rotated Tracking Training (adaptation) and Post-Training (after-effects). Participants experienced a 30^{o} CCW rotation during rotated training while tracking a moving target 180 times (Figure 2.2 B, box 5). This was followed by 30 no-cursor reaches to assess generalization of what was learned during tracking trials towards reaching movements.

2.3.6 Experiment 3: DUAL adaptation experiment

Aligned training (baseline measures). Sixteen participants completed the DUAL adaptation experiment. Like the SINGLE tracking experiment, DUAL participants reached 50 times with aligned visual feedback of the cursor (Figure 2.2 C, box 1), followed by 30 no-cursor reaches. Then, participants tracked moving targets 65 times with an aligned cursor (Figure 2.2 C, box 3), followed by 30 no-cursor reaches. Lastly, participants completed a condition combining both the reaching and tracking tasks. Participants either reached towards a static target 25 times or tracked a moving target 25 times with an aligned cursor (Figure 2.2 C, box 5).

Dual Training (adaptation) and Post-Training (reach aftereffects). During rotated training in the DUAL adaptation experiment, participants experienced opposing visuomotor rotations, each associated with either TRACK or REACH trials, in order to

determine whether dual adaptation can occur when cued by different types of movements. Participants in the DUAL group experienced both a 30^{o} CW rotation (associated with REACH trials) and a 30^{o} CCW rotation (associated with TRACK trials). Again, prior to each trial, participants saw a visual cue to indicate whether to expect a REACH or a TRACK trial (i.e., a “T” appeared before tracking trials and an “R” appeared before reaching trials). Participants completed 180 REACH and 180 TRACK trials (Figure 2.2 C, box 6). REACH and TRACK trials were presented in a pseudo-randomized order such that participants encountered all five possible targets for each type of trial (and thus, rotation) before any target location was repeated. This was followed by 30 no-cursor reaches. Reaches during no-cursor trials were always made towards static targets due to the difficulty in acquiring a moving target without visual feedback, or controlling for tracking speed of the unseen hand.

2.3.7 Data Analysis

Cursor movement data was digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was fixed at 10% of peak velocity for REACH trials and 33% of peak velocity for TRACK trials. Tracking and reach adaptation to a visuomotor rotation can be assessed using a variety of dependent measures. For reaching tasks (including no-cursor trials), performance was quantified using “angular error at maximum velocity” which refers to the angular difference of the target and cursor at peak velocity relative to the home position (Figure 2.1 D). Due to the novelty of the semi-predictable tracking task, we reported several alternative performance measures as well as other movement time descriptors

(described further below). For all our analyses involving blocks, we averaged across blocks of 5 trials (which include a movement to each target).

Analysis of Reaching Adaptation (reach training and no-cursor trials). To compare reach adaptation between groups who received SINGLE or DUAL training, we compared angular reach errors across the first trial, the second block, and the final blocks of trials using a 3 (block) x 2 (group, SINGLE vs DUAL) mixed analysis of variance (ANOVA) followed by post-hoc t-tests with Bonferroni correction. In order to fully show the rapid learning occurring in the initial stages of learning, we chose to analyze the very first trial. Not only does blocking the initial stage of learning mask the rate of adaptation, these rapid trial-dependent changes will lead to a highly variable measure compared to those produced in later stages of adaptation. The overall difference between the first trial and the last block reflect the extent of learning, while the second block (relative to the first) provides a rough estimate of the learning rate. A one-way ANOVA (three levels: first trial, second block, final block) was used afterwards to show whether adaptation has occurred within each group. We also compare the performance between groups during the final block of rotated training to further show the magnitude of adaptation achieved.

Reach aftereffects refer to rotation-dependent, deviated reaching in the absence of visual feedback of the cursor. They were assessed by comparing the first block of trials after rotated-cursor training with the final block of trials after aligned-cursor training. To quantify reach aftereffects, we took the differences in no-cursor reach errors following rotated and aligned-baseline training. Then, to determine whether these reach aftereffects differed across the three groups, we ran a one-way ANOVA with three

levels (SINGLE reaching group, SINGLE tracking group, DUAL group). Follow-up analyses using independent t-tests with Bonferroni correction revealed which pairs of groups had significantly differed in the magnitude of reach aftereffects.

Analysis of Tracking Adaptation (TRACK trials only). We used several measures of tracking performance (Figure 2.1 E). Our main measure was the Root-mean-square-error (RMSE) which we calculated as follows:

$$RMSE = \sqrt{\sum_{i=1}^{N} \left(\theta_{\text{cursor}}(i) - \theta_{\text{target}}(i)\right)^2 / N} \quad (2.1)$$

where $\theta_{cursor}(i)$ and $\theta_{target}(i)$ represent the cursor and target position in Cartesian co-ordinates at the i^{th} sample, respectively, and N is the total number of samples of the tracking trajectory in a trial. As participants adapted to the visuomotor rotation, we expected the RMSE to decrease, such that cursor-to-target tracking trajectories aligned over training trials. As we did with reach training, we assessed this adaptation while participants tracked a moving target by comparing the first trial, the second block, and the final block using a 3 (block) by 2 (group) mixed ANOVA, followed by post-hoc comparisons. These blocks allow us to assess the extent of adaptation, as well as the rate of learning. A one-way ANOVA (three levels: first trial, second block, final block) was used to show whether adaptation has occurred within each group. We also tested whether tracking performance during rotated-cursor training returned to baseline levels by comparing the final block of trials of rotated-cursor training with those for aligned-cursor training for each group using dependent t-tests. The assumed level of significance was $\alpha = .05$, and post-hoc comparisons were Bonferroni-corrected.

Additional Tracking Descriptors (TRACK trials only). To quantify overall tracking ability, we examined the change in the distance and time between the target and the cursor-movement onset (defined as the time when the cursor motion reached 33% of its peak velocity, i.e., tracking-cursor movement onset). Thus, we measured the time it took for the cursor to move in response to target motion ("target pursuit latency") and their respective distance at cursor-movement onset ("cursor-to-target onset distance"). Aside from movement latency, we also analyzed overall cursor movement time from movement onset (passing the onset cutoff at 33% of maximum velocity) until offset (until the offset cutoff at 33% maximum velocity) using the same method as the main tracking measures. This overall cursor movement time is yet another descriptor of how well participants are able to match the target movement of 1.5 s (excluding familiarization trials where target movement is <1.5 s). We applied the same statistical analysis to these additional measures as we did to the main tracking measures.

To further quantify and illustrate the change in reaching and tracking errors across training, we fitted a single exponential function to all datasets across all blocks (of 5 trials) of training and averaged across participants, for each rotation and group using VEEL (http://veel.sourceforge.net/). The equation takes the form:

$$RD = be^{(-ax)}+c \qquad (2.2)$$

where x represents the block number, a the rate of learning, c the asymptotic level of performance, and b the scaling factor.

2.4 Results

We examined whether visuomotor adaptation to tracking movements (towards moving targets) generalize to that of reaching movements (towards static targets) and

further, whether these different types of movements were distinct enough to allow for dual adaptation to opposing perturbations. First, we tested whether participants can adapt tracking movements towards moving targets in response to a visuomotor perturbation and then immediately had them reach towards static targets and compared this to a group that only adapted their reaches to static targets. Next, we associated opposing perturbations to either reaching or tracking movements and presented them within the same experimental block.

2.4.1 Reach adaptation (Performance during training)

Figure 2.3 illustrates mean hand path trajectories for each experiment and condition for the initial and final blocks bounded by 95% confidence intervals. As REACH trials (Figure 2.3 B & D) were associated with a 30° CW rotation, participants compensated with reaches in the counterclockwise direction. Participants produced large, rotation-dependent reaching errors that reduced over training, exhibited by straighter trajectories

that approach pre-training levels.

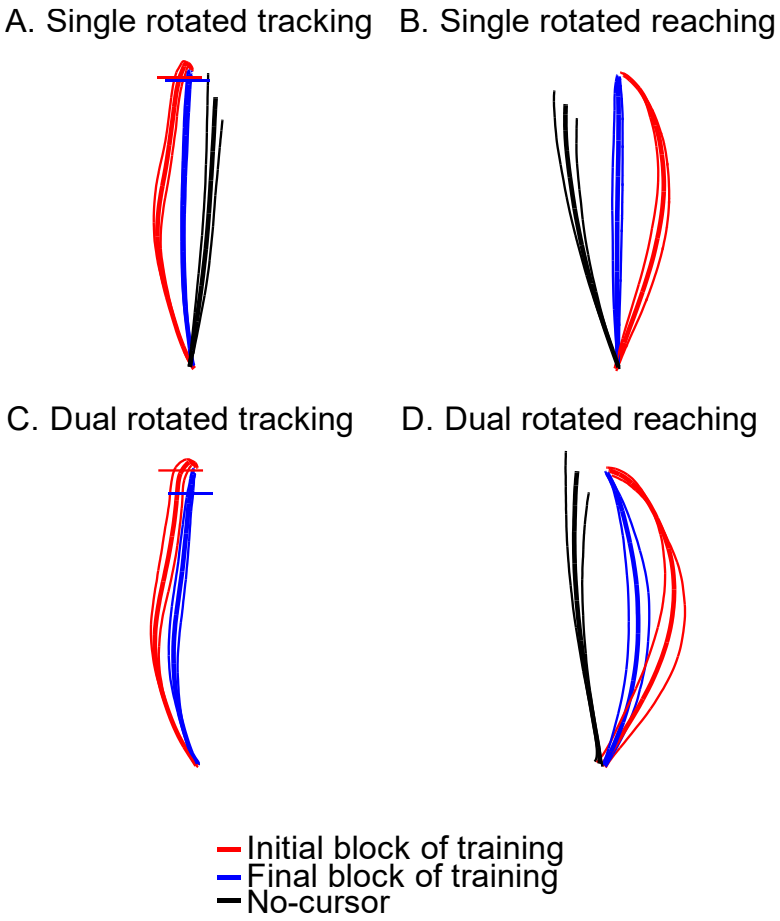

Figure 2.3. Average cursor trajectories for SINGLE and DUAL groups separated by rotations and collapsed across all target locations. Shown are mean hand paths for the SINGLE tracking group (A), the SINGLE reaching group (B), DUAL tracking trials (C), and DUAL reaching trials (D). Mean paths for the first five trials are in red and the last five trials in blue. The mean (central solid line), 95% confidence limits (two thin bordering lines) are plotted across all participants for each groups and rotation. Solid black lines represent mean paths for No-Cursor trials where there was no visual feedback of the cursor. There were no No-Cursor trials associated with the DUAL tracking trials as all No-Cursor trials are considered reaches (i.e., target is static). Horizontal lines for tracking trials depict the location of the cursor when the target halted at its final location.

To illustrate adaptation, Figure 2.4 shows the mean angular reaching errors produced by both the SINGLE group (green) and the DUAL group (blue) across all rotated-reaching trials (A) and for the first trial, the second block, and the final block (B). We

fitted exponential curves to the blocked mean angular errors and show them in red dashed lines for both groups; each curve resembles a typical exponential curve associated with motor learning (Krakauer et al., 2000).

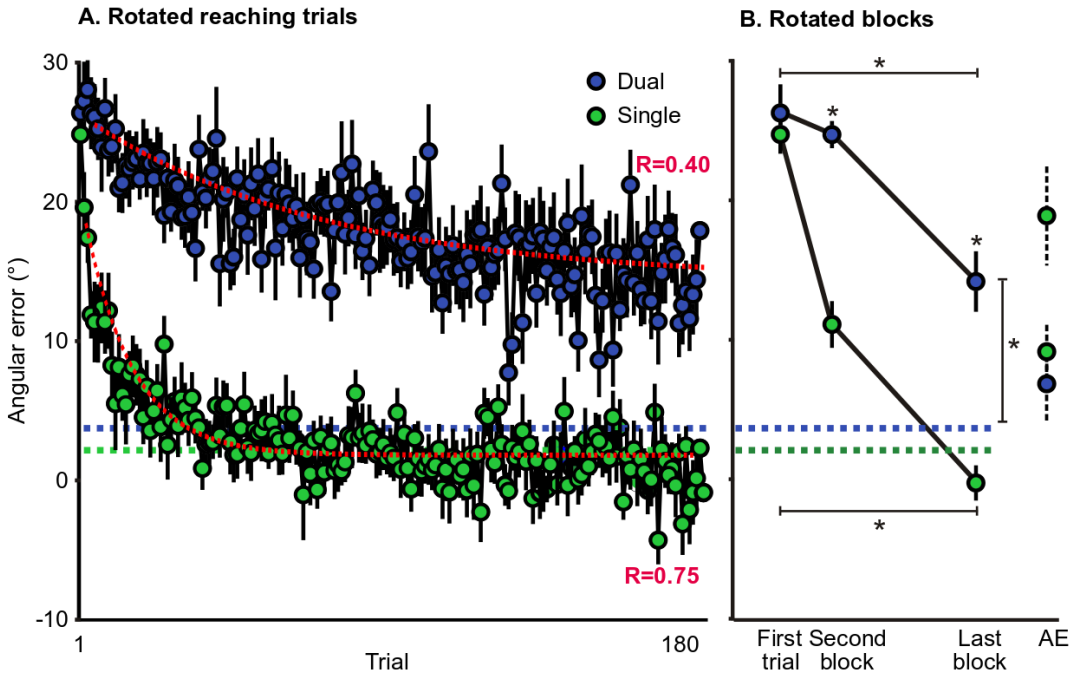

Figure 2.4. Angular reach error across rotated training for the SINGLE and DUAL groups for reaching trials only. Mean reach errors are depicted across all rotated training trials (A) and the initial trial, second block, and final block of 5 trials, in green for the SINGLE reaching-only group and in blue for the reaching trials for the DUAL group (B). Green and blue dashed lines represent baseline levels from aligned reaching conditions. Red dashed lines represent fitted exponential curves for reach deviations for the entire training session with the equation $RD = be^{-ax}+c$. For the SINGLE group, $RD = 16.72^{-0.07x} + 1.65$, and for the DUAL group, $RD = 11.17^{-0.01x} + 14.33$. Single data points with dashed error bars in (B) represent normalized reach aftereffects (AE) for each group (actual reach directions can be seen in Figure 2.7). Error bars represent SEM.

As evidenced by straighter reach trajectories (Figure 2.3) and fit to typical exponential learning curves (Figure 2.4), reaching errors significantly reduced across

the first trial, the second block, and the final block, but this reduction differed significantly between SINGLE and DUAL groups ($F(2,30)=12.25$, $p <0.001$). Nonetheless, we saw a significant reduction in error across training in the DUAL group ($F(2,30)=13.76$, $p<0.001$) although this was smaller compared to that of the SINGLE group ($F(2,36)=116.21$, $p<0.001$). To estimate the learning rate, we compared the second block of training trials between groups, and found that the SINGLE group was already showing a significantly larger reduction in error compared to the DUAL group ($t(33)=-7.47$, $p <0.001$). By the end of training, the DUAL group still made larger reaching errors compared to the SINGLE group ($t(33=-6.69$, $p<0.001$). Thus, it appears that the DUAL group was able to show a significant reduction in error but not at the same rate or to the same extent as that of the SINGLE group. That is, movement type provided a viable context for each opposing visuomotor mapping such that less interference was experienced when both adapting to track a moving target and reach to a static target.

2.4.2 Tracking adaptation (Performance during training and baseline)

Before exploring tracking adaptation (spatial accuracy), we first wanted to verify that participants were able to temporally pursue the moving target. Solid traces in Figure 2.5 A and B show the distance the cursor moved in the direction of the target motion (shown in dotted trace) across time for the final block of training in both the aligned (black solid line) and rotated blocks (red solid line for the initial block and blue for the final block). For aligned training as well as the initial block of rotated-training, participants were reasonably able to keep up with the target, following only approximately a half-second (or a couple centimeters) behind. This suggests that

introducing the rotation did not disrupt how closely participants were able to pursue the target, although it took longer to acquire the target site likely because of the direction-related correction due to the rotation. In other words, altering the visual feedback of the cursor did not disrupt the ability to pursue a moving target with regard to timing.

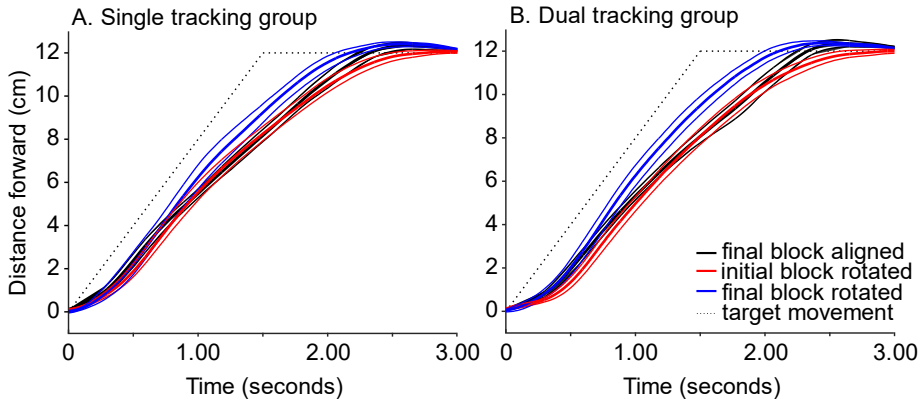

Figure 2.5. Mean cursor displacement. Mean cursor displacement across time for both aligned and rotated tracking trials for the SINGLE tracking group (A) and DUAL (B) tracking trials. Mean paths for the last five aligned tracking trials are depicted in black, while the first five rotated tracking trials are depicted in red and the last five rotated tracking trials in blue. The first block of the aligned trials was omitted as it largely overlaps with the final block of aligned trials. The mean (central solid line), 95% confidence limits (two bordering lines) are plotted across participants for each groups and conditions (aligned or rotated). The dashed line represents the semi-predictable path of the target with an overall movement time of 1500 ms.

After confirming that the visuomotor rotation did not disrupt pursuit speed, we can now examine the effect of the perturbation on pursuit accuracy. This effect can be seen in Figure 2.3A and C, where the 30° CCW rotation (associated with tracking trials) led to large deviations in hand motion during the first block of training (red traces). Evidently, tracking movements became less deviated by the final block of tracking training (blue traces) for both the SINGLE (Figure 2.3 A) and DUAL (Figure 2.3 C) groups.

To assess adaptation during rotated tracking training, we measured tracking

error as the accumulated difference between the moving cursor and target (RMSE). Tracking errors are plotted across trials in Figure 2.6 A and across the first trial, the second block, and the final block in Figure 2.6 B. Tracking errors from the first rotated trials were three times larger than those produced in the aligned tracking condition for both SINGLE and DUAL groups; we found no difference between groups at this point ($t(31)=-0.47$, $p=0.640$). This initial trial was subsequently followed by a reduction in tracking error that varied in magnitude depending on the group ($F(2,32)=8.11$, $p<0.001$). That is, while both tracking errors significantly decreased across training for the both the SINGLE ($F(2,32)=73.24$, $p<0.001$) and DUAL ($F(2,30)=19.50$,$p<0.001$) groups, the rate and amount of reduction differed. To estimate the learning rate, we compared the second block between groups and found faster learning already occurring early on for the SINGLE group compared to the DUAL group ($t(31)=2.34$, $p<0.05$). By the final block, the SINGLE group had reduced their tracking error slightly more compared to the DUAL group ($t(31)=2.27$, $p<0.05$). While final baseline levels did not vary between groups (Figure 2.6, horizontal dashed lines), only the SINGLE group was able to reduce their errors during rotated training to baseline levels ($t(16)=0.90$, $p=0.384$). Thus, as suggested by the performance of the DUAL group, it appears that associating opposing visuomotor mappings with distinct types of movements reduced the amount of interference experienced when adapting to both perturbations concurrently.

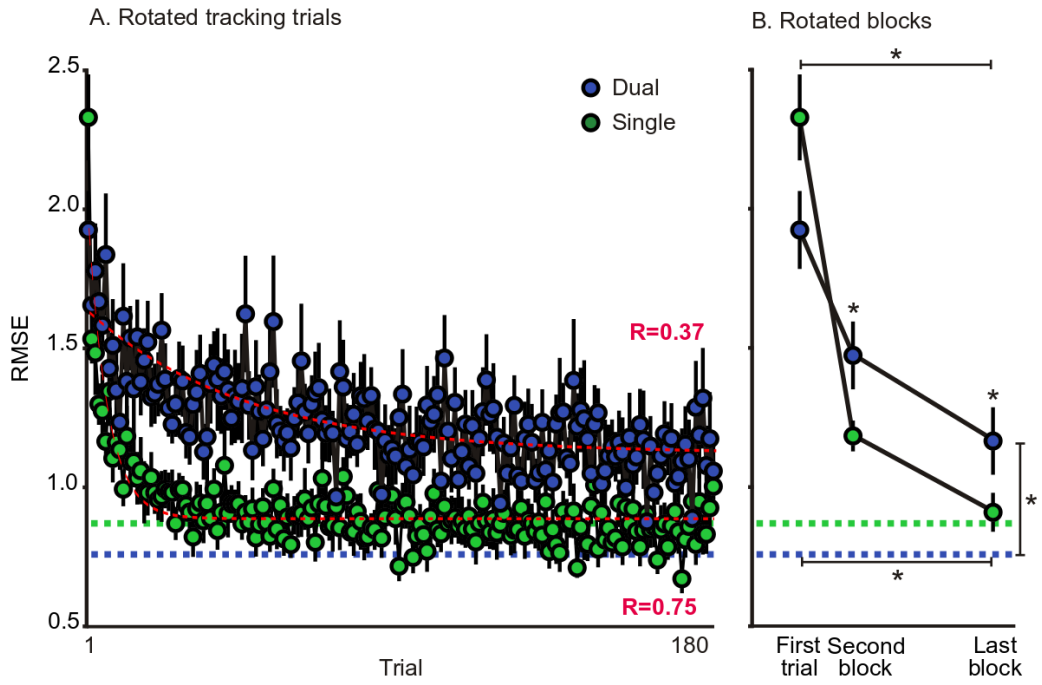

Figure 2.6. Root-mean-square-error (RMSE) across rotated TRACK training for the SINGLE and DUAL groups for tracking trials only. Mean RMSE are depicted across all rotated trials (A), and the initial trial, second block, and final blocks (of 5 trials) in green for the SINGLE tracking-only group and in blue for the tracking trials for the DUAL group (B). The DUAL group also completed aligned trials with both REACH and TRACK trials within the same experimental block (TRACK trials for this condition depicted in turquoise). Green and blue dashed lines represent baseline levels from aligned tracking conditions. Red dashed lines represent fitted exponential curves for tracking deviations for the entire training session with the equation $RD = be^{-ax}+c$. For the SINGLE group, $RD = -1.04^{-0.18x} -0.88$, and for the DUAL group, $RD = -0.51^{-0.01x} -1.12$. Error bars represent SEM.

2.4.3 Additional tracking movement descriptors

As consistent with the results illustrated in Figure 2.5, described briefly above, overall cursor movement time for tracking trials was slightly over 2 s, and did not significantly reduce between the first and final blocks of aligned training ($F(1,31)=3.48$, $p=0.072$). However, introducing the rotation (for either group) lead to a transient

increase in movement time for the first block of about 0.22 s (or ≈10% of the movement time) that returned to the baseline levels by the end of the block ($F(1,31)=0.24$, $p=0.630$). This pattern held for both SINGLE and DUAL training.

Cursor-to-target distance at onset significantly changed over time during rotated trials ($F(2,62)=17.06$, $p<.001$) though this did not change as a function of group. This is likely due to the introduction of the novel rotations, which causes a large discrepancy in the initial stages of training but becomes smaller as participants adapt. For the DUAL condition specifically, cursor-to-target onset distance did not differ between the final block of aligned trials and the final block of rotated trials ($F(1,15)=1.04$, $p=0.323$). This suggests that the distance it initially takes participants to catch up to the moving target becomes uniform over time across conditions.

Target pursuit latency did not significantly change over time in any of the aligned or rotated blocks for both groups (see Figure 2.5). We also analyzed cursor movement time from target-movement onset until target-movement offset and found no significant change over time in any of the aligned or rotated conditions between groups. Thus, it appears that neither the time to pursuit nor the pursuit time change across training.

2.4.4 Reach aftereffects

To illustrate reach aftereffects, the solid black lines in Figure 2.3 depict the mean cursor trajectory during No-Cursor reach trials following rotated training for all groups separated by rotations (or trial type, for the DUAL group). Figure 2.7 depicts the mean reach aftereffects for the SINGLE distortion reaching-only and tracking-only groups (both in green bars), and the DUAL distortion group. Following training with a perturbed cursor, the SINGLE reaching group demonstrated significant reach aftereffects in the

expected (opposite) direction ($t(13)=10.66$, $p<.001$). Likewise, following perturbed tracking training, the SINGLE tracking group demonstrated significant reach aftereffects, also in the expected direction for this opposite rotation ($t(16)=-9.77$, $p<.001$), although to a lesser extent compared to those produced by the SINGLE reaching group ($t(29)=-4.96$, $p<.001$). On average, reach aftereffects produced following only TRACK training were ~+9°, approximately half the size of those produced following REACH training (~-19°). This shows that adaptation to perturbed tracking movements generalizes to reaching movements, as adaptation effects transferred from one movement type (from training trials) to another during no-cursor trials. Altogether, these findings suggest that adaptation to a perturbed cursor when tracking a moving target generalizes to open-loop reaching, such that significant aftereffects manifest despite the difference in the type of movement.

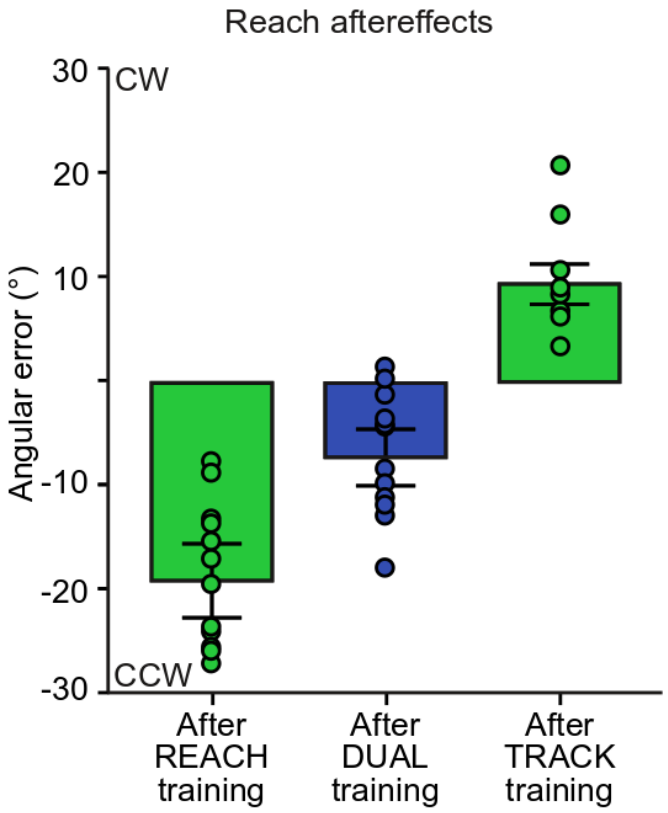

Figure 2.7. Reach aftereffects for SINGLE and DUAL groups. Mean angular error for the first block (of 5 trials) in No-Cursor trials following rotated training (subtracted by mean angular error of No-Cursor trials following aligned training for the first block of trials) are shown in green bars for SINGLE distortion groups and with a blue bar for the DUAL distortion group. Individual subject means are depicted in circles. Error bars represent SEM.

Finally, following concurrent training where reach trials were associated with a CW rotation and track trials with a CCW rotation (DUAL group), participants produced significant reach aftereffects in the direction of what was acquired during reach training, on average ~-7° ($t(15)=5.24$, $p<.001$) and was significantly smaller compared to that of SINGLE reaching ($t(28)=-5.35$, $p<.001$) but not when compared to reach aftereffects following TRACK training. The size of reduction of reach aftereffects was consistent with

the extent of the interference from TRACK training as measured by the reach aftereffects produced when only that condition was performed (producing reach aftereffects of ~+9°). This CW reach aftereffect suggests that some learning remained unimpeded by the opposing perturbation during DUAL training. Overall, these findings suggest that the brain processes tracking movements somewhat independently of reaching movements and vice versa, as generalization of adaptation still tends to occur across these different types of movements.

2.5 Discussion

Our present observations demonstrate three main points. First, we showed significant pursuit adaptation to moving targets (or tracking adaptation) following a small visuomotor perturbation to the hand-cursor. Second, while previous findings show complete interference between opposing visuomotor mappings when each is associated with the same task, we found that tracking adaptation generalized to reaching movements, as reach aftereffects were present when visual feedback was withheld. These reach aftereffects following perturbed tracking movements were smaller in magnitude compared to those produced following perturbed reaching movements. Third, distinct movement types provided a strong contextual cue to the motor system when planning and producing movements for opposing visuomotor mappings. This was evident in the reduction of movement errors for both reaching and tracking trials when both types of perturbed movements were experienced within the same experimental training block. Our findings support the idea that intrinsic or motor-based contextual cues, such as movement type, allow for disambiguation and retrieval of recently learned motor memories.

2.5.1 Visuomotor adaptation with tracking movements

Little is known about how the arm adapts to perturbed tracking movements towards moving targets and how this control process differs from the ubiquitous point-to-point reaching movement. Seminal work by Imamizu and colleagues showed that humans are able to adapt tracking movements in pursuit of randomly moving targets even when the hand-cursor is perturbed by 120° (Imamizu et al., 2000). Similarly, Spapé and Serrien (Spapé & Serrien, 2010) showed a reduction in pursuit errors when participants had to track a moving target with a 60°-rotated cursor. These studies suggested that humans are able to adapt pursuit movements to large perturbations of which participants were aware, although they tended to underestimate their magnitude (Spapé & Serrien, 2010). Humans are also able to adapt pursuit movements to smaller perturbations. In one of their experimental control groups, Tong and Flanagan (Tong & Flanagan, 2003) had participants adapt to a 30° CCW rotation while tracking a target with an unpredictable trajectory and velocity across two training days. They found a significant reduction in tracking errors as well as significant savings on day two (Tong & Flanagan, 2003). These findings demonstrate that humans are able to adapt pursuit movements, regardless of perturbation magnitude and velocity uncertainty. However, since these pursuit type tasks tend to be more complex with changing target positions, velocities, and time constraints, the distinction between point-to-point reaching and pursuit movements remains unclear. Here we show that tracking movements generalize to point-to-point reaching, suggesting overlapping neural mechanisms between these types of movements.

Adaptation of reaching movements has also been shown to be resistant to interference by adaptation to other types of movements such as tracking movements. One key finding by Tong and Flanagan (2003) was a lack of interference in the groups that experienced an opposing perturbation with a different task (i.e., reach-track-reach and reach-draw-reach interference groups). In their tasks, participants reached towards targets with a 30° CCW perturbation, followed by tracking adaptation (or "drawing" adaptation) with a 30° CW perturbation, and a re-test of the 30° CCW-perturbed reach task. They found no retrograde interference at re-test compared to a control group that simply completed reaching tasks on day 1 and day 2 under the same conditions (Tong & Flanagan, 2003). Based on these findings, we should not expect generalization across tracking and reaching trials (i.e., reach aftereffects following tracking training). Indeed, another way to investigate whether similar mechanisms underlie reaching and tracking adaptations is to look at transfer or generalization between these two movements. Here, we found significant reach aftereffects following track training suggesting that some interference occurs between the opposing visuomotor mappings because similar mechanisms process these different types of movements. It appears that the reduced amount of transfer following DUAL training was equivalent to the remainder of transfer from TRACK training alone. That is, the reach aftereffects we saw following DUAL training were what remained unobstructed by training concurrently with tracking movements with an opposing visuomotor mapping. Alternatively, the smaller reach aftereffect following DUAL training may also simply reflect a smaller (or partial) extent of reach adaptation for this group.

It is also possible that the presence of reach aftereffects following tracking training lies in the inherent similarities between our reaching and tracking tasks movements. In Tong & Flanagan (Tong & Flanagan, 2003), the reaching and tracking tasks involved very different target dynamics that made it difficult to tease out exactly whether movement type was the key distinction between tasks. While their reach task was a typical out-and-back movement, the tracking task had a target that moved unpredictably (i.e., a pattern using a sum of 5 sine wave functions) with varying velocity with a large standard deviation. Additionally, their tracking task had no penalty for slow movements, which meant that movements could extend longer than their 35-second trial window (Tong & Flanagan, 2003). All these differences between the reach and the tracking tasks suggest that the movement was not exploring the same space (i.e., not only requiring different movements but also the complete context altogether). In order to isolate the role of different types of movement in visuomotor adaptation, we designed a tracking adaptation task that resembles reach adaptation using a small rotation, a small subset of non-random paths, a constant velocity for all target movement, and the same workspace that requires a similar outward movement for both types of movements. Critically, the same desired trajectory is required across reaching and tracking trials. This ensures that the movement type alone allows for the facilitation of dual adaptation.

Yet another explanation for the transfer of learning between tracking and reaching tasks may be due to the nature of the tracking task itself. In tracking trials, corrections are readily available throughout the movement thereby making it redundant to store a stronger representation of the internal model for that visuomotor mapping. Similar findings by Ikegami and colleagues show that adapted rhythmic movements

show little transfer to reaching movements (Ikegami et al., 2010). Likewise, unpublished work from Morehead et al. (Morehead et al., 2014) show smaller reach aftereffects following adaptation of pursuit movements to randomly moving targets compared to those following discrete reaching towards static targets. Thus, it is possible that when errors can be corrected in flight as in tracking movements, the motor system is less likely to rely on an internal model. Since we found significant reach aftereffects following rotated tracking training (i.e., generalization), tracking adaptation might not be accomplished by online corrections alone, but through a combination of processes which may include the formation of a learned internal model.

One of the main characteristics that distinguishes tracking and reaching movements is the speed of these hand movements. Thus, differences in speed may be contributing to the efficacy of movement types as contextual cues for dual learning. For instance, in one prism adaptation task, Kitazawa and colleagues found smaller reach aftereffects when the movement times during prism exposure and prism removal phases greatly differed, with a small significant difference when the movement times were 2.5 times different; larger differences were found when movement times differed tenfold (Kitazawa et al., 1997). Conversely, Goodbody and Wolpert find that for force-field adaptation tasks, learning generalizes between different speeds (Goodbody & Wolpert, 1998). In our tasks specifically, in order to induce optimal tracking and reaching movement, we used a fixed moving target speed that participate that could easily track during baseline conditions. Likewise, we allow participants to choose their reaching speed. Thus, by definition the two movement types had different speeds and, in our task, tracking took slightly more than twice as long as the ballistic reaches, and

thus, some of our differences in reach aftereffects and learning rate during DUAL training could be related to differences in movement duration. In either case, movement speed or movement types could both serve as sufficient cues to allow for dual adaptation. This may also have some implications on the learned internal models for each type of movement given what type of information is coded during movement planning. In the Module Selection and Identification for Control (MOSAIC) theory, humans are thought to be able to flexibly adapt their movements and choose the right compensatory action given a variable environment with the help of modules consisting of a forward model, inverse model, and responsibility predictor (Haruno et al., 2001; Kawato, 1999). In this model, both feedforward and feedback information (which include velocity) are combined to select the appropriate controller for the context. Thus, it may be possible that for different velocities (and thus, different contexts), different model pairs are selected to produce the correct compensatory action. Thus, it may be possible that both different arm movements and divergent target velocities jointly facilitate dual adaptation. Future studies should explore whether movement velocity can act as a strong contextual cue for facilitating dual learning.

Lastly, although we do not record eye movements during the experiments, it is likely that participants remained fixated or in pursuit of the target due to the absence of other visual stimuli in the task display, as typically seen in reaching tasks (Neggers & Bekkering, 2000; Prablanc et al., 1979; Prablanc & Martin, 1992). Indeed, recent work suggests that for 30° rotations, gaze remains fixated on the target until movement is completed (Neggers & Bekkering, 2000; Rand & Rentsch, 2016; Rentsch & Rand, 2014). Thus, reaches and tracking movements likely were associated with different eye

movements (saccades and tracking) and it is possible that these different eye movements also contributed as intrinsic cues to facilitate dual adaptation.

2.5.2 Explicit strategies

What do the reach aftereffects following single and dual tracking training signify? While it was initially thought that motor adaptation was predominantly an implicit process, more recent work suggests that early stages of motor learning may reflect explicit strategies when compensating visuomotor rotations (Taylor et al., 2014; Taylor & Ivry, 2012). This could explain the reduced learning rate during DUAL training compared to that of the SINGLE training since it may be more difficult to develop an explicit aiming strategy without sufficient contextual cues. We speculate that the slower learning rate during DUAL training reflects a slower development of an explicit strategy or possibly merely reflect only the contribution of the implicit learning as a function of the different movement types. In all three groups, our participants often had no awareness of the perturbation or at the least, were unable explain the nature of the rotations, suggesting that they were not likely forming compensatory strategies. Nonetheless, we do see significant reach aftereffects in all three groups that are consistent with implicit learning (Werner et al., 2015). The smaller reach aftereffects associated when only training with a moving target and or when reaching and tracking in the same training blocks likely reflects the extent of the transfer (or its inverse, interference) of implicit learning. Thus, this may suggest that the contextual cue of movement types is sufficient to allow for concurrent implicit learning of opposing perturbations and perhaps even some contribution of explicit learning during training. Still, it remains unknown to what

extent explicit processes contribute to dual adaptation, laying fertile ground for future investigations.

2.5.3 Incomplete transfer and partial adaptation

When the motor systems constantly experiences opposing error signals, it is not surprising that it learns less as a result (Herzfeld et al., 2014). However, as we have shown, when a context is associated to an error signal, interference may be attenuated. How then does the motor system utilize error to plan and control movement for each context? Nozaki and Scott (Nozaki & Scott, 2009) proposed a multi-compartmental state space model to explain how opposing force-fields can be learned simultaneously when each is associated with a different context for overlapping unimanual and bimanual tasks. In their model, a global update rule is applied to update each component in the system (Nozaki & Scott, 2009). Their model was able to explain why they found significant yet only partial dual learning between unimanual and bimanual movements in their combined learning condition (Nozaki et al., 2006). These findings can also explain the efficacy of learning across our two behavioural contexts: reaching and tracking movements. Much like bimanual movements requiring complex bihemispheric interactions for planning (Donchin et al., 1998; Donchin et al., 2002), tracking movements may require a temporal matching component that engages distinct neural substrates that distinguish them from point-to-point reaching movements. This suggests that both unimanual reaching and tracking compartments of the system use common error information to update the internal state of the system and thus, involve overlapping neural processes.

A related finding is that dual adaptation tends to be partial when the targets are identical across visuomotor mappings. In our present experiments, we observed a significant reduction in reach errors over training that, nonetheless, does not reach baseline levels. When globally comparing between our past experiments which looked at cues such as hand posture, body posture, reach skew (via an obstacle avoidance), and the present experiments, we find that the extent of dual rotation learning ranges from around a third to a half compared to single rotation learning (Ayala et al., 2015; Baldeo & Henriques, 2013). In only one of our experiments, we found near-complete learning – the case for dual adaptation when each perturbation was associated with target workspace location (Baldeo & Henriques, 2013). This is expected given very little generalization tends to occurs for divergent directions (Krakauer et al., 2005). Thus, by using the same target set for all conditions and keeping reach direction constant, any effect would be likely due to the efficacy of the cue itself.

2.5.4 Conclusions

Perturbed tracking of moving targets produced significant reach aftereffects that are smaller than those produced for static targets. This suggests that visually guided changes in tracking movements generalize to reaching movements. Since this generalization is not complete, we tested whether this distinction in movement type can be used to contextualize and thus, facilitate dual adaptation to opposing visuomotor rotations. We found further evidence that motor-based cues such as movement type provide a strong context for the motor system when they are the only cues provided to dissociate between two opposing rotations, and thus, two different visuomotor mappings, even when desired cursor trajectories are identical.

Chapter Three: Dual adaptation to opposing visuomotor rotations by skewing movement trajectories

Ayala, M. N., & Henriques D. Y. P. (Unpublished manuscript).

3.1 Abstract

When planning movement, the human central nervous system (CNS) can actively compensate and adapt to two or more distinct perturbations simultaneously (“dual adaptation”) though this process can occur only when each visuomotor mapping is associated with a valid contextual cue. Because not all contextual cues are effective and only more “intrinsic” or motor-based cues tend to be useful to the CNS for this, we sought to investigate whether movement skewedness allows for dual adaptation of opposing visuomotor rotations. Here, we associated a visual obstacle which effectively skews the reach trajectory thereby acting as a contextual cue preceding target acquisition. Using a virtual reality paradigm, participants manipulated a projected hand-cursor which was rotated 30° clockwise or 30° counter-clockwise, depending on the cue that was presented on a given trial (i.e., a left and right visual obstacle flanking the home position, respectively). Participants completed pre-training where they were instructed to reach towards visual targets with an aligned hand-cursor, training (misaligned cursors), and post-training where they reached without visual feedback of the hand. In the training condition, participants either completed CW trials only, CCW trials only, or both interleaved within the same block (dual distortion group). There was significant adaptation to all targets for both single and dual distortion groups, but unobstructed targets elicited a smaller correction, suggesting that learning was less likely to generalize to obstructed targets. Although reach errors significantly decreased over time for the dual group suggesting that movement skew is a sufficient cue for recalling a previous visuomotor mapping, reach aftereffects were not significant likely due to the unexpectedly large obstacle avoidance response.

3.2 Introduction

As shown in findings from Experiment 1, different movement types can be viable contextual cues for facilitating dual adaptation. Recent work suggested that a critical component for contextual cues requires a distinct motor plan (Sheahan et al., 2016), based on the interpretation that motor preparation involves setting an initial state of neural activity from which point the movement evolves through different neural dynamics upon execution (Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015). This suggests that valid movement contextual cues elicit distinctive motor plans to drive dual adaptation.

In this experiment, I investigated whether movement skewedness allows for dual adaptation to opposing visuomotor rotations. Distinct changes, such as obstacle avoidance, in the reaching movement itself may lead to dual learning since the brain needs to incorporate this information in planning future trajectories, likely involving distinct neural dynamics (Sheahan et al., 2016; Wong et al., 2016). For instance, the hand path can be primed to have a curvature if reaching movements are trained with an obstacle, suggesting that the brain used information about the path obstruction to plan future movements (Jax & Rosenbaum, 2007, 2009; Wong et al., 2016).

I followed up on findings from Chapter 2 experiments with the idea that motor-based cues that elicit a movement change can reduce interference between opposing perturbations. I associated a reach path obstacle which effectively skewed the reach trajectory, thereby acting as a contextual cue preceding target acquisition. Cursor rotations of 30° CW and 30° CCW will each be associated with a left and right visual obstacle partially obstructing the direct path to some targets but not all, allowing for a

comparison of the rate of learning for unobstructed versus obstructed targets. I found that those who experienced distinct obstacles associated with each perturbation were able to dual adapt given the intrinsic contextual cues in the form of movement skew. However, the obstacles elicited an unexpected, exaggerated avoidant response, making conclusions from this experiment unclear.

3.3 Method

3.3.1 Participants

Fifty-three participants (33 females, 23.02 ± 9.08 years old, mean ± SD) were recruited and assigned to participate in the following experiments and were granted a bonus credit for either an undergraduate psychology or kinesiology course. All participants were right-handed, had normal or corrected-to-normal vision, and were naïve to the purpose of the experiment. All participants provided written, informed consent. Procedures were approved by the York University Human Participant Review Committee. Five participants were excluded from analysis due to failure to follow instructions. One participant exceeded the age criteria and was removed from analysis. A final participant did not complete the experiment due to discomfort and was also excluded from analysis.

3.3.2 Apparatus

The same apparatus and set up will be used as in Chapter 2 experiments (Figure 2.1A) with identical target and home stimuli placement (Figure 2.1B).

3.3.3 General procedure

Participants were assigned to one of three conditions: a SINGLE obstacle group that experienced a constant visual obstacle on the left side of the visual workspace

(associated with a CW rotation during training), another SINGLE obstacle group that experienced a constant visual obstacle on the right visual workspace (associated with a CCW rotation during training), and a DUAL obstacle group that experienced both left and right visual obstacles that will change from trial to trial (associated with CW and CCW rotated cursors during training, respectively). The SINGLE obstacle groups serve as control groups to compare the magnitude of adaptation and reach aftereffects from the DUAL obstacle groups.

For each experiment, participants completed pre-training, training, and post-training sessions (Figure 3.1). For both SINGLE obstacle groups, participants completed the task in approximately one hour. Those in the DUAL adaptation condition, participants completed the task in approximately two hours.

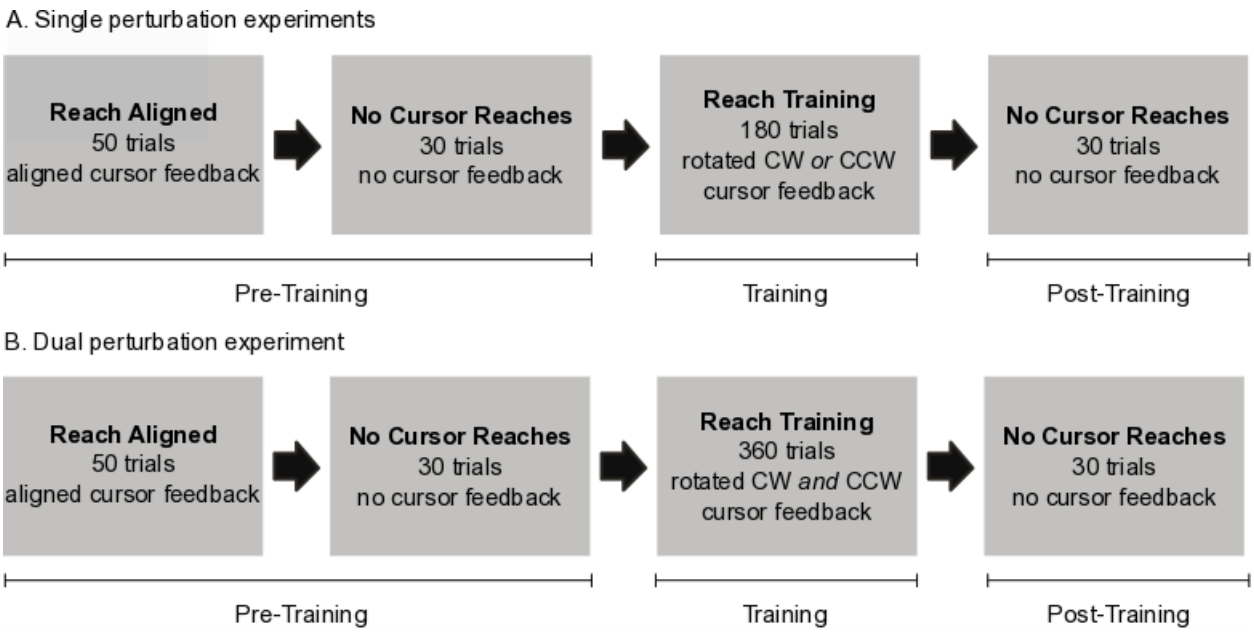

Figure 3.1. Session sequence for A. SINGLE rotation training and B. DUAL rotation training. In both experiments, the SINGLE groups only completed trials under either a 30° CW or 30° CCW rotation, but not both. Those in the SINGLE group completed a total of 180 rotated training trials, while those in the DUAL group completed 360 training

trials of interleaved 30° CW and 30° CCW rotated cursors.

As with Chapter 2 experiments, all tasks involved five radially spaced targets located at 60°, 75°, 90°, 105°, and 120°. All targets appeared in a pseudo-randomized fashion and began at a common starting point located 12 cm away from the home position (Figure 3.2). Participants acquired the targets (1.5 cm in diameter) using a hand-held stylus that they moved across the surface of the tablet, moving a cursor (1 cm in diameter) on the screen. The relationship between the hand and the cursor is similar to using a desktop computer; movements were made with a 1:1 ratio.

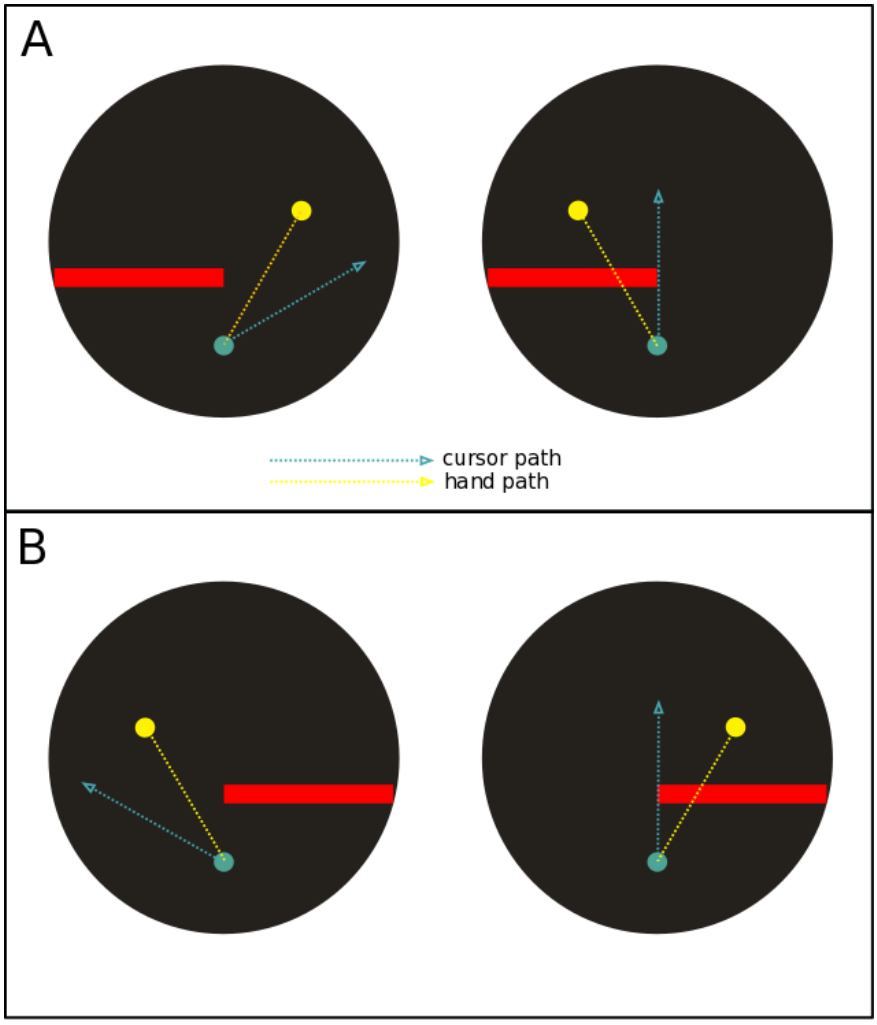

Figure 3.2. Experiment task and display. Participants saw one of five targets (yellow discs), flanked by a box to the left or right (red obstacle). A. Initial exposure to a CW perturbation to an unobstructed target (left) and an obstructed target (right). Teal lines represent the cursor path and yellow lines represent the unseen hand path on initial exposure to the CW rotation. B. Initial exposure to a CCW perturbation to an unobstructed target (left) and an obstructed target (right). Teal lines represent the cursor path and yellow lines represent the unseen hand path on initial exposure to the CCW rotation.

For trials involving visual feedback of the hand-cursor ("closed-loop trials"), participants reached towards a single target, flanked by an obstacle (1 cm in height, Figure 3.2) to the left or to the right, to complete the trial. If any overlap occurred between the obstacle and the hand-cursor, the obstacle turned red and the trial was restarted. For trials involving no visual cursor feedback ("open-loop trials"), participants reached towards the target with their unseen cursor and remained stationary for 500 ms until the home position appeared. Critically, the obstacle remained intact during these open-loop trials, to analyze whether learned compensations during training were elicited in the expected directions (i.e., based on the trained directions).

For both SINGLE and DUAL adaptation experiments, participants started Pre-training by reaching 50 times to one of five targets (Figure 3.1A, 3.1B, first boxes), followed by reaching without visual feedback of their hand-cursor 30 times (Figure 3.1A, 3.1B, second boxes). For the SINGLE rotation experiments, this was followed by Training consisting of 180 reaches with other CW *or* CCW rotated cursor feedback (Figure 3.1A, third box). For those in the DUAL rotation experiment, participants reached 180 times with a CW-rotated cursor, and 180 times with a CCW-rotated cursor, pseudo-randomly interleaved throughout training (Figure 3.1B, third box). Following

Training for both SINGLE and DUAL rotation experiments, participants reached 30 times without visual feedback (Figure 3.1A, 3.1B, fourth boxes).

3.3.4 Data analysis

Cursor movement data was digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was fixed at 10% of peak velocity. For no-cursor trials, performance was quantified using angular error at maximum velocity, while RMSE was used for trials with visual feedback of the cursor (For more detail, see Chapter 2, Data analysis). All R analyses scripts and data can be found in https://github.com/ayalamar/obstacle.

To assess visuomotor adaptation, a 2 (SINGLE or DUAL condition) x 2 (first or final block) mixed ANOVA revealed how reaching errors changed between conditions and across training. Reach aftereffects were analyzed by normalizing errors to flip the negatively signed errors, collapsing across rotations, and comparing these means relative to 0 using a one-sample t-test. Blocks consisted of 5 trials for analyses involving all targets.

Additional analyses of obstructed and unobstructed targets

Unexpectedly, reaching movements were particularly skewed due to the presence of an obstacle. So, for all groups, I also looked at visuomotor adaptation specifically for obstructed and unobstructed target sets. Obstructed target sets for the leftward obstacle (CW-rotated trials) included targets that were blocked by the visual obstacle (i.e., targets at 105°, and 120°); unobstructed targets were thus located at 60° and 75°. For simplicity, the 90° target was excluded as it was only partially obstructed.

To assess visuomotor adaptation, a 2 (SINGLE or DUAL condition) x 2 (obstructed or unobstructed target set) x 2 (first or final block) mixed ANOVA revealed how reaching errors changed between factors and across training. A repeated measured t-test was used to determine whether reaching errors reduced from the first to the final block for obstructed and unobstructed targets, separately.

Lastly, to determine whether reaching to obstructed targets generalized to unobstructed targets, I compared the rate of adaptation between obstructed and unobstructed targets by comparing their reaching errors at block 2 using a repeated-measures t-test. The assumed level of significance was $\alpha = .05$, and post-hoc comparisons were Bonferroni-corrected.

3.4 Results

In this follow-up experiment, I asked whether distinct changes in the reaching movement via the introduction of path obstacles may lead to dual learning, given that information that integrated in the motor plan should elicit a distinct initial neural state (Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015; Sheahan et al., 2016). One group experienced a CW rotation (SINGLE CW group), associated with a left-flanking obstacle, while another experienced a CCW rotation that was associated with a right-flanking obstacle (SINGLE CCW group). To answer the key question of whether dual adaptation can be elicited by distinctly skewed movements as contextual cues, one group experienced both CW and CCW rotations, each associated with left-flanking and right-flanking obstacles, respectively (DUAL group).

3.4.1 Learning across all targets (Obstructed and unobstructed)

Visuomotor adaptation. Figure 3.3 shows the performance of both SINGLE groups (Figure3.3A, B, C) and DUAL groups (Figure 3.3D, E, F) for all targets (i.e., including both obstructed and unobstructed targets). There was a significant reduction in errors across training ($F(1,45) = 53.02$, $p < 0.001$), with those in the SINGLE conditions producing smaller errors in general ($F(1, 45) = 10.50$, $p < 0.01$). However, due to the unexpected influence of the obstacle on kinematic error measures, I present additional analysis on unobstructed target sets in the next section.

Reach aftereffects. Following training, those in the SINGLE conditions produced significant reach aftereffects compared to baseline ($t(24) = 2.82$, $p < 0.01$), but not strongly in the appropriate directions as evident in Figure 3.3C. After collapsing across perturbations in the DUAL group, reach errors following adaptation were no different from those at baseline ($p = 0.91$).

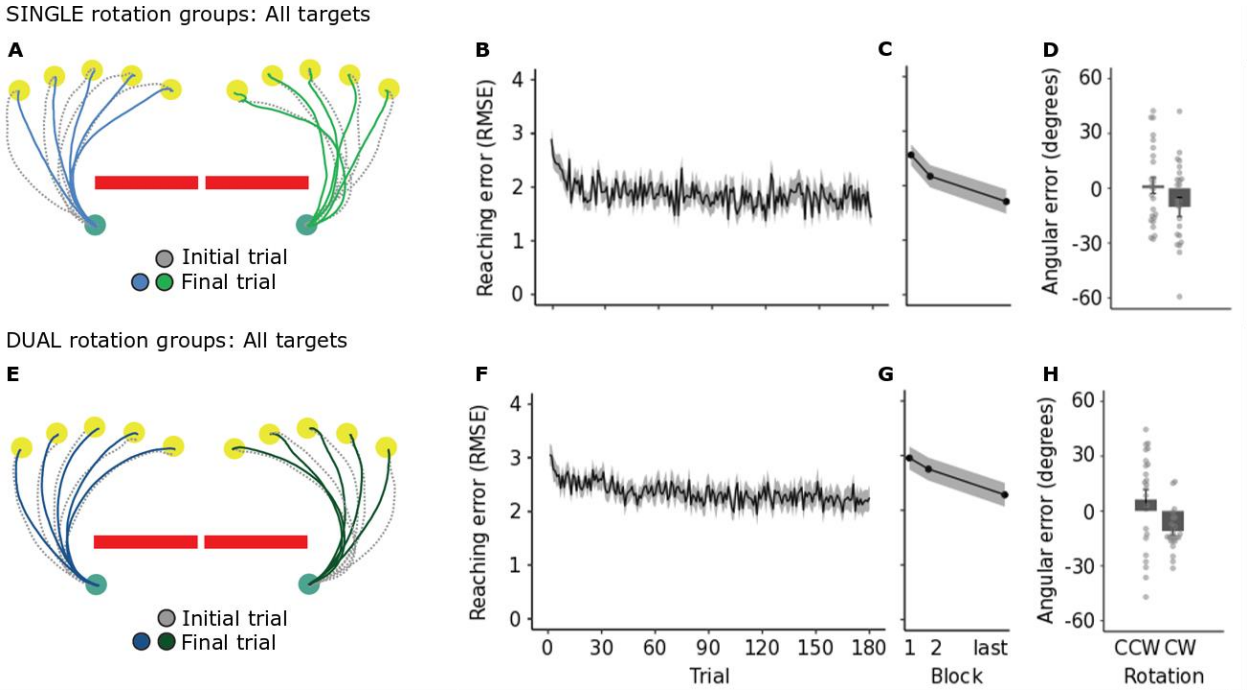

Figure 3.3. Visuomotor adaptation and reach aftereffects to all targets (both obstructed and unobstructed) for both SINGLE groups (top row), and DUAL groups (bottom row). Visuomotor adaptation for the SINGLE groups is shown A. across first and last trials as averaged cursor trajectories for each obstacle type (red rectangle), B. across trials, and C. across the first, second, and last blocks. Reach aftereffects are shown in D. for each SINGLE rotation group. Visuomotor adaptation for the DUAL group is shown E. across first and last trials as averaged cursor trajectories for each obstacle type, F. across trials, and G. across the first, second, and last blocks. Reach aftereffects are shown in H. for each rotation. Shaded regions and error bars represent SEM.

3.4.2 Learning between obstructed and unobstructed targets

Visuomotor adaptation. To assess learning, I compared the mean angular reach errors across the initial trial and final block for all groups. In general, obstructed targets elicited larger deviations ($F(1, 45) = 388.30$, $p < 0.001$), and these errors reduced over training ($F(1,45) = 67.68$, $p < 0.001$). There was no effect of group ($p = 0.06$). More specifically, for unobstructed targets, both SINGLE ($t(23) = 10.16$, $p < 0.001$), and DUAL groups ($t(22) = 3.62$, $p < 0.01$) show smaller errors in the final block compared to the initial block. For obstructed targets, both SINGLE ($t(23) = 2.62$, $p =$

0.02) and DUAL ($t(22) = 5.60$, $p < 0.001$) show smaller errors in the final block compared to the initial block.

Learning rates. To assess differences in learning rates across obstructed and unobstructed targets, we compared the second block for the SINGLE and DUAL conditions. Collapsing across SINGLE conditions, we saw that unobstructed targets elicited smaller errors compared to obstructed targets ($t(23) = 13.67$, $p < 0.001$); this was also true for the DUAL condition ($t(22) = 10.70$, $p < 0.001$).

3.5 Discussion

In the last chapter's set of experiments, I found that movement type (tracking vs. ballistic reaching) sufficiently distinguished two opposing visuomotor mappings. Motivated by recent findings that show the crucial role of motor planning in the retrieval of motor memories, I further try to understand what intrinsic contextual cues elicit dual adaptation. I presented participants with movement obstacles that distinctly skewed the movement trajectory depending on the perturbation they experienced on a given trial and found a significant reduction in error across training for the DUAL condition with no significant reach aftereffects; this finding was difficult to interpret since participants unexpectedly produced exaggerated obstacle-avoidant reaches.

As a result of the unexpected the exaggerated obstacle avoidance response, I saw that the learning rate was worse for the more obstructed targets compared to the less obstructed targets. It's possible that participants were trying to implement a contextual cue that is simply inconsistent for each target. This may be explained by findings from Howard et al. (2017) who showed that a movement cue's execution variability can reduce its ability to facilitate learning. In their force-field experiments, they

saw that increasing the variability of a lead-in movement cue by starting at an inconsistent, highly variable location led to a reduction in the rate of learning (Howard et al., 2017). Thus, the learning rates in the present experiment may have been reduced because the static obstacle was differently located in relation to each target, thereby each eliciting a slightly different obstacle avoidance motor plan, a feature that may be critical to dual adaptation (Howard et al., 2017; Sheahan et al., 2016). To further understand whether skewed movement trajectories can elicit dual adaptation, future experiments will need to control for the possibility that an obstacle can provoke unexpectedly deviant trajectories, possibly by implementing clamped feedback at the point of avoidance, a physical obstruction that can ensure consistency, or even a dynamic visual obstacle that flanks all targets at a consistent relative location.

Some studies suggest that the motor system should be thought of as a dynamical system where the initial neural activity sets up the movements to evolve through the unveiling of the neural dynamics (Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015). The present findings show that skewed trajectories can facilitate dual adaptation, suggesting that planning to avoid an obstacle can be integrated into the motor plan, possibly by engaging separate neural populations at the initial state (Howard et al., 2017; Sheahan et al., 2016). However, given the noise in the present data, it’s difficult to conclude that skewed movements elicit any dual learning. Possibly, the variability captured may simply be attributed to extensive practice with obstacle avoidance.

Chapter Four: Differential contributions of implicit and explicit learning mechanisms to various contextual cues in dual adaptation

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4.1 Abstract

The ability to switch between different visuomotor mappings accurately and efficiently is an invaluable feature to a flexible and adaptive human motor system. This can be examined in dual adaptation paradigms where the motor system is challenged to perform under randomly switching, opposing perturbations. Typically, dual adaptation doesn't proceed unless each mapping is trained in association with a predictive cue. To investigate this, we first explored whether dual adaptation occurs under a variety of contextual cues including active follow-through movements, passive follow-through movements, active lead-in movements, and static visual cues. In the second experiment, we provided one group with a compensatory strategy about the perturbations (30° CW and 30° CCW rotations) and their relationships to each context (static visual cues). We found that active, but not passive, movement cues elicited dual adaptation. Expectedly, we didn't find evidence for dual adaptation using static visual cues, but those in the Instruction group compensated by implementing aiming strategies. Then, across all experimental conditions, we explored the extent by which dual learning is supported by both implicit and explicit mechanisms, regardless of whether they elicited dual adaptation across all the various cues. To this end, following perturbed training, participants from all experiments were asked to either use or ignore the strategy as they reached without visual feedback. This Process Dissociation Procedure teased apart the implicit and explicit contributions to dual adaptation. Critically, we didn't find evidence for implicit learning for those given instructions, suggesting that when explicit aiming strategies are implemented in dual adaptation, implicit mechanisms are likely not involved. Thus, by implementing conscious

strategies, dual adaptation can be easily facilitated even in cases where learning would not occur otherwise.

4.2 Introduction

While it has always been imperative for humans to learn to manipulate new tools, with the rise of modern technologies we are often required to operate and switch under multiple different visuomotor mappings. This ability to switch between different tasks accurately and efficiently is an invaluable feature to a flexible and adaptive human motor system. We can skillfully use a tool, correct for any movement errors while we use it, and then anticipate the consequences of switching to a completely different tool or environment. Often times we make large errors when first learning to move under novel circumstances, but our motor systems quickly adapt, such that eventually, and rather quickly, we produce smooth, accurate movements despite behavioural or environmental constraints.

To study the ability of the motor system to switch between learned visuomotor mappings, variants of the same environment can be introduced serially (i.e., ABA paradigm) or concurrently (i.e., dual adaptation paradigm). ABA paradigms probe how an internal model can be affected by the subsequent learning of another, while dual adaptation paradigms have the advantage of challenging the motor system to learn, acquire, and switch between multiple internal models, mimicking its daily demands. Typically, when faced with unpredictable opposing perturbations to movement that vary from trial to trial, the motor system fails to adapt, or substantially improve, across many blocks of training, leading to interference (Brashers-Krug et al., 1996; Caithness et al., 2004; O Donchin et al., 2003; Karniel & Mussa-Ivaldi, 2002; Krakauer et al., 1999). However, adaptation to two or more visuomotor perturbations (i.e., dual adaptation) can proceed when each visuomotor mapping has been sufficiently cued during training,

although what makes a cue sufficient is still unclear. Usually, the relevance of the cue to the task and possibly the “intrinsic” or motor-based nature of the cue appears to facilitate dual adaptation (e.g., Ayala et al., 2015; Howard et al., 2013a), while cues that are more “extrinsic” or less pertinent to the task lead to mixed findings (e.g., Baldeo & Henriques, 2013; Gupta & Ashe, 2007; Hinder et al., 2008; Osu et al., 2004). Indeed, more recent work has now shown the critical role of motor planning over execution with regards to reducing interference between concurrently-learned visuomotor mappings (Howard et al., 2015; McDougle et al., 2015; Schween et al., 2018; Sheahan et al., 2016). In one pivotal study by Sheahan and colleagues, using distinct follow-through movements as contextual cues, the researchers dissociated the contributions of planning and execution by manipulating the timing of the presentation of the follow-through targets (Sheahan et al., 2016). To isolate the planning component, participants saw both initial (perturbed) and follow-through targets as they initiated their reach, but the follow-through target was extinguished to signal to participants that a follow-through motion is not required. Their main finding, that compensation occurs even in the absence of the execution of the follow-through, suggests that the key component in representing motor adaptation lies in action planning, and not in the act of executing a physically different limb state (Sheahan et al., 2016).

Adaptation to a single perturbation can be characterized by at least two qualitatively different learning mechanisms: [1] an explicit, or conscious process which arises due to the implementation of aiming strategies (Heuer & Hegele, 2008; J. A. Taylor et al., 2014), and [2] an implicit process which is thought to function without awareness, reflect adaptation of internal models in the cerebellum, and largely produce reach

aftereffects (Heuer & Hegele, 2008; Jordan A. Taylor et al., 2010). Explicit and implicit contributions can also be elicited when adapting to opposing visuomotor rotations for some contextual cues, such as when targets are displayed in different workplaces (a cue that usually leads to dual adaptation rates similar to that for single-rotation adaptation, e. g., Baldeo & Henriques, 2013; Woolley et al., 2007), and when the perturbations are large and blocked, as demonstrated by Schween and colleagues (2018). In one of their dual adaptation experiments, Schween and colleagues showed that overlapping strategies led to interference, but when provided with compensatory strategies, participants showed overall learning and reach aftereffects (Schween et al., 2018). Still, it's unclear to what extent these underlying processes are engaged, so here we break down the explicit and implicit contributions to dual adaptation across a diverse set of contextual cues.

In this series of experiments, we explore the efficacy of various cues and implementing explicit aiming strategies in dual adaptation. First, we looked at whether distinct, active follow-through movements and more complex, lead-in movements can facilitate adaptation to opposing visuomotor rotations. This has been similarly demonstrated under force-field paradigms (Howard et al., 2012, 2015), but it's unclear whether the active component of the contextual cue drove dual adaptation, so in the first experiment we isolated the active movement component (i.e., the self-generated follow-through motion) and replaced it with a passive visual-only follow-through that mimicked that motion. We found that both active movement cues elicited dual adaptation and were able to provide a stronger contextual cue compared to the passive movement cue. Using a Process Dissociation Procedure (PDP; adapted from (Werner et al., 2015), we teased apart the implicit and explicit contributions to dual adaptation and found that

implicit mechanisms were involved for cues that elicited dual learning. In the second experiment, we equipped a separate Instruction group with a compensatory strategy about the perturbations (30° CW and 30° CCW rotations) and their relationships to each context (static visual cues) and compared their performance to a Non-instructed group that experienced the same visual cues and their associated perturbations. We didn't find evidence for dual adaptation given only static visual cues, but those in the Instruction group were able to dually compensate by implementing aiming strategies. Critically, we didn't find evidence for implicit contributions for those who were instructed, but found that instruction played a role, suggesting that aiming strategies only elicited explicit mechanisms. Thus, by implementing conscious strategies, dual adaptation can be easily facilitated even when learning would not occur otherwise.

4.3 Method

4.3.1 Participants

One-hundred and thirty-five participants (94 females, 20.40 ± 3.23 years old, mean ± SD) were recruited and assigned to participate in the following experiments and were granted a bonus credit for either an undergraduate psychology or kinesiology course. All participants were right-handed, had normal or corrected-to-normal vision, and were naïve to the purpose of the experiment. All participants provided written, informed consent. Procedures were approved by the York University Human Participant Review Committee (HRPDC # e2017-267) and were in accordance with the declaration of Helsinki. Two participants withdrew from the experiment due to discomfort and were thus excluded from all analyses. Table 4.1 displays the demographic summary of participants.

Table 4.1

Demographic summary.

Experiment	Group	N	Mean age (SD)	Sex (F)
1a	Active Follow-through	28	20.15 (3.64)	22
	Passive Follow-through	30	19.97 (2.22)	17
	CCW-only	10	23.50 (9.42)	8
	CW-only	10	20.60 (2.41)	9
1b	Active Lead-in	31	22.26 (7.09)	17
2	Non-instructed	12	19.53 (2.53)*	11
	Instructed	12	19.09 (0.94)	8

Table 4.1. Demographic summary of experimental groups including sample size, mean and standard deviation of age, and sex (number of female participants). *One participant in this group did not disclose their age.

4.3.2 Apparatus

Participants sat on an adjustable chair facing a digitizing tablet (Wacom Intuos3, 12” x 12” surface, resolution resampled by 1440 x 900 pixels at 60 Hz) and a vertically-mounted monitor (Dell Technologies, 22” P2217 LED screen) located approximately 55 cm from the horizontal tablet workspace. The tablet was placed at waist level so that hand movements were made along the horizontal plane (Figure 4.1A). To prevent participants from seeing their arm movements, an adjustable opaque shield was placed above the tablet (Baldeo & Henriques, 2013; Balitsky Thompson & Henriques, 2010; Dionne &

Henriques, 2008). All tasks required participants to reach to a target disc (1.5 cm in diameter) by moving a digitizing pen that moved a hand-cursor (1 cm in diameter) in a 1:1 ratio. Some tasks required a secondary reach from the target disc to a final target box (3 x 3 cm, e.g., Figure 4.1B). The target disc was radially spaced and located at either 75°, 90°, or 105°, at a distance of 10.5 cm from home position. In all experiments but one, the target disc was flanked by a target box located 7.5 cm to its left or right, but never both at once.

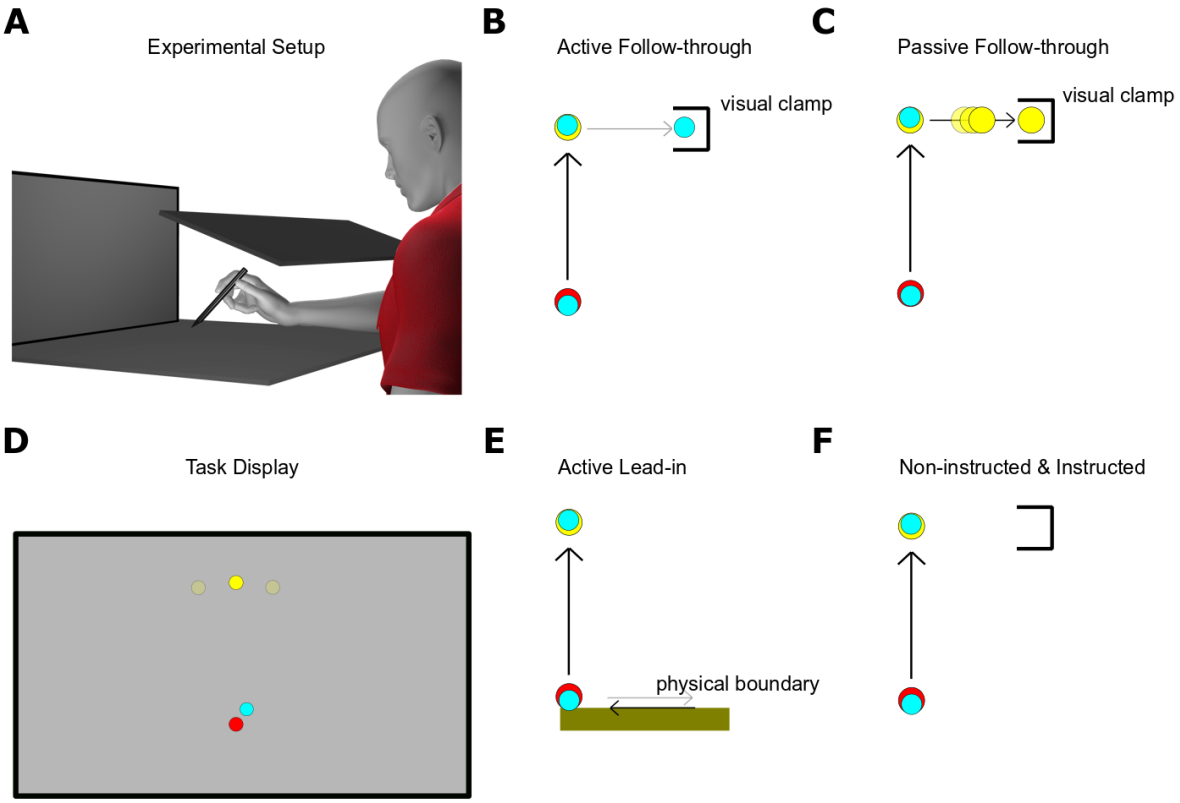

Figure 4.1. Experiment setup and task schematic. A. Participants reached along a horizontally-placed digitizing tablet. An opaque shield occluded the view of their hand. Participants viewed the motion of their hand-cursor on a monitor located at the end of the tablet. B. For Experiment 1a, those in the Active Follow-through condition reached to the yellow target disc, immediately followed by a visually-clamped reach to the box target. CW-only and CCW-only control groups completed the same task but only experienced a single perturbation. C. In the Passive Follow-through condition, participants reached to the yellow target disc, stopped, and only viewed the yellow

target disc move to the target box. D. Participants saw targets discs located at one of three positions. E. For Experiment 1b, participants made an unseen reach along a physical solid edge to the left or right (brown bar), returned to the home position, and then to the yellow target disc, completing a three-part sequence. F. For experiment 2, those in the Non-instructed condition only reached to the yellow target disc, while they saw target boxes that indicated the perturbation in that trial. Those in the Instructed condition saw this same task but were instructed a compensatory strategy.

4.3.3 General Procedure

In Experiment 1a ("Active and Passive Cues Experiment"), we examined how active and passive contextual cues vary in their efficacy in facilitating dual adaptation to opposing visuomotor rotations. In the first group ("Active Follow-through"), we associated distinct follow-through movements with opposing visuomotor rotations (Figure 4.1B). In the second group ("Passive Follow-through"), we removed that follow-through motion and instead associated a distinct visual target consequence to each visuomotor rotation (Figure 4.1C). That is, instead of asking participants to move to the target boxes (follow-through), they only reached to the target discs, then simply viewed that target disc directly move into the target box. In Experiment 1b, we implemented lead-in movements to cue the perturbations: participants made an unseen leftward or rightward reach, then back to the home position, and finally to the target disc, completing a three-part motion (Figure 4.1E). Two groups, "CW-only" and "CCW-onl**y**" served as control groups and learned only a *single* perturbation (thus, under only *one* context; Figure 4.1B).

To better understand the explicit and implicit contributions in dual adaptation, we ran a second experiment ("Instruction Experiment") where in one condition ("Instructed") participants were not only told about the nature of the perturbation and the relationship of the perturbations to the target boxes, they were also given a compensatory strategy. For this instructed condition, participants merely viewed the same target boxes located to the

left or right of the target discs (as in the Active Follow-through and Passive Follow-through groups); no movements to the target boxes were required (Figure 4.1F). In the other condition ("Non-instructed"), left and right target boxes were coupled with different perturbations, but no instructions were provided and no secondary movement to the target boxes occurred; in other words, this condition experienced a purely static visual cue (Figure 4.1F). Across all conditions, the presence of a left-flanking box was predictive of a 30° CCW rotation while the right-flanking box was predictive of a 30° CW rotation.

All participants started at the same home position and were told to make smooth and direct reaches to the target disc. Although there were no hard time restraints, participants were encouraged by the experimenter to move in a quick and uniform pace across training and were warned on screen if they moved toward the target too slowly. For trials involving visual feedback of the hand-cursor (also referred to as "closed-loop trials"), participants simply reached and attained the target disc. For trials involving no visual cursor feedback (also referred to as "open-loop trials"), participants reached towards the target disc with their unseen cursor and remained stationary for 500 ms until the home position appeared. To facilitate returning to the home position and proceed to the next trial during open-loop trials, a line on the home position appeared following target acquisition and changed in orientation depending on the position of the pen. A physical solid edge was also placed just below the home position to help participants find the home position. Likewise, visual feedback of the hand-cursor appeared when participants were within a 2 cm radius of the home position.

Across all groups, participants completed pre-training, training, and post-training sessions (Figure 4.2). For the CW-only and CCW-only control conditions, participants

completed the task in approximately one hour (Figure 4.2A), while the rest completed the task in approximately two hours (Figure 4.2B - C). Apart from the Instructed condition in Experiment 2, participants were not informed about the presence or nature of the rotation at the start of the experiments. After the experiment, participants answered a series of questions to assess their awareness of the rotation and the experimental objectives.

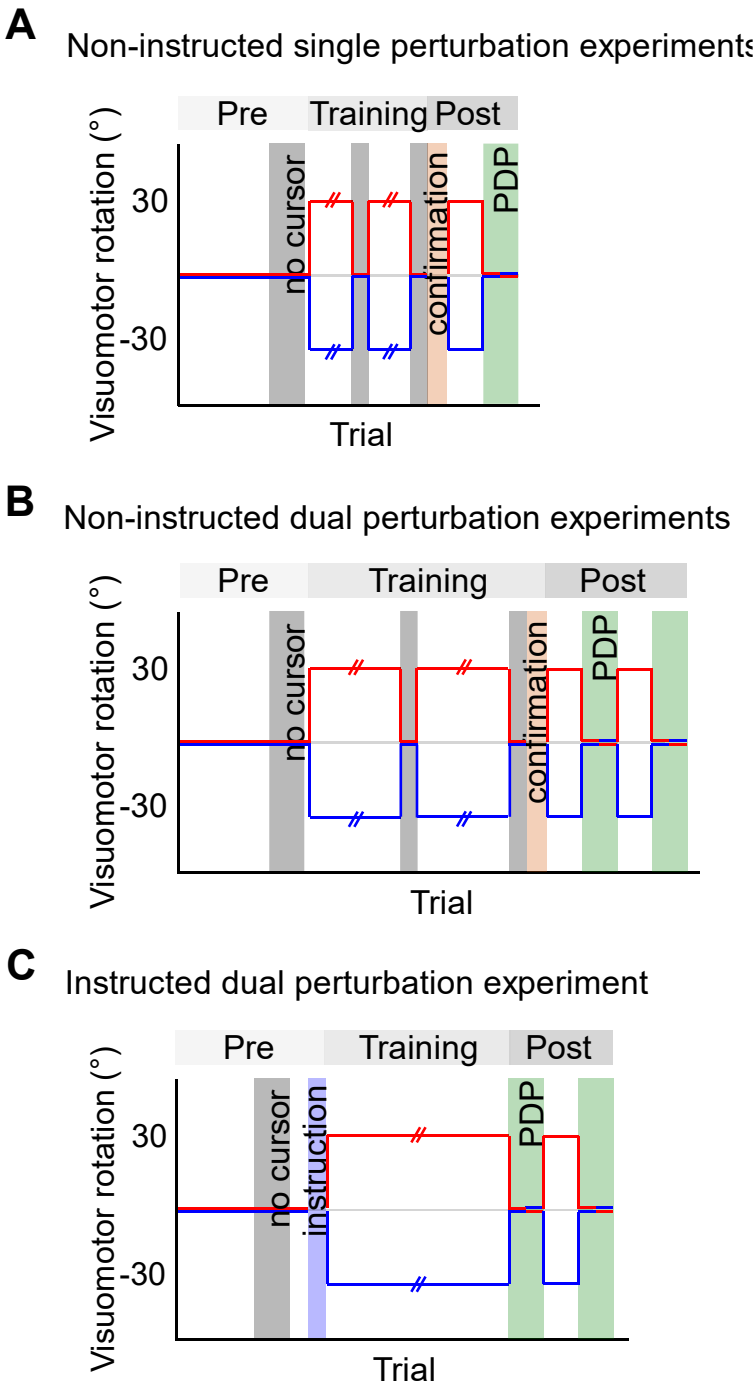

Figure 4.2. Perturbation schedule. Experiments consisted of Pre-training, Training, and Post-training periods. Pre-training captured baseline reaching movements, void of any perturbations. Grey bars depict blocks where participants do not receive visual feedback of the cursor (No-cursor). During training, perturbations were introduced depending on the condition. Post-training involved PDP tests (green bars) interleaved with additional training (perturbed) blocks to preserve any learning. A. Non-instructed single perturbation experiments. Two groups follow this perturbation schedule: CW-only and

CCW-only control groups. B. Non-instructed dual perturbation experiments. Four groups fall into this perturbation schedule category: Active Follow-through, Passive Follow-through, and Active Lead-in. The Non-instructed condition from Experiment 2 also completed this protocol. During Training, participants experienced interleaved trials with CW and CCW rotated cursors. B. Instructed Group (Experiment 2) session schedule. Only the Instructed group in the Instruction Experiment followed this perturbation schedule. All PDP trials, shaded in green, were counterbalanced.

4.3.4 Experiment 1a: Active and Passive Cues Experiment

Experiment 1a consisted of 4 groups: [1] Active Follow-through, [2] Passive Follow-through, [3] CCW-only control, and [4] CW-only control.

Active Follow-through Group. Twenty-eight participants completed the Active Follow-through condition (Figure 4.2B). Participants reached towards the target disc followed by a reach to either its LEFT or RIGHT to a target box (Figure 4.1B). After acquiring the target disc (Figure 4.1B, yellow disc), the hand-cursor was visually clamped to only show the horizontal component of movement (i.e., only show movement along the x-axis) as they moved towards the target box (Figure 4.1B, left-opened black box). Considering findings by Howard and colleagues (Howard et al., 2012), we minimized the dwell time at target disc acquisition and encouraged participants to try to make their reach and follow-through movements as continuous as possible.

Pre-training (Baseline measures). The aim of the pre-training session was to obtain baseline performance and familiarize participants with the task. Participants reached towards the target disc 60 times with visual feedback of the aligned cursor (veridical), followed by 24 reaches with no visual feedback of the cursor (i.e., No-Cursor) in order to record baseline open-loop reach errors (Figure 4.2B, Pre-training).

Rotated Training (Adaptation). The aim of reach training was to expose participants to a visuomotor rotation in order to assess the learning rate and later, reach aftereffects. Participants reached 360 times with interleaved 30^{o} CW and CCW rotated cursors followed by 12 “Within-Training” No-Cursor reaches (Figure 4.2B, Training). This was repeated for a total of 720 rotated training trials. During training, each rotation was associated with either a LEFT or RIGHT target box (Figure 4.1B) in order to determine whether dual adaptation can occur when cued by different movement contexts. At the beginning of every trial, participants saw both the initial (Figure 4.1B, yellow disc) and final targets (Figure 4.1B, left-opened black box). CW and CCW trials were presented in a pseudo-randomized order such that participants encountered all three possible targets for each cursor rotation before any target location was repeated.

Post-training (Analysis for awareness). Immediately after Training, we confirmed with participants that the cursor would not move in the same direction as their hand, and that they needed to compensate and keep that compensatory strategy in mind (Figure 4.2B, Confirmation, in orange) as they will later be prompted by the screen to either use a “strategy” (Include-Strategy) or *not* use a “strategy” (Exclude-Strategy). This Process Dissociation Procedure (PDP; adapted from Werner et al., 2015) allowed us to make inferences about the participants’ awareness, which in turn allowed us to tease apart implicit and explicit contributions to dual adaptation. After Confirmation, participants reached with both CW- and CCW-rotated cursors for 24 trials to preserve any dual adaptation. This was followed by 12 Include-Strategy No-Cursor trials, then 12 Exclude-Strategy No-Cursor trials (Figure 4.2B, Post-training). Finally, they again reached with

both CW- and CCW-rotated cursors for 24 trials, followed by another 12 Include-Strategy trials and 12 Exclude-Strategy trials. All post-training tasks were counterbalanced.

CW-only and CCW-only Control Groups. Twenty participants served as CW- or CCW-only controls for all dual groups. The task is identical to the Active Follow-through group, except participants in these groups experienced either a 30º CW *or* 30º CCW rotation of the cursor during training. The experiment began with a Pre-training session, consisting of 60 aligned reaches followed by 12 No-Cursor reaches.

Rotated Training (Adaptation). During training, these participants reached 180 times with a rotated cursor (30º CW *or* 30º CCW) followed by 15 No-Cursor reaches twice (Figure 4.2A, Training). This was repeated for a total of 360 rotated training trials. Since participants in these groups only experienced a single perturbation, they only saw either a left or a right target box across training.

Post-training (Awareness analysis). As in the Active Follow-through group, immediately after Training we confirmed with participants that the cursor would not move in the same direction as their hand and that they needed to compensate for this (Figure 4.2A, Confirmation). After Confirmation, participants reached with CW- *or* CCW-rotated cursors for 24 trials to preserve any adaptation. This was followed by 12 Include-Strategy No-Cursor trials, then 12 Exclude-Strategy No-Cursor trials (Figure 4.2A, Post-training). All post-training tasks were counterbalanced.

Passive Follow-through Group. Thirty participants completed the Passive Follow-through condition. Unlike the Active Follow-through group, participants simply had to reach to the initial target (disc), stay stationary on the disc, which initiates the

movement of the disc into the final target (box; Figure 4.1C). Participants were told to stay on the initial target location until the disc has fully migrated into the final target box. When participants failed to remain still, a high-pitched beep and the visual message “Stay still!” signaled them to stop moving until all stimuli disappear.

Participants in the Passive Follow-through Group followed the same perturbation schedule as the Active Follow-through Group (Figure 4.2B).

4.3.5 Experiment 1b: Active Lead-in Cue

In a follow-up experiment, we implemented a lead-in movement to cue the perturbations (Figure 4.1E). Thirty-one participants completed the Active Lead-In experiment. Instead of making a secondary movement to the box target, participants made a lead-in movement: first, an unseen initial reach to the left or right along a physical edge, whose direction is signaled by a black arrow superimposed on the home position, followed by a visually-clamped reach to the home position, then finally to the target disc (Figure 4.1E). Three participants fell in the extreme outlier range and were excluded from analysis.

The Active Lead-in condition followed the same perturbation schedule as the Active Follow-through and Passive Follow-through conditions (Figure 4.2B).

4.3.6 Experiment 2: Instruction Experiment

Experiment 2 consisted of 2 conditions: the [1] Instructed, and the [2] Non-instructed group.

Instructed Group. Twelve participants completed the Instructed condition. While these participants saw the static visual cues (target boxes), they did not reach towards

the boxes or see any visual motions toward the boxes; they simply had to reach to the target disc and stay stationary (Figure 4.1F). When they failed to remain still, a high-pitched beep and the visual message “Stay still!” signaled them to stop moving until all stimuli disappear. Critically, these participants were instructed about the nature of the perturbations and their relationship to the static visual cues (target boxes). They were explicitly given a strategy on how to counter the perturbations.

Figure 4.2C shows the perturbation schedule for those in the Instructed condition. During Pre-training, participants reached towards the initial and final targets 60 times with visual feedback of the aligned cursor, followed by 24 reaches with no visual feedback of the cursor (Figure 4.2C, Pre-training). After Pre-training, participants were informed about the nature of the rotations and were provided with a strategy to counteract the rotation so that they can move the cursor in a straight path to the targets (Figure 4.2C, Instruction, shaded in blue). More specifically, they were instructed to visualize the location of the home position as the center of a clock face. They were told that for trials where they saw the box on the left side, reaching towards a number on the clock would result in the cursor heading an hour behind, so they should aim an hour ahead to make a straight path to the target. They were told that the opposite was true for trials where they saw the box on the right side. Full instruction scripts can be found in this experiment’s OSF repository (https://osf.io/v2hwp/).

During training, participants reached 720 times with interleaved CW- and CCW-rotated cursors (Figure 4.2C, Training). Post-training followed the same protocol as in the Active Follow-through, Passive Follow-through, and Active Lead-in conditions (Figure 4.2C, Post-training).

Non-instructed Group. Twelve participants completed the Non-instructed condition. This experimental group served as controls for the Instructed group; participants only saw the final target and were not informed about the rotations, the coupling between the rotation and target box, nor were they given any compensatory strategy (Figure 4.1F). Participants reached to the target disc and stayed stationary (and were otherwise alerted as described above in the Instructed condition if they failed to do so). Figure 4.2B shows the perturbation schedule for the Non-instructed condition**.** Pre-training, training, and post-training followed the same protocol as in the Active Follow-through, Passive Follow-through, and Active Lead-in conditions (Figure 4.2B).

4.3.7 Analysis

Cursor movement data was digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was fixed at 10% of peak velocity. The experimental data was analyzed offline using R (preprocessing and analysis scripts can be found in https://github.com/ayalamar/sequence), using kinematic error (operationalized as angular deviation at maximum velocity) during training and No-Cursor trials. Our main error measure, angular error at maximum velocity, refers to the angular difference of the target and cursor at peak velocity relative to the home position. Other error proxies for trials with visual feedback of the cursor include cursor path length, which refers to the length of the cursor movement in centimeters, and maximum angular deviation, which refers to the maximum angular difference of the target and the cursor (relative to the home position) along the cursor trajectory. For trials without visual feedback of the cursor, along with angular deviation at maximum velocity, we also looked at endpoint angle which refers to the angular difference of the target and the cursor

(relative to home position) at the end of the reach (target-disc acquisition). For all our analyses involving blocks, we averaged across blocks of 3 trials to include a movement to each target. The assumed level of significance for all statistical tests was $\alpha = .05$, and post-hoc comparisons were Bonferroni-corrected. Angular error was subject to tests of normality, and corrections for unequal variances were applied where necessary. When the normality assumption was not met, we instead applied non-parametric tests (i.e., Wilcoxon rank-sum and signed rank tests for t-tests). Finally, post-hoc power analyses were completed for key comparisons. All raw and processed experimental data can be found on the project's OSF (https://osf.io/v2hwp/).

Visuomotor adaptation. Classic analysis of visuomotor adaptation in dual adaptation studies typically includes comparisons between single-perturbation groups and dual-perturbation groups to compare rates of learning. However, as it has been shown in the literature, dual adaptation rarely parallels the learning rate to that of single adaptation, so we opted to report only dual learning statistics for brevity. For those who are interested, omnibus tests are available on the project OSF.

The overall difference in reaching error between the first trial and the last block reflect the extent of learning. Since CW and CCW rotations were not expected to elicit different rates of learning, we analyzed normalized errors, but we provide visualizations of signed errors to show whether compensation occurs in the expected directions. A planned repeated-measures t-test (first block vs. final block; one-sided) was used to show whether adaptation has occurred within each experimental group. To further visualize learning and provide a more intuitive measure of effect size, we compared performance from the beginning of rotation training (*Initial block error*) to the final block of experiencing

the rotation (*Final block error*), for each rotation. We quantified this Percent Improvement (PI) for experiments 1a, 1b, and the Non-instructed condition for experiment 2:

$$Percent\ Improvement = \frac{Initial\ block\ error - Final\ block\ error}{Initial\ block\ error} \times 100 \qquad (4.1)$$

Positive PIs indicate reduction in errors over time while negative PIs indicate worsening of errors over time. PIs for the Instructed condition were calculated relative to the size of the rotation, since some participants show near-perfect compensation at the initial block of training that yield inflated PIs. In a follow-up analysis, we collapsed across active conditions from Experiment 1 and compared their PI to that of the Passive Follow-through condition using a Wilcoxon rank-sum test.

Reach Aftereffects. An alternative measure to test whether adaptation has occurred is the presence of reach aftereffects during No-Cursor trials. Reach aftereffects refer to rotation-dependent, deviated reaching in the absence of visual feedback of the cursor. Using the PDP (Werner et al., 2015), reach deviations can be analyzed to segment explicit and implicit components. It is thought that implicit learning is reflected in No-Cursor trials where participants are told not to implement any strategies in their movements (i.e., Exclude-Strategy No-Cursor trials). To this end, we subtracted any biases from the final block of No-Cursor trials following Pre-training from the first Exclude-Strategy No-Cursor trial and determined whether this was significant from zero using a one-sample t-test (one-sided) for all experimental groups.

Include-Strategy No-Cursor trials consist of not only explicit, but also implicit processes. Thus, to determine whether participants were using a compensatory strategy, we compared the reach deviations for the first Include-Strategy No-Cursor trials and the

first Exclude-Strategy No-Cursor trials, after accounting for baseline biases, using a repeated-measures t-test (one-sided) for all experimental groups.

The role of instruction. In this final set of analyses, in Experiment 2 we set off to understand the role of explicit strategy in dual learning by comparing the results between the Instructed group and the Non-instructed group. To confirm that participants in the Instructed condition could implement the strategy, we compared their first block of training to those from the Non-instructed condition using a Welch independent-measures t-test.

First, to assess whether any implicit learning occurs following training, we ran a 2 X 2 Mixed Repeated-Measures ANOVA comparing reach aftereffects across Pre-training No-Cursor tasks and Exclude-Strategy No-Cursor tasks between the Instructed and Non-instructed groups. A significant effect of No-Cursor task would indicate the presence of reach aftereffects even when participants are excluding strategy, suggesting the presence of an implicit learning mechanism.

Then, to examine the effect of instruction, we ran a 2 X 2 Mixed Repeated-Measures ANOVA comparing across Exclude-Strategy No-Cursor tasks and Include-Strategy No-Cursor tasks between the Instructed and Non-Instructed groups. If participants are aware and are using the instructed strategy, we would see a significant difference between Include-Strategy No-Cursor trials (in the expected directions) and Exclude-Strategy No-Cursor trials. Finally, this analysis was followed by planned comparisons within each group (Instructed and Non-instructed groups) to determine whether having instructions significantly affects the magnitude of reach aftereffects.

4.4 Results

To investigate the underlying mechanisms behind dual adaptation, we implemented various contextual cues in the first experiment, and provided detailed instructions on how to counter the perturbations given the contexts in the second experiment. In the first experiment, those in the Active Follow-through and Active Lead-in conditions made active movements that cued the perturbations either after or before the perturbed reach, respectively. Those in the Passive Follow-through condition reached to the target disc and only saw that target move to a secondary target whose location cued the perturbation. In the second experiment, one group was given a compensatory aiming strategy to dual adapt (Instructed group), while another group was not given any strategies (Non-instructed group). Across all experiments, a leftward sequence (or visual location of the box) was indicative of a 30^{o} CCW rotation, while a rightward sequence (or visual location of the box) was indicative of a 30^{o} CW rotation.

Participants of Experiment 1a in the CW-only and CCW-only control groups exhibited typical visuomotor adaptation since they only encountered one perturbation, with large errors approximately the size of the rotation at the beginning of training that gradually reduced to near baseline levels (Figure 4.3B) and rotation-dependent reach aftereffects (Figure 4.3C).

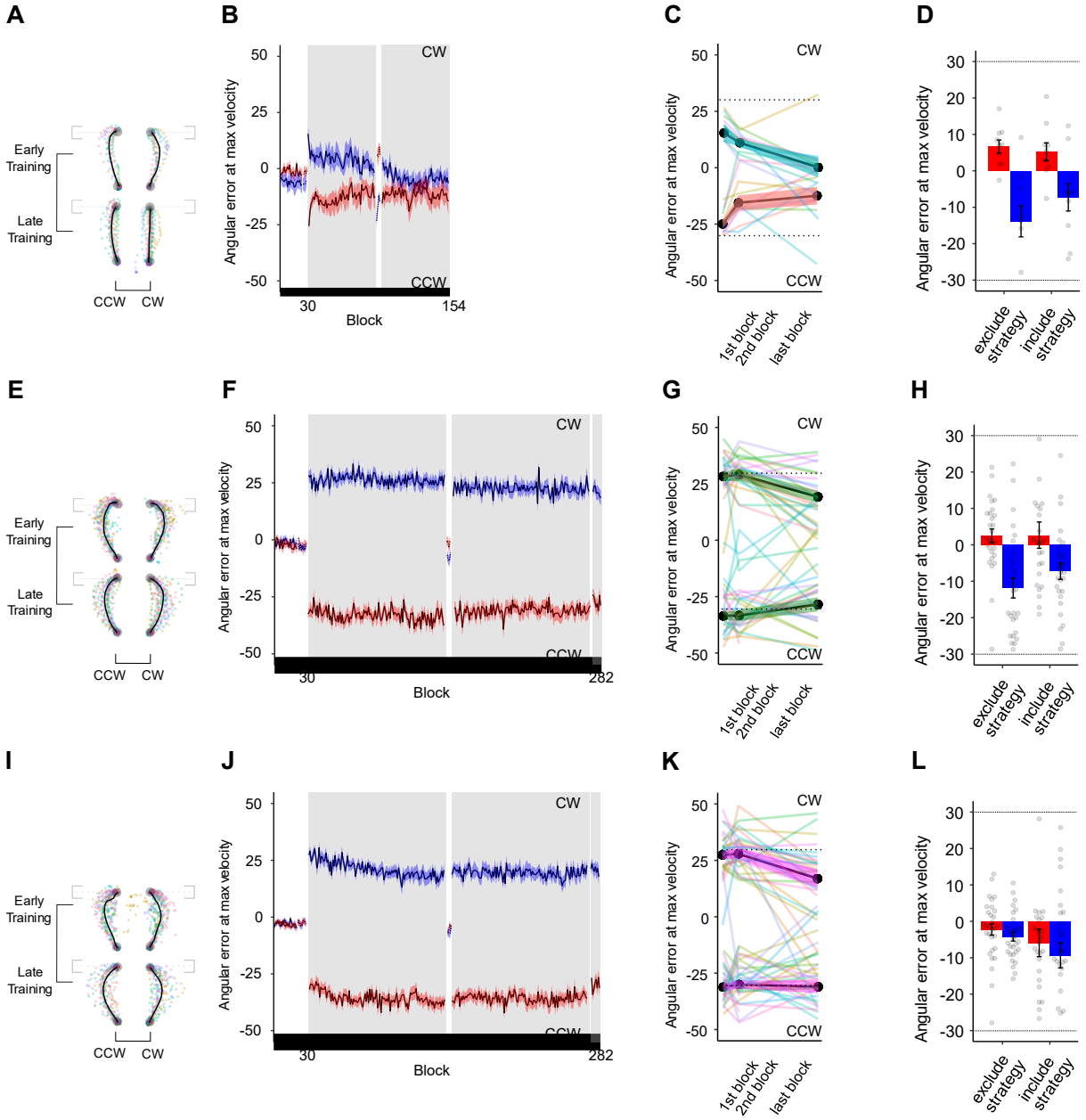

Figure 4.3. Experiment 1a performance. A. Averaged hand-cursor trajectories for CW- and CCW-only control groups. Coloured translucent dots represent individual trajectories. B. Visuomotor adaptation across all training blocks for CW- and CCW-only control groups. The learning curve for the CW-only group is in blue, and the CCW-only group in red. C. Truncated visuomotor adaptation across training for CW- and CCW-only control groups. Colored translucent lines represent individual learning curves for CW- and CCW-only control groups. D. Reach aftereffects in post-training for CW- and CCW-only control groups. Grey dots represent individual participant errors. Red bars

represent CW errors and blue bars represent CCW errors. Dashed lines represent rotation magnitude experienced during training (30° CW and 30° CCW). Error bars represent SEM. E. Averaged hand-cursor trajectories for the Active follow-through group. F. Visuomotor adaptation across training blocks for the Active follow-through group. G. Truncated visuomotor adaptation across training for the Active follow-through group. H. Reach aftereffects in post-training for the Active follow-through group. I. Averaged hand-cursor trajectories for the Passive follow-through group. J. Visuomotor adaptation across training blocks for the Passive follow-through group. K. Truncated visuomotor adaptation across training for the Passive follow-through group. L. Reach aftereffects in post-training for the Passive follow-through group.

4.4.1 Visuomotor adaptation

Experiment 1a: Active and Passive Cues Experiment

Active follow-through group

Participants made a two-part, active follow-through movement involving a reach to the target disc followed by a secondary, visually clamped reach to the target box. Figure 4.3F and 4.3G (green) shows the extended and truncated learning curves for Active Follow-through group, respectively. We saw a small, significant reduction in reaching errors at maximum velocity across training ($t(27) = 2.07$, $p = 0.02$, one-tailed, $d = 0.39$). Similarly, cursor path length reduced across training ($t(27) = 4.24$, $p < 0.001$), along with maximum deviation along the cursor trajectory ($t(27) = 2.52$, $p < 0.01$). To intuitively show the effect of the cue and individual performance, Figure 4.4 depicts percent improvement per experimental group and per rotation. Distinct active follow-through cues led to improved performance for both rotations as seen in Figure 4.4 (green bars); on average, participants improved across training by a modest 14.72% for the CCW rotation and 30.81% for the CW rotation. Post-hoc analysis of errors at maximum velocity revealed that for a moderately sized effect ($d = 0.50$) and our modest sample size, we had obtained power of 0.72 for this condition.

When we removed visual feedback of the cursor but kept the cues intact, we found significant reach aftereffects in their expected directions ($t(27) = 4.06$, $p < 0.001$, one-tailed, $d = 0.77$; Figure 4.3H, exclude strategy), also indicated in endpoint angles significant from zero ($t(27) = 4.49$, $p < 0.001$, $d = 0.85$). When asked to implement a compensatory strategy, we did not find a significant difference in reach errors relative to those during Exclude-Strategy No-Cursor trials ($t(27) = -0.80$, $p = 0.78$; Figure 4.3H, include strategy); endpoint angle was similarly not significant from 0 ($t(27) = -0.88$, $p = 0.81$). These findings further support that distinct active follow-through motions can facilitate dual adaptation, but we found that this compensation was largely implicit.

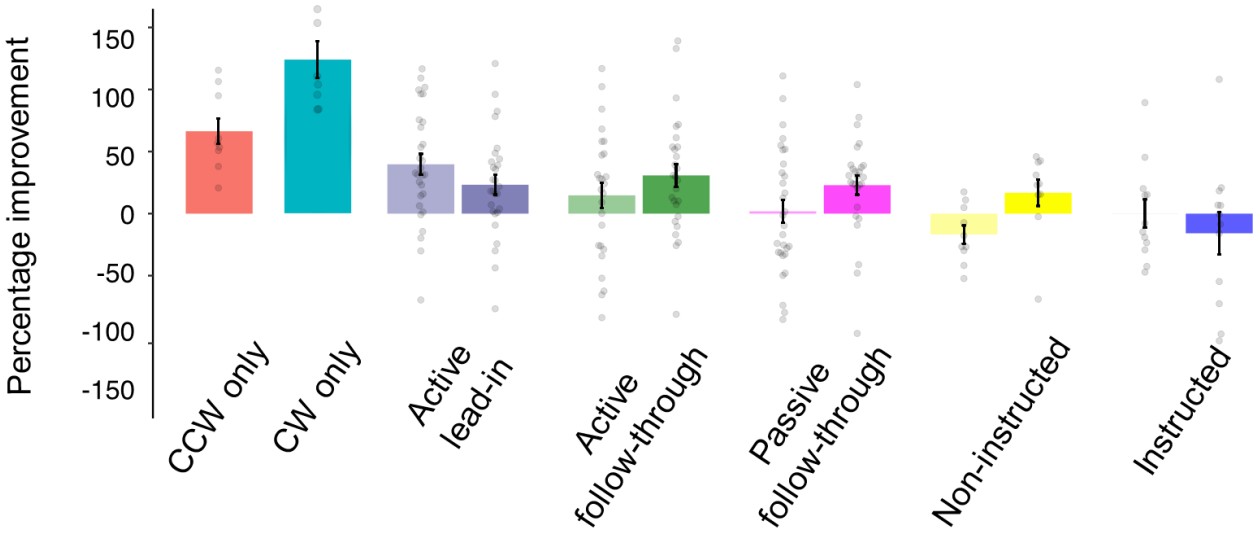

Figure 4.4. Percent improvement across training for all experimental groups and rotations. For dual conditions, bars with a darker hue represent PI for CW trials, and vice-versa. Grey dots represent individual improvement scores. Positive values reflect improvement, and vice-versa. Error bars represent SEM.

Passive follow-through group

In contrast to the Active Follow-through condition, in the Passive Follow-through condition participants were required to reach to the target disc with a CW- or CCW-rotated

cursor, and then simply observe their target disc move towards the target box. Training performance is illustrated in Figure 4.3J and 4.3K (pink). This cue was insufficient at facilitating dual adaptation as suggested by large reaching errors that did not significantly reduce across training ($t(29) = 0.91$, $p = 0.18$), also reflected in their percent improvement which was close to zero (Figure 4.4, pink bars). Using a two one-sided equivalence test (TOST) with $a = 0.05$ and equivalence bounds of $d = -0.50$ and $d = 0.50$ signifying a moderate effect size, we found that the observed effect is statistically not different from 0 ($t(29) = 0.911$, $p = 0.370$) and statistically equivalent to 0 ($t(29) = -1.828$, $p = 0.039$). Similarly, maximum cursor deviation did not reduce over time ($t(29) = 1.65$, $p = 0.05$), although path length decreased over time ($t(29) = 4.20$, $p < 0.001$). Expectedly, reach aftereffects were not in the expected directions, although significant from baseline as participants erroneously compensated ($t(29) = 1.86$, $p = 0.04$); Figure 4.3L). Endpoint angle was not significant from baseline ($t(29) = 0.87$, $p = 0.20$). Furthermore, comparing Exclude-Strategy and Include-Strategy No-Cursor trials, we did not find a significant difference in reach error (nor were they in the correct directions) for both the error at maximum velocity ($t(29) = -1.09$, $p = 0.86$) or at the end of the movement ($t(29) = 0.21$, $p = 0.42$). Thus, merely viewing the movement sequence did not elicit dual adaptation.

Experiment 1b: Active lead-in group

To explore whether a more complex lead-in movements can elicit dual learning, we had participants make a three-part movement sequence where the final portion of the reach was perturbed but the preceding motions were predictive of that perturbation. In the Active Lead-in group, participants reached along an edge from the home position, back to the home position, and finally, to the target disc. This active lead-in cue was able

to elicit significant dual learning over training ($t(26) = 3.44$, $p < 0.001$, one-tailed, $d = 0.66$; Figure 4.5B, 4.5C). Likewise, cursor path length reduced significantly over time ($t(26) = 5.46$, $p < 0.001$), but maximum deviation did not ($t(26) = 0.41$, $p = 0.34$), but this may have been driven by a few outlying participants. On average, participants reduced their errors by 26.95% for the CW rotation and 46.30% for the CCW rotation (Figure 4.4, purple bars). Post-hoc power analysis of errors at maximum velocity revealed that for a moderately sized effect ($d = 0.50$) and our modest sample size, we obtained a power of 0.28 for this condition.

Failing normality assumptions ($W=0.96$, $p = 0.02$)), a follow-up Wilcoxon rank-sum test indicated that active cues (Active Follow-through and Active Lead-in) tend to elicit larger PIs compared to passive cues (Passive Follow-through; $W = 1049$, $p = 0.01$, $\delta = 0.30$).

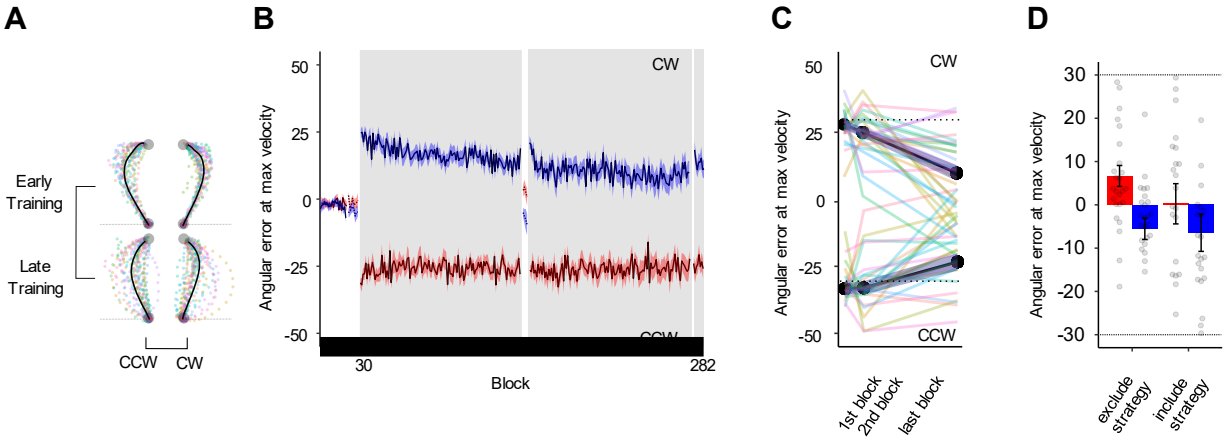

Figure 4.5. Experiment 1b performance. A. Averaged hand-cursor trajectories for the Active Lead-in group. Coloured translucent dots represent individual trajectories. B. Visuomotor adaptation across training blocks. The learning curve for CW trials is in blue, and CCW trials in red. C. Truncated visuomotor adaptation across training for the Active Lead-in group. Colored translucent lines represent individual learning curves. D. Reach aftereffects in post-training. Grey dots represent individual participant errors. Red bars represent CW errors and blue bars represent CCW errors. Dashed lines represent

rotation magnitude experienced during training (30° CW and 30° CCW). Dashed lines represent the rotation magnitude. Error bars represent SEM.

Reach aftereffects for the Active Lead-in group were in the expected directions (Figure 4.5D). When asked to exclude any explicit strategy used, participants showed significant reach aftereffects in their expected directions, suggesting the involvement of an implicit mechanism ($t(29) = 2.95$, $p = 0.003$, $d = 0.54$). Endpoint angle was not significantly different from 0 ($t(29) = 0.68$, $p = 0.25$), but this is likely driven by an outlying participant. Conversely, when asked to include a strategy, participants did not show any additional reach deviations in the expected directions as would be expected if they had used a strategy ($t(29) = -0.97$, $p = 0.83$); endpoint angle mirrored these findings ($t(29) = -1.27$, $p = 0.89$).

4.4.2 The role of instruction in dual adaptation

To examine the explicit and implicit contributions to dual adaptation, we instructed a group about the nature of the perturbations and how to compensate for them given the contextual cue (Instructed condition) and compared their performance to a group who completed an identical task but were not provided any instruction (Non-instructed condition). In the Non-instructed condition, we eliminated any active or passive sequences; participants saw the box targets but only reached towards the target discs. Expectedly, reaching errors at maximum velocity did not reduce across training ($V = 28$, $p = 0.81$; Figure 4.6B, 4.6C), with both cursor path length ($t(11) = 0.05$, $p = 0.48$) and maximum angular deviation mirroring this finding ($t(11) = -2.15$, $p = 0.97$). On average, for those who only received a static cue, percent improvement was -16.85% for the CCW rotation and 16.76% for the CW rotation which suggests that

participants failed to adapt using this visual cue (Figure 4.4, yellow bars).

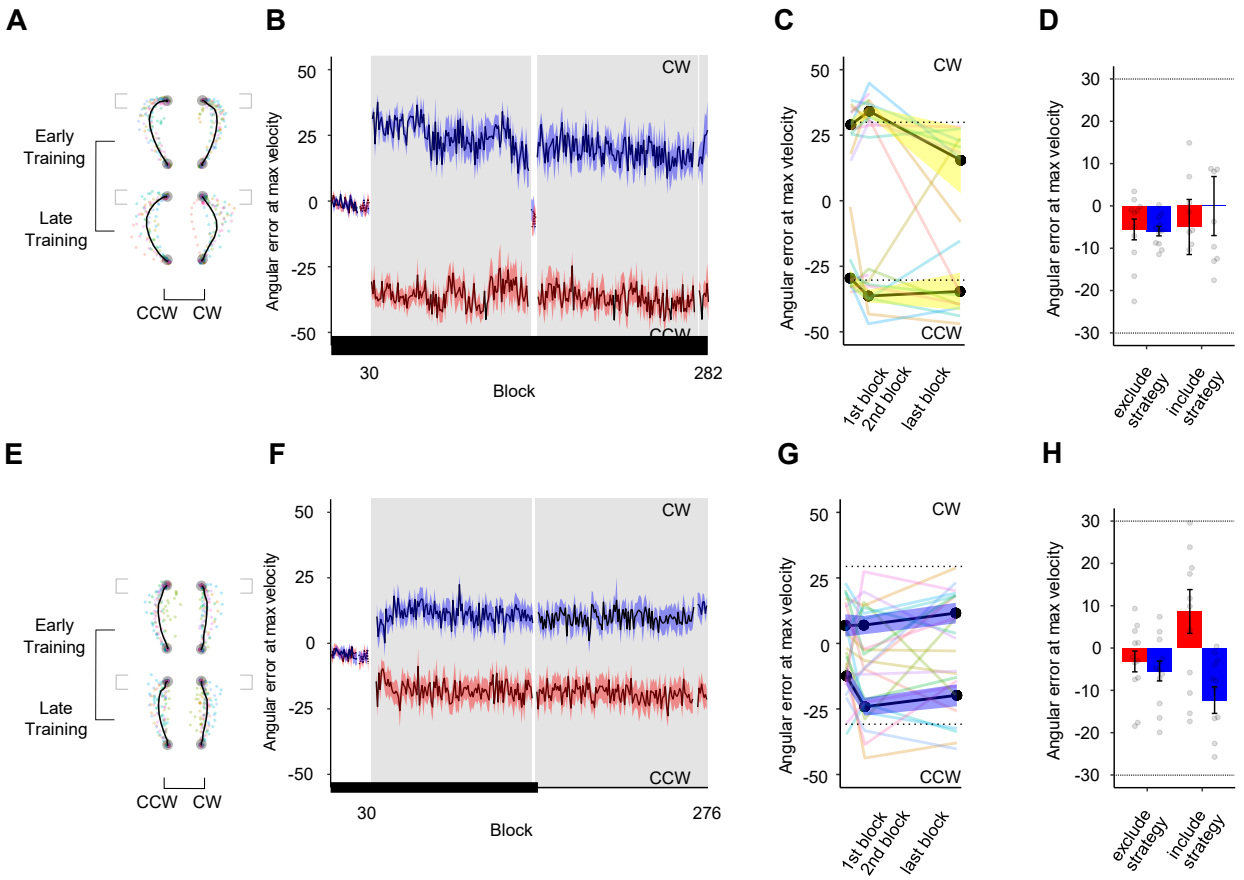

Figure 4.6. Experiment 2 performance. A. Averaged hand-cursor trajectories for the Non-instructed group. Coloured translucent dots represent individual trajectories. B. Visuomotor adaptation across training blocks for the Non-instructed group. The learning curve for CW trials is in blue, and CCW trials in red. C. Truncated visuomotor adaptation across training for the Non-instructed group. Colored translucent lines represent individual learning curves. D. Reach aftereffects in post-training for the Non-instructed group. Grey dots represent individual participant errors. Red bars represent CW errors and blue bars represent CCW errors. Dashed lines represent rotation magnitude experienced during training (30° CW and 30° CCW). Dashed lines represent the rotation magnitude. Error bars represent SEM. E. Averaged hand-cursor trajectories for the Instructed group. F. Visuomotor adaptation across training blocks for the Instructed group. G. Truncated visuomotor adaptation across training for the Instructed group. H. Reach aftereffects in post-training for the Instructed group.

Participants in the Instructed condition showed immediate benefits of strategy-use such that they made smaller errors right at the beginning of training. On average, those given instructions only had a 14.98° error in the first block of training, which is significantly smaller than that of the Non-instructed group at 32.54° ($t(18.02)= -7.72$, $p < 0.001$, $d = 3.04$). Failing normality assumptions ($W = 0.68$, $p < 0.001$), a Wilcoxon rank sum test on maximum deviation mirrored these results ($W = 34$, $p = 0.03$), but path length did not differ ($t(16.00) = 0.68$, $p = 0.51$) again likely due to two outlying participants. This advantage was fleeting, however, as participants in the Instructed condition did not further reduce their reaching errors across training ($t(11) = -1.78$, $p = 0.87$), suggesting that instruction benefits were immediate and not moderated by more training (Figure 4.6F, 4.6G); this was reflected in the maximum deviation measure ($V = 47$, $p = 0.28$) but not in path length ($t(11) = 2.79$, $p < 0.01$). Those in the Instructed condition did not show any improvement over time; their average reaching error by the end of training was only 17.98°, compensating for only about 40.07% of the rotation, implying that the role of instruction was limited and exerted most of its effects in the early stages of learning (Figure 4.6F, 4.6G).

Comparing No-Cursor trials across the Instructed condition (Figure 4.6H) and Non-instructed condition (Figure 4.6D), we found no implicit learning such that Exclude-Strategy No-Cursor trials were no different from Pre-Training No-Cursor trials ($F(1,22) = 0.00001$, $p = 0.99$); this was similarly reflected when comparing endpoint angles from Pre-Training and Exclude-Strategy trials across groups ($t(39.68) = -1.85$, $p = 0.07$). In particular, using a TOST ($a = 0.05$, lower bound $d = -0.50$ and upper bound $d = 0.50$), we saw that the observed effect in the Non-instructed condition was not statistically different

from 0 (t(11) = -0.0703, p = 0.945) and statistically not equivalent to 0 (t(11) = 1.662, p = 0.0624). Likewise, the Instructed condition similarly show indeterminate outcomes; the observed effect was not statistically equivalent to 0 (t(11) = -0.0634, p = 0.475) and not statistically different from 0 (t(11) = 1.669, p = 0.123). Further studies are thus needed to sufficiently support that implicit processes are not involved during Instructed or Non-instructed dual adaptation.

To probe the effect of instruction, we compared Exclude-Strategy and Include-Strategy No-Cursor trials between Instructed and Non-instructed conditions and found that having instructions significantly elicits more deviated reaches in the expected directions (angle at peak velocity F(1,22) = 17.71, p < 0.001, one-sided, η_G^2=0.19; endpoint angle F(1,22) = 11.86, p < 0.001, η_G^2=0.20). Together, these findings suggest that when contextual cues convey no information, the motor system may instead rely on an explicit mechanism to support dual adaptation.

To assess whether explicit processes are engaged within *each* experimental group, we compared Include-Strategy No-Cursor trials with Exclude-Strategy No-Cursor trials for the instructed and non-instructed groups separately. For the Instructed condition**,** we found that explicit mechanisms are engaged such that Include-Strategy and Exclude-Strategy No-Cursor reaches significantly differed (angle at peak velocity t(11) = 3.24, p < 0.01, one-sided, d = 0.94; endpoint angle t(11) = 2.32, p = 0.02, d = 0.67; Figure 4.6H). Using a TOST with a = 0.05 and equivalence bounds of d = -0.50 and d = 0.50 signifying a moderate effect size, we saw that the observed effect was not statistically different from 0 (t(11) = 0.756, p = 0.465) and statistically not equivalent from 0 (t(11) = -0.976, p = 0.175), yielding undetermined outcomes. Altogether these findings suggest that when

given an explicit compensatory strategy to dual adapt, the motor system likely relies on explicit processes exclusively.

4.5 Discussion

To better understand what allows for dual learning, we investigated various contextual cues including both actively-generated and passively-viewed follow-through motions. In another experiment, we explicitly provided participants with a compensatory strategy. Across all these conditions, we teased apart the explicit and implicit mechanisms underlying dual adaptation by separating the influence of strategy. We found that active movement cues facilitated dual adaptation, while passive cues did not. These simple active follow-through and lead-in movements were largely learned without awareness since we found implicit but not explicit contributions in their reach deviations during PDP trials. Expectedly, we didn't find evidence that static visual cues convey useful information to the CNS, instead finding interference. However, when given instructions about the rotations and their relationships to the static visual cues, dual learning was able to proceed but only in the form explicit learning, as we didn't find evidence for the presence of reach aftereffects attributed to implicit processes.

4.5.1 The role of active vs. passive cues in dual learning

Previous work on dual adaptation has largely demonstrated that motor-based or "intrinsic" cues tend to be more successful at reducing interference and facilitating learning (Ayala et al., 2015; Ayala & Henriques, 2018; Baldeo & Henriques, 2013; Galea & Miall, 2006; Schween et al., 2018; Wang & Musseler, 2014; Woolley et al., 2011). We further explored this idea by investigating whether self-generated movement sequence cues, which are motor-based by nature, can facilitate dual adaptation. In both our Active

Follow-through and Active Lead-in groups we found significant dual adaptation as evidenced by reduced reaching errors and significant reach aftereffects in the former experiment. Our findings support the force-field work by Howard and colleagues, who found that distinct follow-through motions can sufficiently cue the motor system to compensate for opposing force-field perturbations (Howard et al., 2015). Other force-field work showed that peripherally-moving visual cues do not facilitate learning, while passively-viewed lead-in visual cues do (Howard et al., 2012, 2013b). Thus, it was unclear if follow-through movement cues needed to be self-generated in order to facilitate dual adaptation. To explore whether the *active* lead-in or *active* follow-through was the key component in this contextual cue, we removed that active component of the cue, as in the Passive Follow-through condition, and found no reduction in reaching errors or any reach aftereffects in the expected directions. This suggests that even dynamic visual cues—likely extrinsic like that used in the Non-instructed condition**,** are insufficient even when it is temporally linked as a consequence of the perturbed reach.

Research by Howard and colleagues also found that lead-in motions can be coupled with opposing force-fields to produce significant reach aftereffects (Howard et al., 2012). They found that in their most effective dwell condition cued by a distinctive lead-in motion, participants were able to compensate up to 75% of the necessary force to overcome the perturbation. With these findings in mind, we designed the Active Lead-in condition to have minimal dwell times at the home position (100 ms) and found that participants compensated for less than half the size of the rotation in the Active Lead-in condition. There are a few factors that may account for this. One key difference is the complexity of our lead-in cue—participants were asked to make a three-part motion in

which the final reach was perturbed. So, not only did participants in the Active Lead-in condition have to access the past motion as a cue (second lead-in motion to the home position), they also had to go one step back to access the motion cue prior to that (first lead-in motion from the home position). Thus, one possibility is that cues that take longer to execute hampers its efficacy. Indeed, Howard and colleagues have found that a complex combination of lead-in and follow-through motion cues elicited dual adaptation to opposing force-fields, but only after intensive training across 5 days (Howard et al., 2015). Additionally, in a previous study of ours, we saw that doubling the training (from 360 to 720 trials) did not sufficiently induce greater improvement nor larger reach aftereffects (Ayala et al., 2015), making it possible that there is a maximum level of dual adaptation for a specific cue. Thus, future work should investigate if, and to what extent, longer sequences elicit dual learning. An alternative and less prevalent account might be that certain cues are more effective at facilitating dual adaptation to more dynamic tasks (i.e., force-field perturbations), and less to visuomotor rotations like we saw in our present experiments. Together, these may account for a proportion of why we saw a smaller mean level of compensation compared to previous force-field work implementing similar cues.

Interestingly, knowledge about the perturbations alone does not seem to dictate whether dual adaptation will occur. While not reflected in *more deviated* Include-Strategy No-Cursor reaches, post-experimental interviews revealed that a large proportion of those in the Active Lead-in condition were aware of the perturbations (post-experimental responses can be found in the project's OSF). In fact, in the Active Lead-in group, nearly 42% (13 out of 31) of participants were able to explain the nature

of the perturbations and their relationships with the cues, compared to 8 out of 28 participants (28.57%) in the Active Follow-through group. This didn't seem to lead to any advantage as both *active* experiments achieved a similar level of percentage improvement. For the experiments where dual adaptation did not occur, only one participant in the Non-instructed group and an intriguing 8 out of 30 (26.67%) participants in the Passive Follow-through group were able to explain the nature of the perturbations and their relationships to the cues. These post-hoc observations highlight the critical role of how explicit and implicit components of motor learning are assayed (Maresch et al., 2020). In a recent set of experiments, Maresch and colleagues found that more frequent sampling of explicit components via verbal report amplified explicit contributions, and that verbal report yielded larger explicit components compared to that of exclusion tests (i.e., PDP, as we adapted here) when matched for reporting frequency. Here we saw that post-experiment, some participants accurately report the nature and contextual associations of the perturbations, but not necessarily make the compensations *during* training. Possibly, this may be due to explicit mechanisms consisting of subcomponents, some of which are accessible depending on whether re-aiming is simply cached or recalculated (McDougle & Taylor, 2019), with our PDP measures likely placing greater emphasis on the latter. We should also recognize that explicit knowledge of the perturbation altogether does not necessarily imply that participants were obliged to make corrections (Hadjiosif & Krakauer, 2020). Lastly, minute differences in how participants are informed about the perturbation have the potential to influence the differential contributions of these sub-mechanisms. Thus, future work should assess these key differences in determining the optimal way on how

explicit learning can be extracted from behaviour. It should be also noted that some differences lie between conditions and it's unclear how these factors affect our findings; for instance, the Active Lead-in condition involved a motion elicited a movement cue toward the starting position, while the Active Follow-through condition elicited a movement cue around the target disc. Thus, it seems that even with a sizeable portion of participants having knowledge about the nature of the perturbation, we still do not see significant strategy application. Possibly, insufficient cues might require the implementation of explicit aiming strategies to be successful.

An alternative explanation has been put forth by Sheahan and colleagues (Sheahan et al., 2016), who showed that distinctive motor plans, not movement execution, allow for concurrent adaptation to opposing force fields. They found that participants still compensated in the direction depending on the follow-through target even when they did not execute a follow-through motion, suggesting that the representation of the motor plan drives this dual adaptation (action selection), not the follow-through movement itself (action execution) (Sheahan et al., 2016). This provides an alternative explanation to the lack of dual adaptation in our Passive Follow-through condition**,** where it was unlikely that participants produced a motor plan relevant to the cue, since they only viewed a visual consequence of their movement. Our finding that passive cues don't lead to significant dual learning provide further support to their proposition that dual adaptation is more likely to be associated with a distinctive internal state which is separate from the neural dynamics involved during execution (Sheahan et al., 2016).

Use-dependent learning can alternatively explain how those in the Active Follow-through and Active Lead-in conditions were able to adequately adapt to both rotations.

Here, use-dependent learning can alter the learning process since perturbations were applied in a redundant dimension of the movement (Diedrichsen et al., 2010). Since leftward-flanking lead-in and follow-through motions were always paired with CCW perturbations, it's possible that participants developed a bias toward repeated movement directions (i.e., by always aiming to the right-hand side).

4.5.2 Insufficient cues can be salvaged by aiming strategies

As expected, static visual cues did not show any predictive strength, so in addition we provided participants in the Instructed condition with aiming strategies that depended on that context. This implementation led to significant learning which suggests that when cues are insufficient (e.g., static visual cues), the CNS can tap into explicit mechanisms to support dual learning. This purely explicit learning, however, comes at a cost. We saw that those in the Instructed condition could immediately compensate by implementing the aiming strategy, but they failed to improve, only retaining a small portion of the aiming strategy by the end of the training session, and later reflected in the lack of implicit reach aftereffects. In contrast, using a strongly predictive cue of target workspace separation, Schween et al. (Schween et al., 2018) nicely demonstrated significant implicit reach aftereffects in their group that received verbal instructions about how to counter their blocked 60° CW and CCW rotations (Schween et al., 2018) that were otherwise shown to interfere. Indeed, we found a similar effect whereby dual adaptation as cued by separated target sets were able to elicit reach aftereffects that decreased in size as a function of the distance between workspaces (Baldeo & Henriques, 2013). Critically, we show here that moderately predictive cues can indeed elicit implicit learning, but in the case of the Non-instructed

and Instructed groups, an ineffective cue even in conjunction with aiming strategies will be unsuccessful.

Finally, it should be emphasized that our Instructed group are by proxy provided some explicit component of learning (i.e., through the aiming strategy), while those in Non-instructed groups (e.g., in Schween et al., 2018) were able to derive it from visuomotor learning alone. In fact, Schween et al. (2018), participants had relatively decent estimates of the rotations, estimating over half of the rotations' magnitudes in their explicit judgment task, while our explicit reach aftereffects in the Instructed group only reached about a third of the size of our rotations. In light of these differences, these findings bring up the critical point that explicit strategies can support dual learning but only to a limited extent. Here we found that explicit strategies can aid an impoverished context, while more recent work by Schween and colleagues have found more interactive contexts can elicit dual learning (Schween et al., 2019a). There is also the potential that the mechanisms behind dual adaptation differ for smaller and larger rotations. Finally, it remains unclear how rotation presentation schedules influence this dual learning (i.e., pseudo-randomized trial-by-trial vs. alternating blocks of 8 trials per rotation).

4.5.3 Limitations

Post-hoc power analyses revealed that limited statistical power due to our modest sample sizes may have played a role in limiting the significance of some of the statistical comparisons we conducted. While we were able to obtain a power of 0.71 for our Active Follow-through condition, still shy of the recommended level of 0.80, we would have needed a sample size of approximately 64 in our Active Lead-in condition.

Relative to the literature, Experiment 2 had an adequate sample size but due to its exploratory nature, future experiments looking at the role of instruction in dual adaptation should approach it with a larger N, with sizes at least comparable to those in Experiment 1; this need was additionally confirmed by findings from equivalence testing.

We additionally observed small effects in our Active Follow-through condition, with an effect size of d = 0.39 and a percentage improvement that was much larger in the CW condition (30.81% vs. 14.72%). Thus, it is possible that one perturbation elicited most of the learning, and this imbalance may signify that the CW condition was primarily being learned over the other.

4.5.4 Conclusion

Altogether our findings show that while intrinsic cues (such as active lead-in and follow-through cues) provide an avenue for the motor system to learn two or more visuomotor mappings at the same time, it is single-handedly the underlying explicit mechanism that drives learning when the cues are insufficient. This has significant implications in short-term rehabilitation where time is constrained and the motor system must rely on explicit processes to re-learn multiple motor skills, so future studies should investigate how to enhance this explicit process so that learning can be retained over extended periods of time.

Chapter Five: Dual adaptation in VR

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This chapter is in preparation for submission.

5.1 Abstract

Motor adaptation has long been studied in virtual reality environments, using two-dimensional displays where participants typically experience a perturbation to the visual feedback of their movements. Now more than ever, head-mounted virtual reality (HMD-VR) is increasingly used in laboratory settings to understand motor control under a more ecologically valid yet still experimentally rigorous lens, but still little is known about the underlying mechanisms at play in this novel setting. Building on recent work that shows differential contributions of implicit and explicit learning in HMD-VR, here we try to understand the subprocesses in two phenomena in motor learning: (1) how error is attributed in object manipulation, and (2) whether a richer contextual environment can facilitate adaptation to opposing perturbations where it would typically lead to interference. In the first experiment, participants trained on transporting a perturbed object with their right hand. They were additionally asked to transport a novel object, with either the trained hand or with their untrained, contralateral hand. We did not see an attribution of error to the end-effector; participants transferred a similar amount of learning when using their untrained, contralateral hand to transport either the trained or novel object. Likewise, transfer of learning was similar when transporting a trained object versus a novel object with the trained right hand, suggesting that there was no attribution of error to the object itself. This suggests a different learning profile for object manipulation in the HMD-VR setting. In the second experiment, we used a dual adaptation paradigm, each object identity (sphere and cube) predicted a distinct and opposing visuomotor rotation and applied a Process Dissociation Procedure to look at the explicit and implicit contributions that may underlie this process. In a follow-up

experiment, another group completed the same paradigm with a perturbation set that was double the size, to understand how rotation magnitude may play a role in dual adaptation. We found weak evidence for dual adaptation to opposing visuomotor rotations, suggesting that object identity does not facilitate dual learning even in an immersive, and more realistic experimental paradigm. Together, these findings highlight that although HMD-VR presents a novel way to understand motor learning, there remains critical differences in how adaptation proceeds in 3D virtual reality environments.

5.2 Introduction

Head-mounted virtual reality (HMD-VR) provides an exciting new avenue to test motor learning in a more immersive environment that allows researchers to make more ecologically valid conclusions from their paradigms. Unlike conventional virtual reality, HMD-VR allows for a richer study of behaviour by providing a more realistic simulation of the world and allowing experimenters to powerfully manipulate context and feedback. Beyond its experimental utility, participants usually feel more engaged and motivated in HMD-VR tasks, as evidenced by greater feelings of presence and embodiment (Finkelstein et al., 2011; Ijsselsteijn et al., 2006; Osimo et al., 2015). With a growing body of work across a variety of fields, HMD-VR becomes an increasingly compelling approach to study motor learning that allows for experiments that are not only well-controlled, but also realistic.

Still, very little is known about how motor learning and its sub-processes proceeds differently in HMD-VR, given the limited number of studies conducted with this novel tool. For instance, it's now recognized that motor adaptation can be characterized by at least two qualitatively different learning mechanisms: [1] an explicit, or conscious process which arises due to the use of aiming strategies, and [2] an implicit process which is thought to function without awareness, reflecting adaptation of internal models in the cerebellum (Heuer & Hegele, 2008; Taylor et al., 2014; Taylor et al., 2010). Recent work has now shown that adaptation to visuomotor rotations in HMD-VR may consist of different contributions from explicit and implicit sub-mechanisms in motor learning, as compared to conventional VR (Anglin et al., 2017). Specifically, adaptation in HMD-VR may elicit greater cognitive or explicit strategy compared to conventional

VR, while conventional VR elicits more implicit learning compared to HMD-VR. Additionally, motor skills learned in HMD-VR tend to transfer less to conventional VR compared to vice-versa, or not at all for certain sequence learning tasks (Anglin et al., 2017; Juliano & Liew, 2020). Given its novelty to the motor learning literature, we sought to validate this approach, and take advantage of its powerful capacity to manipulate context to better understand how the motor system learns.

Due to its relative novelty in motor learning research, it's unknown how the motor system assigns experienced error when manipulating objects in virtual 3D space. In the real world, when we interact with objects, we efficiently construct an internal representation of the object's properties from trial to trial (Flanagan et al., 2001; Gordon et al., 1993). However, learning from experienced error brings up a critical question: where is the source of error? In other words, did the error arise because I misestimated properties of my body or that of the object? (Berniker & Kording, 2008; Kluzik et al., 2008). Kong et al. (2017) were first to examine this question with an integrated approach, since this question is typically explored by looking at how learning transfers between effectors or transfers between objects; they looked at how much learning can be attributed to the body and the object by having participants adapt to picking up a glass of water of a certain mass with their right hand. To determine how much learning can be attributed to the object, participants picked up the trained object with the contralateral hand. To determine how much learning can then be attributed to the hand, participants used the trained hand to pick up a novel object. They found transfer distinct to the hand and to the object, on top of learning the task itself (Kong et al., 2017). Still, it's unclear how this underlying process might differ in HMD-VR, especially since

learning in this novel environment appears to be more reliant on cognitive, explicit mechanisms (Anglin et al., 2017). For instance, Just et al., (2014) showed that movement in HMD-VR and conventional VR training have similar kinematic profiles, but HMD-VR elicited longer reaction times, which can have implications in the extent to which learning in this environment relies on more cognitive subprocesses (Haith et al., 2015; Just et al., 2016). Thus, it's important to understand how error is assigned in the HMD-VR environment, since VR-based interventions are increasingly being adapted, and how we learn differently in this space may have significant implications on rehabilitation prognosis.

HMD-VR additionally opens a new avenue for researchers seeking to understand the role of context in motor learning. To study this in a way that mimics the daily demands on the motor system, we can use a dual adaptation paradigm where participants are presented with opposing visuomotor perturbations, randomly interleaved within the same training period. Typically, when faced with two (or more) visuomotor perturbations within the same training session, participants fail to "dual adapt" such that movement errors do not reduce significantly over time for both perturbations, leading to interference (Brashers-Krug et al., 1996). A body of literature now shows that the CNS can flexibly adapt to two or more perturbations, but only if each visuomotor mapping is extensively trained with a sufficiently distinctive contextual cue. Still, it's unclear why certain contextual cues help the motor system predict the impending perturbation, nor what the cues are themselves. So far, it's been found that these cues tend to be motor-based or "intrinsic" in nature, with cues such as movement direction, type, sequence, or posture, sufficiently facilitating dual adaptation (Ayala et

al., 2015; Ayala & Henriques, 2018; Baldeo & Henriques, 2013; Howard et al., 2012, 2013a; Woolley et al., 2007). Non-motor (or “extrinsic”) cues such as background colour and object identity show mixed findings (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Hegele & Heuer, 2010; Hinder et al., 2008; Osu et al., 2004; Woolley et al., 2007), while more recent work shows that visual cues can elicit dual learning when they show an interactive action effect such as distinctively “exploding” targets (Schween et al., 2019b) or dynamic tools (McGarity-Shipley et al., 2020). So, it remains unclear if this discrepancy in dual learning is due to a more engaging task and task structure.

We decided to further understand how motor learning proceeds in HMD-VR with a unified approach: first, by seeing how transfer of learning occurs between distinct objects, and second, by exploring whether these distinct objects can elicit dual adaptation, and if so, how much of this learning is due to implicit and explicit mechanisms. Using HMD-VR to mimic an analogous 3D environment to our typical lab set-up, we had participants transport spheres or boxes on a table, to a location as indicated by the object shape (e.g., a sphere can only be transported to a circular receptacle). In the first experiment, participants adapted to either a 30° CW *or* 30° CCW visuomotor rotation with their right hand with an initial object. They were then asked to pick up both trained and novel objects with either their trained, right hand or their untrained, contralateral hand. With these conditions also serving as control groups for the dual adaptation conditions, we then had another group experience both CW and CCW rotations, each predicted by object identity and thus, receptacle shape. Since some work has shown dual adaptation with extrinsic cues (i.e., tool identity) in conditions where larger perturbations were imposed (Schween et al., 2018, 2019a), in a

second dual condition, participants experienced 60° CW and 60° CCW rotations, again predicted by object identity on a given trial. Together, these findings further elucidate the key differences in motor learning in HMD-VR, and whether this immersive and engaging environment will be sufficient at eliciting learning where it typically would not occur.

5.3 Method

5.3.1 Participants

Seventy-seven participants (55 females, 19.99 ± 3.14 years old, mean ± SD) were recruited, assigned to participate in the following experiments, and granted a bonus credit for either an undergraduate psychology or kinesiology course. All participants were right-handed, had normal or corrected-to-normal vision, and were naïve to the purpose of the experiment. All participants provided written, informed consent. Procedures were approved by the York University Human Participant Review Committee.

5.3.2 Apparatus

Participants sat on a height-adjustable chair facing a table placed at waist level. They wore an Oculus Rift Consumer Version 1 (resolution 1080 by 1200 for each eye, refresh rate 90 Hz) and held an Oculus Touch controller with their right hand. Participants were instructed to place their left hand on the magnetized docking apparatus (7.5 cm in diameter) at the centre of the table to aid them in returning to the home position (dock) to restart the next trial. To ensure accurate tracking, three Oculus Constellation sensors tracked the head position and the Oculus Touch VR controller.

In the VR environment, participants were presented with their avatar's right hand, representing the movement of their own right hand (Figure 5.1). To initiate a trial, participants first docked and aligned their hand to the home position (radius of 1 cm, corresponding to the physical dock), until an object spawned (depth of 2 cm) on the table. Objects spawned 10 cm away from the home position, and receptacles (depth of 2 cm) spawned around the target location 15cm away from the object (3 radially spaced targets located at 45°, 90°, and 135°; Figure 5.1, seen as hollow receptacles). Object and target stimuli were presented in a pseudo-random order. Participants were instructed to pick up the spawned object by first overlapping their hand avatar at its location, making a pinching motion using the index finger and thumb by pressing the VR controller buttons. To highlight the object identity, the hand avatar disappeared once the object was picked up. Participants then had to transport the object to its correct receptacle (i.e., sphere to circular receptacle, box to square receptacle). All movements were made with a 1:1 ratio.

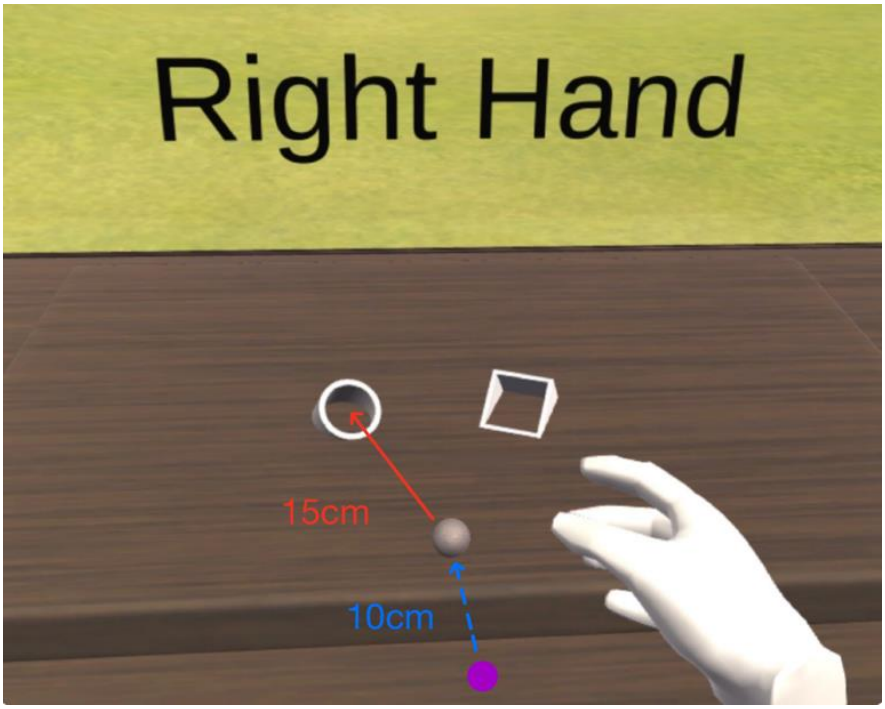

Figure 5.1. Experiment display. Participants grasped an object (box or sphere) and placed it into the matching receptacle (i.e., box object to box receptacle as seen above, or sphere to the sphere receptacle). An animation of the experimental task can be found https://osf.io/gv64a/ in the project OSF and in https://deniseh.lab.yorku.ca/.

5.3.3 General procedure

In the following experiments, we explored the underlying mechanisms in motor learning in HMD-VR to understand any differences from widely used conventional VR methods. In the first experiment, we looked at how much learning is transferred between trained and untrained hands when transporting trained and untrained objects, to understand how the motor system is attributing experienced error. In the second experiment, we looked at whether object identity (i.e., shape) can elicit dual adaptation. Using both groups from Experiment 1 as control groups, in Experiment 2 we had a third group ("Dual-30") of participants who adapted to both 30° CW and 30° CCW rotations within the same training block, with each perturbation predicted by the same object (and thus, receptacle) identity association as in the control conditions (30° CCW for sphere

trials; 30° CW for cube trials). Then, to understand whether rotation size plays a role in dual adaptation, in a follow-up dual condition (“Dual-60”) participants adapted to both 60° CW and 60° CCW rotations within the same training block, again as predicted by object identity. Across all experimental groups, sphere trials were associated with a CCW visuomotor rotation, while cube trials were associated with the opposing CW visuomotor rotation.

All participants started at the same home dock and were told to produce smooth and direct movements throughout the experiment. Although there were no hard time restraints, participants were encouraged by the experimenter to move in a quick and uniform pace across training and were warned if they moved toward the target too slowly.

Across all trials, participants had visual feedback of the object being transported. During aligned feedback trials, participants transported objects without any perturbation being imposed (Figure 5.2A). During rotated feedback trials, participants experienced a perturbation to the visual feedback of the object being transported (Figure 5.2B). During clamped feedback trials, participants saw the transported object move straight from its starting position to the receptacle location. Clamped feedback trials reveal behaviour in the absence of visual error feedback, potentially showing movement aftereffects that would otherwise be difficult to capture in the VR setup.

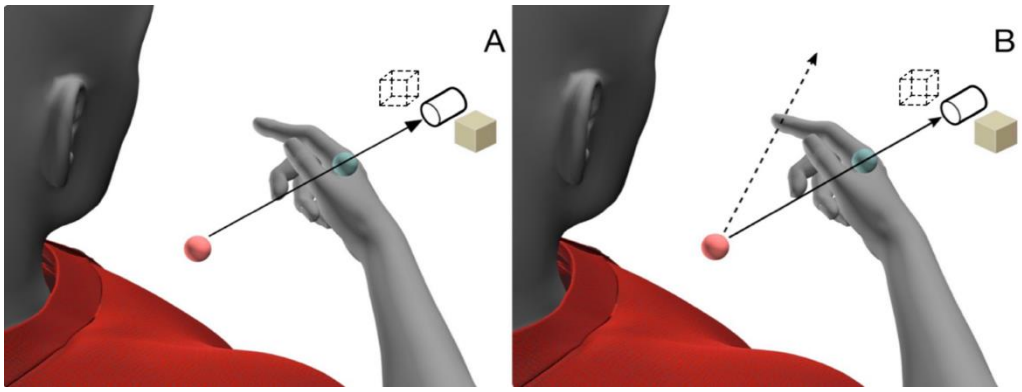

Figure 5.2. Trials types. A. During the aligned condition, participants transported an unperturbed object to the square receptacle. The solid black line represents the movement of the participants hand and the object. B. During the rotated condition, participants transported an object that was perturbed by 30° CW or 30° CCW, depending on its identity (and thus, receptacle type), relative to the object's spawn location. The dashed line demonstrates the path of the participants hand movement, while the solid line is the path the object takes. Trials alternated between cubes or spheres, and participants were required to move the object to the correctly shaped receptacle. The cylinder is at the 90° position, the solid cube is at the first possible spawn location, and the dashed cube demonstrates the second possible receptacle spawning position.

5.3.4 Trial structure

Participants started with their right hand on the magnetized home dock where their location is initially calibrated, and their hand avatar appears. Once the VR system sensed the docked right hand was held stationary at the home location, an object would spawn 10 cm away from the home dock. Participants picked up the object by making a pinching motion by pressing on the Oculus Touch VR controller index and thumb buttons, and overlapping their pinch aperture over the location of the object. Once the object was picked up, the avatar of the participant's hand would disappear, and they now must transport this object to its final location–the appropriate receptacle (e.g., circular receptacle for the sphere). In both experiments, regardless of the object being transported, participants always saw both types of receptacles to encourage them to pay

attention to the object identity; the correct receptacle appeared at one of the three possible target locations (45°, 90°, and 135°) while the incorrect receptacle spawned randomly at one of the remaining 2 target locations. All trials ended once the participant placed the object in the correct receptacle by overlapping the object with the receptacle opening, coinciding with a high-pitched, pleasant sound effect which indicated a completed trial; objects were not accepted into the incorrect receptacle. After dropping off the object, participants returned their right hand to the home dock, where the VR system can then sense a docked position to proceed to the next trial.

Across all groups, participants completed pre-training, training, and post-training sessions (Figure 5.3). Participants were given a practice block of aligned trials prior to the start of the experiment. For the control conditions, participants completed the task in approximately 30 minutes (Figure 5.3A), while those in the dual conditions completed the task in approximately 45 minutes (Figure 5.3B). Participants were not informed about the presence or nature of the rotation at the start of the experiments. After the experiment, participants answered a series of questions to assess their awareness of the rotation and the experimental objectives.

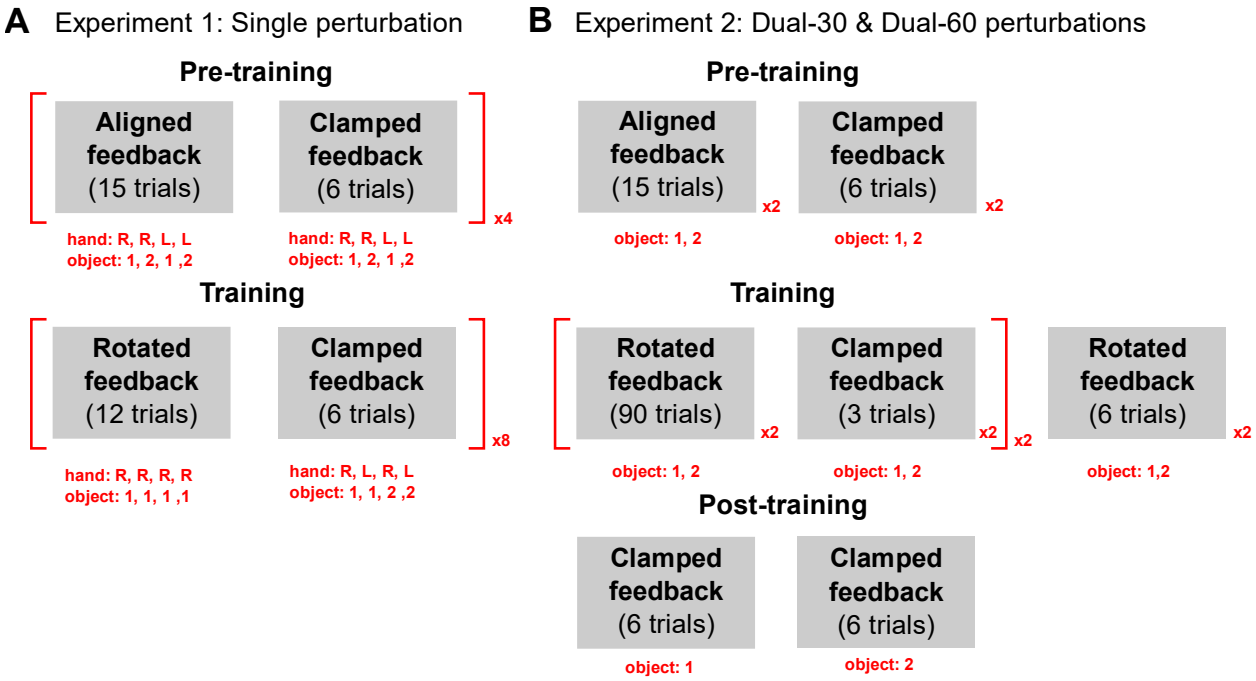

Figure 5.3. Session sequence for the Chapter 5 HMD-VR experiments. A. Single perturbation experiments. Pre-Training consisted of Aligned and Clamped feedback trials for both right (R) and left (L) hands for each object 1 and 2. Training consisted of Rotated and Clamped feedback trials for both R and L hands and objects 1 and 2. B. Dual-30 and Dual-60 perturbation experiments. During Pre-training, participants experienced aligned and clamped feedback for both objects. This was followed by Training, which consisted of Rotated and Clamped feedback trials for both objects, and a final top-up Rotated feedback training. Post-training consisted of Clamped feedback trials where participants were first prompted not to apply any strategies they may have developed during training.

5.3.5 Experiment 1 protocol

Single groups (CW- or CCW-only). Thirty-two participants (20.03 ± 3.21 age, 24 females) completed Experiment 1 and served as CW- or CCW-only controls for both conditions in Experiment 2. Sixteen participants trained with a cube and experienced a 30° CW visuomotor rotation during training (Figure 5.3A, Training), while the remaining 16 trained with a sphere and experienced a 30° CCW visuomotor rotation during training. Participants picked up their trained object and transported it to its appropriate receptacle (Figure 5.1).

Pre-Training (Aligned object motion)

Participants started with three blocks of practice, consisting of 45 trials. The experiment then commenced with a Pre-training session, consisting of a series of 15 aligned feedback trials (veridical) followed by 6 clamped feedback trials (i.e., no visual error feedback) four times, to experience all possible hand and object permutations (Figure 5.3A, row 1, Pre-training).

Training (Rotated object motion)

During Training, participants transported an object that was perturbed with a visuomotor rotation of 30° CW **or** 30° CCW. Participants who trained with object 1 (sphere) experienced a 30° CCW, while those who trained with object 2 (cube) experienced a 30° CW rotation. Participants transported their trained object 99 times. Then, to measure transfer while maintaining adaptation, the trained object was transported 12 times followed by 6 clamped feedback trials, and this training sequence was repeated 8 times (Figure 5.3A, Training). Clamped feedback trials consisted of all hand and object permutations to obtain a complete set of measures of transfer.

5.3.6 Experiment 2 protocol

Dual-30 group

Thirty participants (19.69 ± 3.14 age, 23 females) completed the Dual-30 condition (Figure 5.3B). Participants picked up an object (sphere or cube) and transported it to its appropriate receptacle (Figure 5.1).

Pre-training (Aligned object motion)

To obtain baseline performance and familiarize participants with the task, participants first transported both objects 60 times with aligned visual feedback, followed by 12 trials with clamped visual feedback to record baseline errors (Figure 5.3B, row 1, Pre-training).

Training (Rotated object motion)

The aim of training was to expose participants to a visuomotor rotation to assess adaptation. Participants transported objects 180 times with alternating blocks (of 3 trials) of 30° CW and CCW rotated feedback followed by 6 clamped feedback (Figure 5.3B, row 2, Training). This was repeated for a total of 360 rotated training trials and 12 clamped feedback trials. To determine whether dual adaptation can be elicited by object identity, during training participants transported spheres that were rotated 30° CCW and boxes that were rotated in the opposite direction (30° CW). At the beginning of every trial, participants saw a spawned object (box or sphere), a box receptacle, and a sphere receptacle. On a given rotation block, the location of the correct receptacle was pseudo-randomized such that every receptacle location appeared once before the next object type was presented. Since we did not give any instructions for clamped trials during training, participants likely used whatever strategy they employed for rotated training trials. Additionally, in a previous experiment we confirmed that reach errors within training blocks compared to those after being explicitly asked to exclude any strategies do not significantly differ in size (Ayala & Henriques, In Review). So, we assumed that errors during these clamped trials as inclusive of strategy (Include-Strategy) to later use for the Process Dissociation Procedure (PDP; adapted from Werner et al., 2016; Modchalingam et al., 2019). PDP allowed us to make inferences about the participants'

awareness, which in turn allowed us to tease apart implicit and explicit contributions to dual adaptation.

Post-training (PDP)

Following Training, we confirmed with participants that the objects would not move in the same direction as their hand when they are transporting it, and that they needed to compensate and keep that compensatory strategy in mind (Figure 5.3B, Confirmation, in orange) as they will later be prompted by the screen to not use a "strategy" (Exclude-Strategy). Following Confirmation, participants reached with both CW- and CCW-rotated cursors for 12 trials (in alternating blocks of 3 trials) to preserve any dual adaptation. This was followed by 6 Exclude-Strategy clamped feedback trials for one object, then 6 Exclude-Strategy clamped feedback trials for the other object (Figure 5.3B, row 3, Post-training). All post-training tasks were counterbalanced.

Dual-60 group

Sixteen participants (20.50 ± 5.02 age, 8 females) completed the Dual-60 condition (Figure 5.3B). As in the Dual-30 condition, participants picked up an object and transported it to the appropriate receptacle (Figure 5.1A). The key difference of this condition compared to the Dual-30 group is the size of the opposing perturbations experienced during rotated trials (i.e., 60° CW and 60° CCW). The same protocol as in the Dual-30 was followed.

Data Analysis

All kinematic data were recorded by Unity 3D (2020.1.17, Unity Technologies, San Francisco, CA). The experimental data was analyzed offline using R

(preprocessing and analysis scripts can be found in https://github.com/ayalamar/dual-vr), using kinematic error (operationalized as hand angle, i.e., heading error) during rotated and clamped feedback trials. Hand angle was defined as the angular deviation (from a straight-line path connecting the object starting location and receptacle location) at 3 cm after the object was picked up. For all our analyses involving blocks, we averaged across blocks of 3 trials to include a movement to each target. The assumed level of significance for all statistical tests was $\alpha = .05$, and post-hoc comparisons were Bonferroni-corrected. Hand angle was subject to tests of normality, and corrections for unequal variances were applied where necessary. All data can be found in the project OSF (https://osf.io/2t6ak/).

Experiment 1: Credit assignment

Visuomotor adaptation. To quantify overall learning in these single rotation conditions (CW- and CCW-only conditions), we ran a planned repeated-measures t-test between the first block vs. final block of training for each condition. All data were normalized to reflect counterclockwise errors to enable easy comparisons.

Transfer between trained and untrained hands. Next, to see whether transfer took place between hands, we determined whether there was a difference in hand angle between the right and left hand. The difference in hand angles between the two hands would indicate the extent to which adaptation in the trained right hand benefits the untrained, left hand. More specifically, complete transfer would be indicated in the same level of adaptation between hands, while partial transfer would be indicated in a hand angle above baseline levels but less than that of the trained hand. No transfer would be indicated in left hand angles showing similar levels as baseline. To this end, we looked

at clamped feedback trials during Training, collapsed across objects, and compared the two left-hand clamp blocks with that of the right-hand blocks using a repeated-measures t-test.

Transfer between trained and untrained objects. To see whether transfer took place between objects, we determined whether there was a difference in hand angle between objects. To do this, we looked at clamped feedback trials during Training, pooling together blocks sharing that same object identity (i.e., trained object vs. novel object) and comparing the hand angle between them using a repeated-measures t-test.

Experiment 2: Dual adaptation

Visuomotor adaptation. Typically, analyses of adaptation involve comparisons between the single perturbation conditions and the dual perturbation conditions about their rates of learning. However, it has become abundantly clear from the past work that dual adaptation rarely parallels the learning rate of single adaptation, so for brevity we opted to only report statistics on dual learning.

To study whether object identity elicited dual adaptation, we looked at whether there were differences in early versus late adaptation by comparing the initial block and the final block of rotated training. First, using a 2 (block: first, last) by 2 (object: sphere, cube) repeated-measures ANOVA, we looked at whether there was a significant reduction in hand deviations over time. Then, since CW and CCW errors are not expected to elicit different rates of learning, we analyzed normalized errors, but visualize signed errors to show whether compensation occurs in the expected directions. A planned repeated-measures t-test (first block vs. final block of training;

one-sided) was used to show whether adaptation has occurred within each experimental group (i.e., Dual-30, Dual-60).

PDP. Since it is difficult to obtain movement aftereffects in the HMD-VR setup compared to conventional VR, we opted to capture angular deviations when there is no visual error feedback. Like reach aftereffects in conventional VR (i.e., rotation-dependent, deviated reaching in the absence of visual feedback of the cursor), errors during these clamped feedback trials can also reveal whether dual learning has occurred. These errors during clamped trials can further be analyzed to reveal explicit and implicit components using the PDP (Modchalingam et al., 2019; Werner et al., 2015). Implicit learning can be reflected in clamped trials where participants were told not to implement any strategies in their movements (i.e., Exclude-Strategy; Figure 5.3B, row 3, Post-training). To this end, we subtracted any biases from the final block of clamped trials during Pre-training from the first block of Exclude-Strategy clamped feedback and determined whether this was significant from zero using a one-sample t-test (one-sided) for each object type per group.

Include-Strategy clamped feedback trials consist of not only explicit, but also implicit processes. Here, we opted to apply clamped feedback trials immediately following training with both perturbations, but before confirmation (Figure 5.3B, row 2, Training). We subtracted baseline biases (again from the final block of clamped trials during Pre-training) from the first block of Include-Strategy clamped feedback and tested whether this was significant from zero using a one-sample t-test (one-sided) per object and group.

To determine whether participants were using a compensatory strategy, we compared the hand deviations for the first Include-Strategy clamped trials and the first Exclude-Strategy clamped trials, after accounting for baseline biases, using a repeated-measures t-test (one-sided) for all experimental groups.

5.4 Results

We sought to validate the use of HMD-VR to study motor learning by building on recent work looking at how explicit and implicit learning may differ compared to conventional VR. In the first experiment, participants trained on transporting a perturbed object (30^o CCW or 30^o CW) with their right hand. They were additionally asked to transport a novel object, with either the trained hand or with their untrained, contralateral hand. In the second experiment, to understand whether task-relevant extrinsic cues facilitate dual adaptation, we leveraged the powerful capacity of HMD-VR to create our most realistic and ecologically valid experimental paradigm. Here, we assigned participants to the Dual-30 condition where they had to transport distinct objects (sphere vs. cube) whose identity predicted the perturbation they experienced on a given trial (30^o CCW or 30^o CW). To understand whether perturbation size plays a role, in a follow-up condition those in the Dual-60 condition completed the same task as Dual-30 but with larger perturbations (60^o CW or 60^o CCW). The two conditions in Experiment 1 served as control groups – a CW-only (cube-only) condition and a CCW-only (sphere-only) condition. Across all conditions a cube always predicted a CW perturbation, while a sphere always predicted a CCW perturbation.

5.4.1 Experiment 1

Visuomotor adaptation. Both CW-only and CCW-only control groups exhibited typical visuomotor adaptation since they only encountered only one perturbation, with hand deviations approximately at baseline levels at the beginning of training, then gradually matching the size of the imposed rotations (Figure 5.4A). Participants who transported spheres, and thus experienced a CCW perturbation during training, significantly approached the correct compensatory hand angle across training ($t(15) = 7.01$, $p < 0.001$, $d = 2.33$; Figure 5.4A). Similarly, those who transported cubes exclusively (and thus experienced a CW perturbation during training) improved their performance over time, significantly approaching the imposed rotation by the end of training ($t(15) = -10.98$, $p < 0.001$, $d = 4.20$).

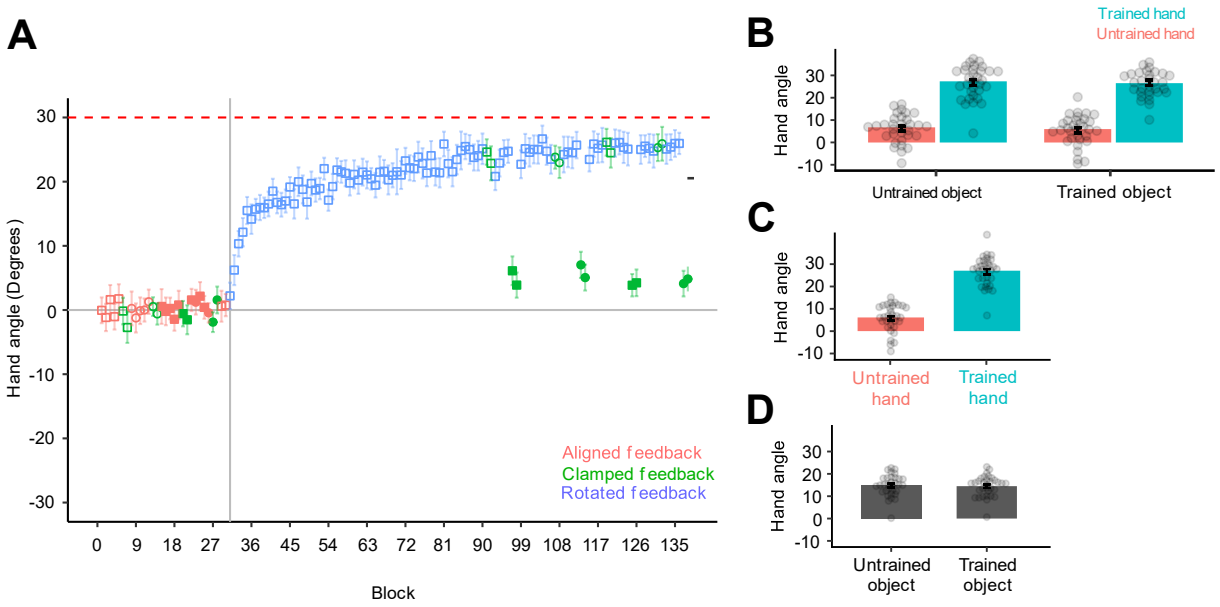

Figure 5.4. Averaged performance across all blocks. A. Aligned feedback trials are displayed in red, with the vertical grey line displaying the end of aligned training, and the beginning of rotated training. Blocks involving the trained right hand are depicted as hollow data points, while untrained (left) hand blocks are depicted as filled data points. Trained objects are depicted as square datapoints, while untrained objects are depicted as circles. Rotated feedback trials are in blue, and a red dashed line is included to show the 30° rotation, indicating perfect adaptation. Clamped feedback trials are depicted in green. Familiarization (practice) trials are not depicted. B. Averaged hand angle of all clamped feedback trials. Trained hand performance for both trained and untrained objects are depicted in blue, while untrained hand performance for trained and untrained objects depicted in red. Grey dots show individual performance for each condition. C. Averaged hand angle during clamped feedback trials for each hand, collapsing across objects. D. Averaged hand angle during clamped feedback trials for each object, collapsing across hands. Error bars represent the SEM.

When we removed visual feedback of the hand deviations (i.e., via clamped feedback trials), we saw reach aftereffects in the expected directions (Figure 5.4D, Single groups). Hand deviations were in the expected compensatory directions and significant from 0 for both CW-only ($t(15) = 12.71$, $p < 0.001$, $d = 3.18$) and CCW-only ($t(15) = -7.79$, $p < 0.001$, $d = 1.95$) control conditions. Together, these findings

demonstrate robust, classic motor adaptation to visuomotor rotations but captured in an HMD-VR setup, adding to the currently limited literature using the novel tool.

Transfer between trained and untrained hands. First, we determined the extent to which transfer occurred between hands by looking at clamped feedback trials which probed performance in both the trained and untrained hand (Figure 5.4A, filled data points). We saw a larger correction for the perturbation when transporting objects with the untrained hand relative to baseline ($t(31)=19.31$, $p < 0.001$), demonstrating that there was significant transfer to the left hand, although substantially reduced compared to compensations made by the trained right hand (Figure 5.4C). The untrained, left hand compensated by only 6°, while the trained, right hand adapted by 26°, indicating that the trained hand had adapted by 86% while the untrained hand had benefitted from that adaptation by only 20% of the total 30° rotation. Thus, assuming the right hand's compensation of 26° is at the peak of adaptation, we can conclude that only 23% of adaptation had transferred to the untrained left hand, likely because participants attributed the errors to the objects they were transporting. Additionally, hand angles when transporting objects with the untrained, left hand during clamp trials were significantly smaller than when transporting objects with the trained right hand ($t(63)=-18.02$, $p < 0.001$). This suggests that participants had a marginal amount of external error attributing to the objects, evidenced by their reduced compensatory response after switching to the untrained hand (Figure 5.4C).

Transfer between trained and untrained objects. Next, we wanted to understand the extent to which error was attributed to the specific object they were transporting. We saw that hand angles when transporting untrained and trained objects

were similar; there was no difference in their compensatory response regardless of the object type ($t(63)= 0.73$, $p =0.23$; Figure 5.4D). Thus, in the HMD-VR setting, participants partly attribute errors to the objects, as indicated by a bimanual transfer of 23%, but this attribution was not specific to the trained object.

5.4.2 Experiment 2

Visuomotor adaptation. Participants in the Dual-30 condition completed the typical dual adaptation paradigm with object identity distinguishing the perturbation experienced on a given training trial (Figure 5.5A, 5.6A). Although angular deviations headed towards the appropriate compensatory response for each distinct object ($F(1, 29) = 15.45$, $p < 0.001$, $ges = 0.12$), we saw that participants were adapting to one perturbation more than the other (Figure 5.5B). Overall, when collapsing across rotations, we found a moderate significant reduction in error across training for those in the Dual-30 condition ($t(29) = -2.17$, $p = 0.02$, $d = 0.56$). Those in the follow-up Dual-60 condition completed the same task as the Dual-30 condition but instead experienced larger perturbations of 60^o CW and 60^o CCW during training (Figure 5.6B). For this larger perturbation dual condition, hand angle did not significantly change over the course of training ($t(14) = -0.26$, $p = 0.30$; Figure 5.5C).

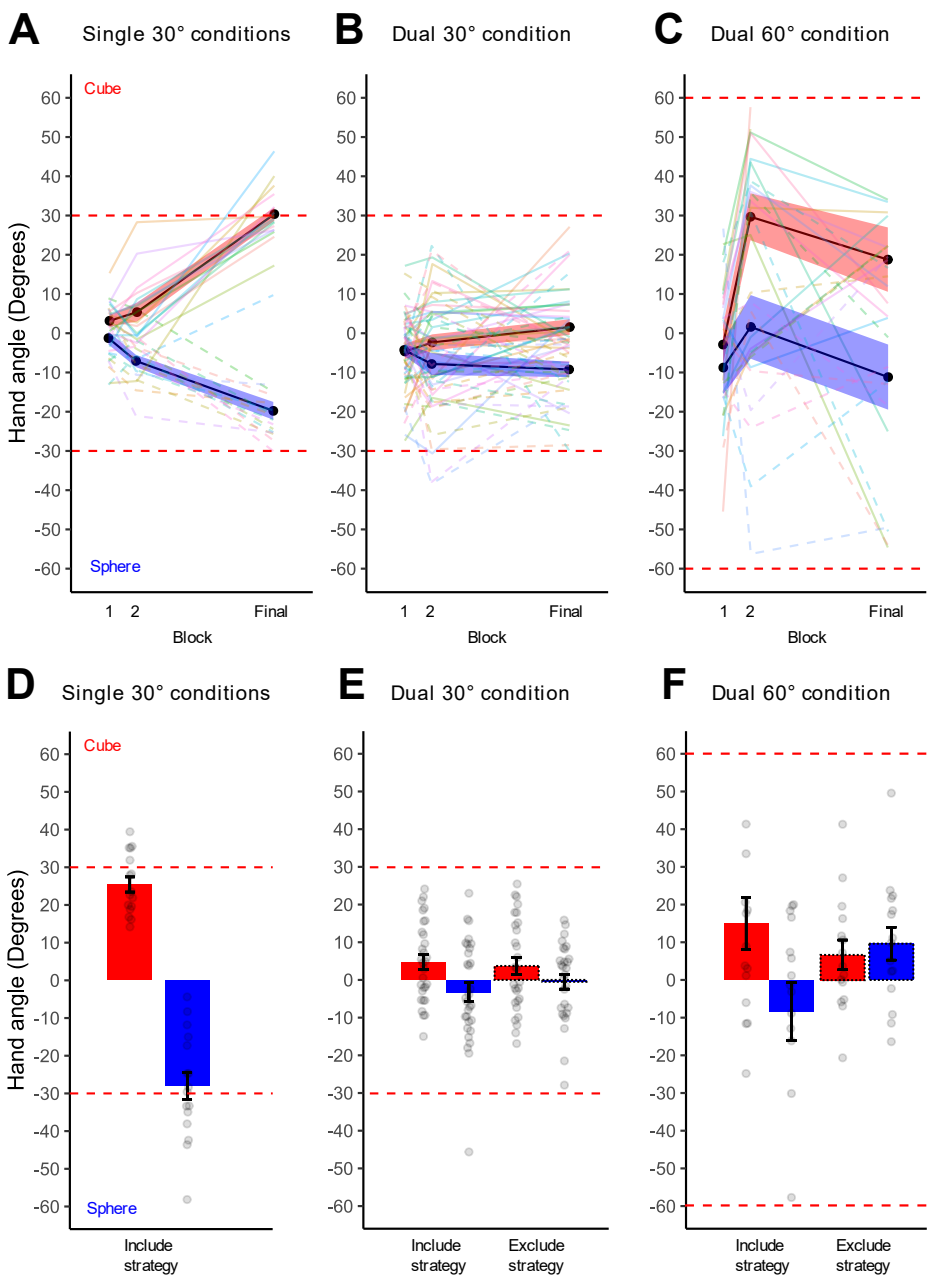

Figure 5.5. Visuomotor adaptation across training blocks. A. Single conditions (Sphere/CCW-only group in blue, Cube/CW-only group in red), B. Dual-30 condition, C. Dual-60 condition. Colored translucent lines represent individual learning curves, with sphere blocks depicted in dashed. Dashed horizontal lines represent rotation magnitude experienced during training. Hand angle during clamped feedback trials for D. Single control conditions (CW-only and CCW-only), E. Dual-30 condition, F. Dual-60 condition. Grey dots represent individual participant errors. Red bars represent errors during cube trials, while blue bars represent errors during sphere trials. Dashed lines represent rotation magnitude experienced during training. Error bars represent SEM.

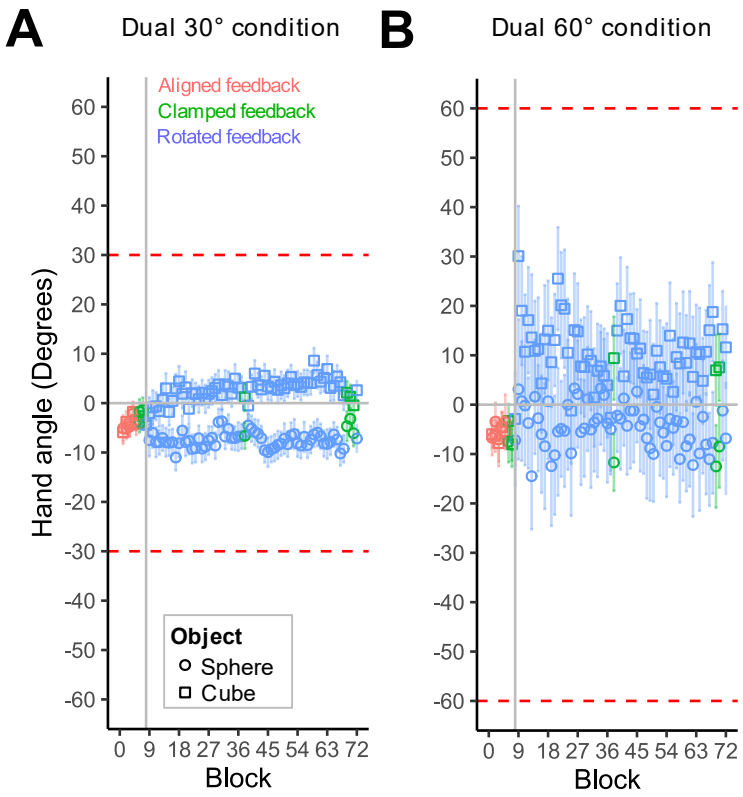

Figure 5.6. Visuomotor adaptation across all blocks. Aligned feedback trials are depicted in red, clamped feedback trials in green, and rotated feedback trials in blue. Sphere trials are depicted in circle data points, while cube trials are depicted in square data points. A. Dual-30 condition. B. Dual-60 condition. Dashed lines represent rotation magnitude experienced during training. Error bars represent SEM.

PDP (explicit vs. implicit learning). Include-strategy clamped feedback trials are thought to consist of both explicit and implicit learning mechanisms. For the Dual-30 condition, when we removed visual feedback of their hand deviations via clamped feedback trials, we saw errors in the expected directions for each distinctive object, but they were not consistently significant from 0 (Figure 5.5E, Dual-30 group). That is, we saw a significant aftereffect for the Dual-30 cube clamped feedback trials ($t(29) = 2.46$, $p = 0.009$, $d = 0.45$), but not for sphere clamped feedback trials ($t(29) = -1.30$, $p = 0.10$).

Exclude-strategy clamped feedback trials are thought to consist of only implicit components, since participants are expected to omit any strategies they may have developed during training. When we asked participants to exclude strategies during clamped feedback trials, we again did not fit significant aftereffects for both cube ($t(27) = 1.58$, $p = 0.06$) and sphere trials ($t(27) = -0.25$, $p = 0.40$). Together, these findings make it less likely that participants were concurrently adapting to both perturbations, suggesting that object identity alone cannot elicit dual adaptation.

Mirroring the results of those in the Dual-30 condition, those in the Dual-60 condition did not show any significant aftereffects in their expected directions for neither the cube ($t(14) = 2.17$, $p = 0.02$) nor the sphere ($t(14) = -1.09$, $p = 0.15$) during include-strategy clamped feedback trials (Figure 5.5F, Dual-60 group). When asked to exclude any strategies from training, we did not find direction-dependent compensation for neither cube ($t(14) = 1.69$, $p = 0.06$) nor sphere trials ($t(14) = 2.21$, $p = 0.98$). Taken together, these findings further reveal that object identity is unable to elicit dual adaptation with neither smaller nor larger perturbations, despite a more immersive and engaging 3D paradigm.

5.5 Discussion

In this set of experiments, we leveraged the power of HMD-VR to mimic real-life movements to more meticulously look at two key questions in motor learning in this novel setting: (1) how error is attributed, and (2) whether the motor system can use extrinsic contextual information to inform motor planning. In the first experiment, we tried to understand credit assignment in HMD-VR by looking at patterns of learning

transfer from having participants transport trained and novel objects using both their trained, right hand and untrained, left hand. We found small transfer to the untrained hand, suggesting that error was attributed to the object, but no difference in compensation between object types suggesting that this correction was not limited to the trained object. In the second experiment, we used object identity as distinctive cues, and found more evidence to support that extrinsic cues tend not to elicit dual learning, even in a more immersive and engaging set-up. In the critical Dual-30 condition, we saw inconsistent patterns of learning for both rotations, while in the Dual-60 condition, we saw no significant adaptation across all metrics. In the control conditions, participants adapted to a single perturbation, where we saw robust typical adaptation, and compensatory deviations when error feedback was withheld. Altogether, our findings further support that extrinsic cues are unlikely to facilitate dual adaptation. Still, HMD-VR clearly shows great potential to study motor learning and its subprocesses since it allows us to manipulate context in such a way that 2D set-ups cannot.

5.5.1 Transfer of learning between objects and hands

Our results also showed a modest transfer of learning between hands, suggesting that some error is being attributed to an external source. Indeed, estimates about the world should readily transfer across limbs, since this represents information that is independent of the effector (Berniker & Kording, 2008). Conversely, error attributed to the hand would manifest in transfer to novel objects, but should not generalize to the untrained hand, since this information is specific to the trained effector. Here, we saw that participants transferred learning between hands, suggesting an assignment of error to the external world, but complete generalization between objects,

suggesting that at least in the HMD-VR environment, the motor system expects novel objects to require the same correction as familiar objects.

We also saw that clamped feedback trials for the trained hand were quite large, as evidenced by a rather continuous level of compensation from rotated feedback trials (Figure 5.4A, hollow green data points). Indeed, trained hand clamped feedback trials show no decay, a characteristic usually observed with true adaptation (Krakauer et al., 2019). One explanation for this might be that the motor system became accustomed to a certain movement pattern to achieve its goal. In this use-dependent learning, participants develop an effective strategy and apply it continuously since they are getting positive reinforcing feedback based on previous trials (Diedrichsen et al., 2010). This may alternatively explain why untrained hand clamped feedback performance were quite reduced in comparison to the right hand (Figure 5.4C), since switching hands breaks the participant's motor pattern of continuously reaching in the same direction.

But, critically, we found that participants showed the same level of learning between trained and untrained objects. So, the motor system simply applied the same rule to plan movements regardless of the object identity. A couple of parsimonious reasons for this might be that the untrained object was not relevant enough to have an overall meaningful impact on the outcome of the task, or, simply, that participants did not notice the identity of the object change. Future work can tackle this issue by making the task even more engaging by either allowing participants to perform different movements with each object or by making the objects less abstract and more meaningful in the way they interact with them (e.g., placing a key into a lock). This may

make object identity more salient, thereby giving them more relevance and possibly attributing more error to them.

5.5.2 Extrinsic cues fail to facilitate dual adaptation

Our findings provide yet more evidence that extrinsic (or non-motor based) cues tend not to be encoded by the CNS in motor planning. That is, despite using a more immersive and engaging paradigm where the task very clearly requires the recognition of each distinct object, we still saw no consistent reduction in error across training in the Dual-30 group, and no trace of learning in the smaller Dual-60 group. This contrasts with findings by Osu et al. (2004), whose group saw significant learning to opposing force-field perturbations when distinctly cued by background colour. This discrepancy is unclear; likely, the experiment set-up and trial structure combined with the structure of the colour cue (coloured arrows depicting force-field direction) sufficiently elicited dual learning. These results by Osu et al. (2004) led us to provide further evidence that task engagement alone cannot facilitate dual adaptation. Anglin et al., (2018) suggested that task engagement might elicit more cognitive strategy, but since we did not see learning in the dual conditions, it remains a question to what extent explicit and implicit processes are engaged in dual adaptation in HMD-VR. Still, using HMD-VR allowed us to not only test our questions but also to give further support for studying motor learning with this more ecologically valid paradigm.

5.5.3 HMD-VR as a novel tool for studying motor learning

Motor learning is classically studied using 2D paradigms, using a flat display and a cursor to represent the movement of the unseen hand to simplify the solution space and maximize control of all mediating factors. With modern technologies, it has now become

inexpensive to employ 3D virtual reality tasks using equipment such as the Oculus Rift used in the present experiments. In one key study, Anglin et al., (2017) were first to compare visuomotor adaptation in conventional training (CT) and HMD-VR and show that visuomotor adaptation comparably occurs in HMD-VR. They first replicated their CT task to the HMD-VR environment, by matching the size and lighting of the room, the objects within it, and the computer monitor where the task was completed. During training, participants trained with a 45^{o} CCW-rotated cursor, reporting their aiming direction prior to every trial (adapted from a task by Taylor et al., 2014). This reporting method allowed them to tease apart the implicit and explicit contributions to visuomotor adaptation and to compare the extent of each sub-mechanisms between paradigms. CT led to greater implicit learning compared to HMD-VR training, while HMD-VR training led to greater use of cognitive strategies. In our single perturbation conditions, we indeed saw typical, robust adaptation, further adding to the currently sparse literature on motor adaptation in HMD-VR. It remains a question why HMD-VR might elicit more cognitive strategy, with others suggesting that the sheer novelty of the environment leads to capturing the attention and engagement of participants, triggering an increased reliance on cognitive strategies (Anglin et al., 2017). Future work should explore how motor learning in HMD-VR generalizes to real life, and how this may affect rehabilitation interventions that rely on simulated environments.

Still, HMD-VR allowed us to study the contextual cue of object identity in the most realistic and seamless way possible. Other contextual cues can be studied in HMD-VR in such a way that we cannot execute in conventional 2D setups, like manipulating object (or tool) movements or environmental conditions like surface tilt, to name a few.

Chapter Six: General discussion

The primary goal of my dissertation was to understand what allows the motor system to concurrently adapt to two opposing perturbations and the sub-mechanisms behind this process. Typically, when presented with two opposing perturbations that constantly change from trial to trial, the motor system experiences anterograde interference, where the learning of perturbation A interferes with the ability to learn perturbation B. However, when a sufficient and distinctive context is associated with each perturbation, interference can be reduced, and some level of dual adaptation occurs. This is further complicated by the issue that only some contextual cues succeed at facilitating dual learning. Understanding the characteristics about these viable contexts remains an active field of research in motor control.

Previous research from our lab demonstrated that motor-based (intrinsic) cues tend to facilitate dual learning (Ayala et al., 2015; Baldeo & Henriques, 2013), and my objective was to further unravel these various contexts and their key characteristics to understand what information is useful to the motor system when adapting and switching between different visuomotor mappings. This research will help us further understand some key guiding principles of motor planning. Using a series of experiments, I manipulated various contextual cues that I hypothesized would impact whether learning occurs based on past work, and later, inspired by the advances of the field, started to also test the contributions of the different mechanisms involved in motor adaptation. Finally, with the help of a novel and powerful 3D VR experimental set-up, I looked at whether this learning is feasible in an immersive environment, where results have been highly variable in the impoverished, conventional set-up.

Guided by findings from my master's thesis which showed that different hand and body postures facilitate dual adaptation, in experiment 1 I investigated the efficacy of intrinsic cues, specifically, movement type. In the key condition of this experiment, participants adapted to opposing perturbations (30° CW or 30° CCW) within the same training block, with each perturbation predicted by a distinctive movement type (ballistic reach to a static target or pursuit tracking movement to a linearly moving target). In experiment 2, inspired by recent findings that suggested that distinctive motor plans differentiate motor memories (Sheahan et al., 2016), I followed up on experiment 1 by looking at distinctively skewed movements can facilitate dual adaptation. To elicit skewed movements that are thought to elicit distinctive motor plans (Jax & Rosenbaum, 2007, 2009), participants saw an obstacle to the left or to the right of the visual workspace, each predicting a distinct perturbation. In experiments 3 and 4, I asked two questions: (1) whether movement cues need to be actively produced to be effective at facilitating dual adaptation, and if so (2) to what extent are implicit and explicit sub-mechanisms of learning involved? To this end, I ran three experimental conditions looking at whether active follow-through, passive follow-through, and active lead-in movements elicits dual adaptation, while simultaneously measure the implicit and explicit contributions, regardless of whether learning occurs. Then, I equipped one group with explicit strategies to counter the opposing perturbations, comparing their performance to a group who received no instructions and only tried to dual adapt to static visual cues. Finally, in experiment 5, in the pursuit for a more ecologically valid understanding of dual motor adaptation, I leveraged the powerful capacity of HMD-VR to create a more immersive and engaging adaptation of the conventional reaching task.

Little is known about how motor learning proceeds in HMD-VR, and some have already found key differences in the sub-mechanisms behind it compared to conventional VR. So, I looked to understand two key questions: (1) how does the motor system attribute error in this novel 3D setting? And (2) does a more engaging HMD-VR dual adaptation task facilitate learning to visual cues that would otherwise not elicit any learning?

By examining performance patterns across these different conditions, this research furthered theoretical knowledge about how the motor system overcomes various and changing challenges by using context to support learning. More specifically, this research found a series of cues that aid in reducing interference when adapting to multiple visuomotor perturbations, as well as how this learning is differently made up of implicit and explicit subcomponents. This is profound because it shows that interference when simultaneously learning two visuomotor mappings is not inevitable; likely, the motor system salvages adaptation by leveraging high level cognition to associate cues to mappings (Krakauer et al., 2019; Sheahan et al., 2016). Lastly, I examine the practical implications stemming from my findings and provide areas of future research.

6.1 Extrinsic vs. Intrinsic cues

Results from my experiments revealed that certain contextual cues facilitate dual adaptation—in particular, those that tend to be motor-based or “intrinsic” in nature. In the first experiment, I found that associating different movement types to each visuomotor mapping can reduce interference and allow for both perturbations to be learned. Likewise, findings from experiment 2 show that skewed movement trajectories can facilitate learning, but due to the unexpected effects of participants obstacle

avoidance compounded by the opposing perturbations, it was difficult to draw direct conclusions. In the third and fourth set of experiments, I looked at whether intrinsic contextual cues need to be actively produced, or if merely viewing a passive representation of a distinct cue is sufficient, and found that active cues elicited dual adaptation, while passive cues did not. As expected, static visual cues did not elicit any learning. In the final experiments, I saw that even with an engaging and immersive task interface, task-relevant extrinsic cues still do not elicit dual adaptation. Taken together, these findings support the idea that the types of contexts that tend to prevent anterograde interference tend to be motor-based.

An explanation as to why additional movement cues tend to work was offered by Sheahan et al., (2016) who found that a critical characteristic of an effective cue is that it can be related to a distinct goal. In their experiment, they used follow-through movements (i.e., secondary movement following acquisition of the target) to cue opposing force-field perturbations and found that even if the cueing motion isn't produced, the necessary compensation manifests. This is insightful because it shows that when certain contexts do not elicit learning, it is not because the motor system is limited to a low-level process (i.e., anterograde interference) but because it simply fails to produce a high-level cognitively motivated plan (Krakauer et al., 2019).

Yet, in my final dual adaptation experiment using HMD-VR, I implemented object identity which is an inherently extrinsic cue was tied to a task goal but still did not lead to any dual learning. So, this suggests that there is an added component to just simply associating a distinct goal and a distinct cue – possibly, the cue still needs to be intrinsically based in order to lend utility to a motor plan. The findings by Sheahan et al.

(2016) tells us *why* movement cues work, but it remains unclear why extrinsic cues do not, seeing as clearly very task-relevant cues as in my final experiment, (e.g., spherical object to a spherical receptacle) still do not elicit learning. Alternatively, this may be an issue with defining what a different movement goal entail. Thus, future work needs to elucidate what it means to associate a movement goal to a cue, and to better define what a goal is, beyond vague psychological parameters.

6.2 Explicit and implicit contributions to dual adaptation

With advances in the field of motor control proceeding while I was completing the experiments in my dissertation, it became apparent that motor adaptation cannot simply be characterized by a single process governed by a single learning rule. This first became apparent in early prism adaptation experiments where it was noted that reach aftereffects following adaptation were not the same magnitude as the prism shift (Redding & Wallace, 1993). The most prominent way in which adaptation has been characterized as multiple processes is with the implicit and explicit adaptation dichotomy. First characterized by Mazzoni & Krakauer (2006) in a conventional visuomotor rotation paradigm, implicit adaptation is thought to arise due to a mismatch between the intended movement of the unobserved hand and the observed direction of the cursor movement. This became evident in their experiment when participants produced errors despite having been given the perfect compensatory strategy, and this was further manifested in implicitly driven reach aftereffects when participants were asked to discount the aiming rule (Mazzoni & Krakauer, 2006). This hallmark finding demonstrated that classic models of motor adaptation need to account for multiple learning processes at play—both implicit and explicit mechanisms.

This dual process model is further compounded by the characteristics that each learning process exhibit. First, the explicit mechanism seems to map onto a fast-learning, fast-forgetting process, while the implicit mechanism arises slowly, and produces more long-term learning (Krakauer et al., 2019). To further understand the components of learning that lead to dual adaptation, I used the Process Dissociation Procedure (PDP; adapted from Werner et al., 2015) to distinguish between explicit and implicit learning processes. In the third and fourth sets of experiments, I found that contextual cues that elicited learning also showed implicit but no explicit contributions. However, when given an explicit strategy on how to counter the perturbations, participants only showed explicit learning and no implicit contributions. Thus, contextual cues that reduce interference are largely learned without awareness, and cues that would typically elicit interference can be learned with the use of strategies, but it appears to be an entirely explicitly mediated process.

Ongoing work on contextually-driven dual adaptation points to the idea that effective cues can be dichotomized as direct and indirect cues depending on how they relate to the dynamic state of the body (Forano et al., 2021). We proposed an analogous conceptualization of cue efficacy using the intrinsic and extrinsic distinction (Ayala et al., 2015a). Informed by this work by Forano and colleagues (2021), along with findings from Chapter 4, it appears that effective, intrinsic cues tend to elicit implicit learning, while extrinsic cues can rely on explicit learning. Figure 6.1 shows the conceptualization of the findings from this dissertation. In this conceptualization, dual adaptation is achieved by the CNS using intrinsic and extrinsic cues, with intrinsic cues owing its efficacy entirely to implicit processes (Chapter 4, Experiment 1, Active follow-

through and Active lead-in experiments) and extrinsic cues to explicit processes (Chapter 4, Experiment 2, Instructed group). Older theoretical models of dual adaptation do not account for the differences in how different types of cues are used by the motor system, for instance, the Modular Selection and Identification for Control (MOSAIC) theory, which posits that a contextual switching mechanism exists in order to change between internal models of specific motor commands and sensory states (Haruno et al., 2001). Along with our findings, Forano and colleagues (2021) are only now starting to show that the understanding the explicit and implicit distinction will be key to understanding the efficacy of contextual cues in dual adaptation. Newer theoretical models of dual adaptation suggest that the motor system uses a generative model whereby latent contexts give rise to both contextual cues and dynamics. The motor system is then thought to infer the statistical relationships between these latent contexts and selected movements based on prior expectations about context-dependent dynamics (Heald et al., 2018), with other groups speculating that this inferential process occurs primarily for explicitly-mediated cues (Forano et al., 2021). Still, future work needs to elucidate what enables some individuals to benefit from extrinsic or indirect cues, while others fail to dual adapt.

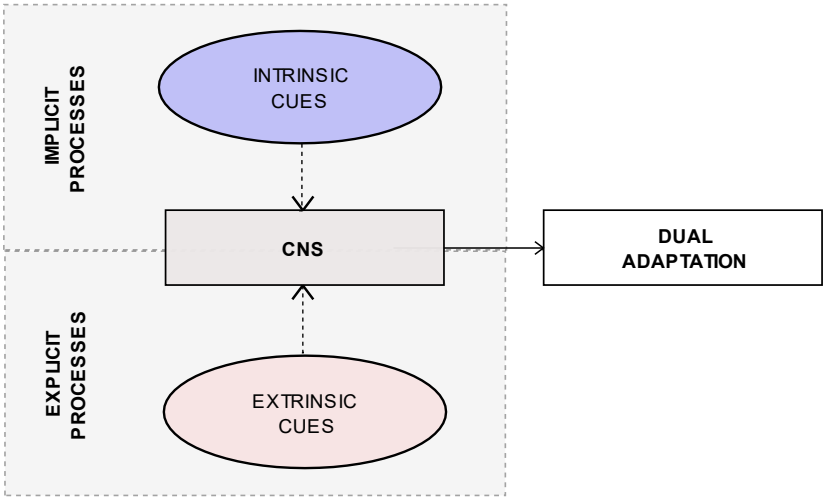

Figure 6.1. Conceptualization of findings. Extrinsic cues such as static visual cues (Chapter 4, Experiment 2) may lead to dual adaptation if it elicits explicit processes. Intrinsic cues such as movement type (Chapter 2), or active movement sequences (Chapter 4, Experiment 1), solicit implicit mechanisms to drive learning.

6.3 Future steps using HMD-VR in motor learning research

While my final set of experiments showed the viability of using HMD-VR in motor control research, it also highlighted some differences in how people behave in this type of environment. This experiment built upon more recent findings that implicit and explicit contributions to motor adaptation differs in HMD-VR relative to conventional VR (Anglin et al., 2017). Another study found that reaching movements in HMD-VR produced similar movement profiles, but longer reaction times compared to reaching to real objects (Just et al., 2016). Given how HMD-VR is becoming more commercially available for use both in the lab and clinical settings, it is important to characterize the differences in how we learn in this novel setting.

In my final set of experiments in HMD-VR, I asked two questions: (1) when manipulating objects in this novel environment, how does the motor system assign error? And (2) does a more immersive and task-relevant context elicit dual learning? In the first experimental groups, I saw that error was attributed externally, as evidenced by transfer of learning between limbs. However, I found that when manipulating a novel object, the motor system completely generalizes learning from the trained object, suggesting that error was not being attributed to the object.

Next, I found that task-relevant object identity was insufficient at facilitating dual adaptation. In the past, these findings have been mixed, with some static contextual cues such as background colour eliciting learning (Osu et al., 2004), and others showing no learning (Baldeo & Henriques, 2013; Hinder et al., 2008). I found that in my first HMD-VR dual adaptation condition, participants who experienced 30 CW and 30 CCW perturbations negligibly reduced their errors significantly over time but did not show any direction dependent reach aftereffects. Those in the large perturbation condition similarly did not show any learning, although these results may be underpowered due to a small sample size. This is interesting because even with very distinct visual goals (i.e., matching shape to receptacle), participants failed to dual adapt. In contrast, more recent work by McGarity-Shipley et al. (2020) showed that the relationship of a visual control point and the location it contacts a target. Thus, it's possible that with a richer association between goal and visuomotor mapping, dual adaptation can be elicited, but perhaps not merely by providing the motor system with distinct object identities. Likely, a higher-level association needs to take place between the mapping and the goal that may rely on more explicit processes (Krakauer et al.,

2019; Wong et al., 2016). Altogether, these insights point to the critical work we need to do before further using HMD-VR to deploy motor tasks asking novel questions, or even for rehabilitation; that is, we need to further characterize how basic motor learning processes in humans differ in this environment compared to conventional VR.

6.4 Conclusion

This dissertation enhanced our current understanding of how the motor system uses contextual cues to facilitate learning and the issue of uncovering these cues that are involved. Findings across these experiments provide a cohesive view that actively produced, motor-based (or “intrinsic”) contextual cues can elicit dual adaptation, and these cues tend to be governed by implicit mechanisms. Lastly, this work further shows that the visuomotor learning paradigm can be brought to the HMD-VR setting to mimic a more unified, immersive experience.

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Appendices

Appendix A: Disclaimer for Coauthored Chapters

Chapter 2 in this dissertation has been published with my supervisor Denise Y.P. Henriques as coauthor. Denise Y.P. Henriques is also coauthor of Chapter 3, which is now published in PLoS ONE. Chapter 5 is currently being written up for publication, with coauthors Shanaa Modchalingam and Denise Y.P. Henriques.

Denise and I conceived and designed the experimental methodology, created the experimental methods and stimuli. Experiments were programmed by Errol Cheong (Chapters 2 and 3), Alireza Tajadod (Chapter 4), Marius ’t Hart (Chapter 4), and Shanaa Modchalingam (Chapter 5). I performed the experiments and collected the data for all chapters, with assistance from undergraduate students Priyanka Sharma (Chapter 2) and Nabil Abdelmoneim (Chapter 5). I analyzed all the data and wrote the manuscripts.