THE EFFECTS OF LEARNING SCHEDULES AND VISUAL CUES ON IMPLICIT SENSORIMOTOR ADAPTATION OF ARM MOVEMENTS

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Abstract

Implicit motor adaptation is vital for maintaining accurate movements when faced with changes in the environment or our own bodies. Using both simple and complex motor tasks, this dissertation investigates the limits of implicit adaptation in upper-limb motor adaptation, and its sensitivity to visual context cues. We first demonstrate that the extent of implicit adaptation depends on how motor errors are introduced during a training paradigm. We find the largest extents of implicit adaptation when participants can adapt to small but noticeable motor errors before experiencing further perturbations to their movements. This method of error introduction led to significantly larger adaptation compared to both abruptly introducing large errors or introducing small errors in a ramped manner. Next, we determined that when adapting to opposing perturbations simultaneously, task-relevant object-shape cues that predict the presence of a given perturbation are insufficient to consistently trigger the formation of object-specific motor memories. Finally, we show that when perturbations can plausibly assign the source of errors to environment causes, context-dependent motor learning can readily occur. Overall, this dissertation highlights the adaptability of implicit motor learning, emphasizing the need to consider perturbation methods, contextual influences, and task complexity when designing effective motor learning paradigms.

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Chapter 1: General Introduction

Effectively and reliably accomplishing movement goals is essential for performing the actions that make up daily living, and for self expression. When we fail to accurately predict the consequences of our planned movements, however, our planned actions may have unintended outcomes leading to motor errors. Effectively minimizing such errors is crucial for accomplishing daily activities. Accordingly, the human motor system reduces persistent motor errors over time both explicitly, through the development of conscious strategies, and through the updating of implicit mental models that map movement goals to executed motor activity (Krakauer et al., 1999, 2019; Miall & Wolpert, 1996; Shadmehr et al., 2010; Shadmehr & Krakauer, 2008).

Motor learning can be generally divided into two broad categories: de novo skill learning and motor adaptation. De novo skill learning constitutes learning new motor tasks, whereby the motor system may create new internal models that generate efferent activity to achieve desired movement outcomes given the current internal and external states (Krakauer et al., 2019). As developing new skills often requires many repetitions of a motor task over long periods of time (Krakauer et al., 2019), studying de novo learning in a well-controlled laboratory setting is difficult; although there has been recent advancement in the field using simplified de novo tasks (Gastrock et al., 2018, 2023; Telgen et al., 2014; Wang & Taylor, 2021; Yang et al., 2021). Motor adaptation is the process of returning to previous levels of performance when errors arise in already-known tasks. This process can be rapid, occurring in seconds to minutes, making it a more accessible paradigm in laboratory settings, and thus has been extensively studied (Helmholtz, 1867; Ruttle et al., 2016, 2021). Alongside studying properties of error reduction in controlled environments, understanding the processes involved in motor adaptation itself is necessary. Many training and rehabilitation programs involve regaining a once-established level of

performance in response to injury, or changing movement contexts, like using new equipment for familiar tasks.

To effectively perform motor tasks in changing environments, the human motor system relies on both explicit adaptation processes that require the use of conscious, recallable strategies (Mazzoni & Krakauer, 2006; Miyamoto et al., 2020), and implicit adaptation processes that are automatic and require no cognitive resources (Hwang et al., 2006; McDougle et al., 2016). Implicit adaptation processes allow for consistent motor adaptation to systematic errors in movements while freeing up cognitive resources for other tasks while executing movements (Leow et al., 2017). Explicit processes on the other hand can be quickly engaged or disengaged and allow for flexibility in rapidly changing conditions. Implicit and explicit processes of adaptation can evolve over time independently of each other, but often act in tandem to stabilize or buffer movement changes caused by each other (Albert et al., 2022; Brennan & Smith, 2015; Miyamoto et al., 2020). Both processes are important for effective and efficient motor performance and require individual attention when designing learning tasks and paradigms. In this dissertation, we focus on implicit adaptation mechanisms and explore the limits of implicit motor adaptation as well as the role of visual contexts in driving implicit motor adaptation. Although we focus on implicit learning processes, it will be in the context of evolving alongside explicit learning mechanisms.

Implicit motor adaptation consists of altering mappings between a set of neural signals that initiate patterns of muscle activations, known as motor commands, and intended movement consequences. These mappings, known as internal models, or motor memories when they are context-specific, both determine the appropriate motor command for a given goal, and estimate the sensory changes that should follow a given motor command (Fig 1.1). When an individual initiates a familiar movement, they generate a prediction of the sensory consequences of the movement of both the effector and the environment. These predictions are generated using a “forward model”, where a copy of

the motor command, known as an “efference copy”, is used to simulate predicted consequences of the movement (Blakemore et al., 1998). When the motor command for familiar movements results in unintended sensory consequences, e.g., the arm moves slightly faster than predicted during a reach, this internal forward model can be recalibrated to better match the predicted and real sensory consequences of the motor command. This recalibration in turn changes future estimates of the states of the moved limb, affecting choices in future motor commands. Alternatively, in the presence of errors in the motor task, implicit motor adaptation may also occur by changing the control policy of the “controller” for the intended movement, termed the “inverse model” (Haith & Krakauer, 2013) (Fig 1.1).

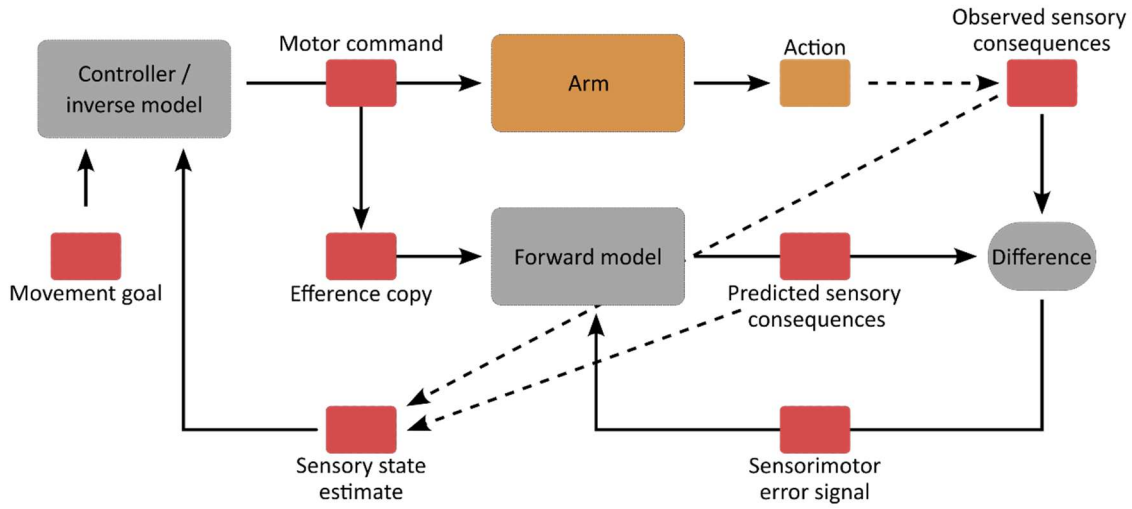

Figure 1.1: Internal models for the motor control of arm movements.
Grey boxes represent internal models. Red boxes represent neural signals. Orange boxes represent physical consequences.

To effectively reduce errors during the motor adaptation process, existing internal models may be modified to better map their predictions to altered outcomes of intended movements, or new context-specific motor memories created. In response to a variety of plausible sources of motor errors,

motor learning processes themselves are varied; ranging the development of explicit strategies to counter perceived perturbations, implicit and unconscious updating of internal motor control models that map movement intentions to outcomes, and the creation of new internal models for specific motor contexts. It is clear that the motor adaptation process itself is a combination of multiple learning processes (Baddeley et al., 2003; M. A. Smith et al., 2006). Although motor learning as a whole follows a stereotyped pattern of exponential error reduction, where error-reduction rates depend on the reliability of observed errors (van Beers, 2012; Wei & Körding, 2010), features of re-learning recently experienced contexts suggest the presence of two or more distinct processes, with their own learning and forgetting rates (M. A. Smith et al., 2006; van der Kooij et al., 2016). These learning processes each may comprise of multiple mechanisms, such as model based learning, reinforcement learning and use-depended plasticity (Huberdeau et al., 2015).

To elicit motor adaptation in laboratory settings, systematic perturbations are introduced to well-learned movements, which lead to discrepancies between observed consequences of planned and executed actions. These observed discrepancies are termed “motor error signals.” Perturbations can be introduced either to the path of movements by applying external forces during a movement (Krakauer et al., 1999; Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994; M. A. Smith et al., 2006) or strictly to the perceived path of movements by providing altered visual feedback of the movement (M. M. Cohen, 1967; Cressman & Henriques, 2009; Fernández-Ruiz et al., 2004; Mazzoni & Krakauer, 2006; Redding & Wallace, 1988, 2000). In response to both experimental paradigms, participants reduce motor errors over time by altering their movements to compensate for the imposed perturbations and return to near-baseline performance levels. Although learning of dynamic perturbations and perturbations to visual paths can be independent (Krakauer et al., 1999), many underlying learning mechanisms overlap, allowing researchers to investigate these mechanisms using either paradigm. In this dissertation, we use visuomotor perturbations as they can be individually and independently applied to the movement paths

of end effectors or objects in the environment. Here, we alter the visual path if either the hand movement, or the movement of objects of interaction, allowing us to investigate motor learning to both body-based and environment-based perturbations.

To study the underlying mechanisms of motor learning, we must first ensure we have viable methods of measuring sub-processes of motor learning. When dissociating implicit and explicit sub-processes of visuomotor adaptation, currently there are three common methods. The first method, termed “aiming”, consists of asking participants to report their desired reach direction using visual landmarks on the workspace before initiating a movement (Taylor et al., 2014) (Fig 1.2 a). The discrepancy between the aiming direction and the actual target of the reach is widely considered to be the explicit component of the movement. This new aiming target can be assumed to be the actual target of the reach and any further shifts in the movement direction of their hand is considered to be implicit adaptation. A major advantage of this method is that implicit and explicit processes can be measured throughout learning. However, it is possible that asking participants to actively aim to something other than the target during a visuomotor task, may cue participants toward effective cognitive strategies and lead to an overexpression of the explicit process (Maresch et al., 2021).

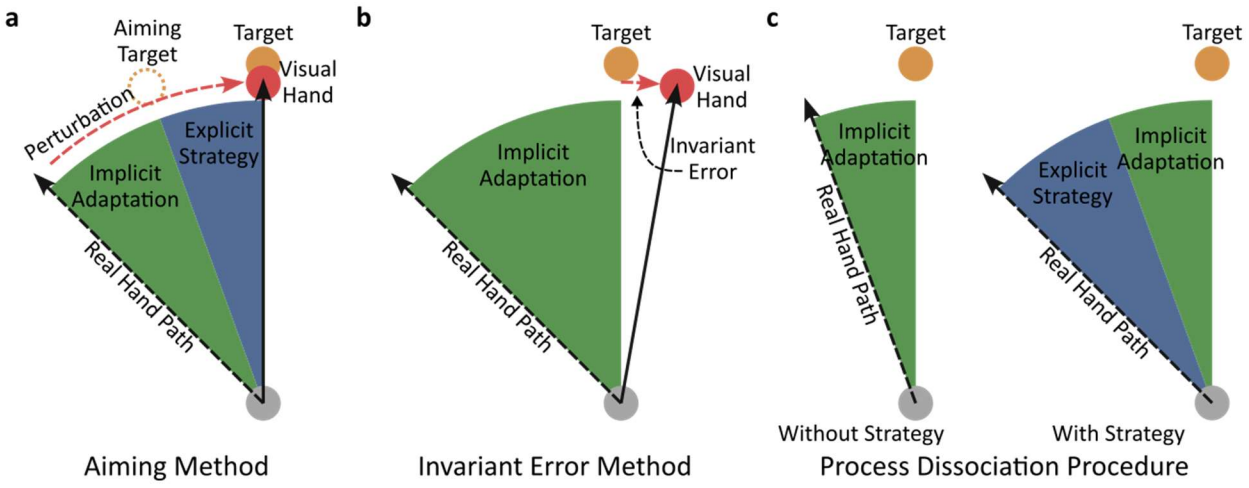

Figure 1.2: Measures of implicit adaptation.

a: In the aiming method, participants first indicate an aiming target, then reach toward a visible target while experiencing a visuomotor rotation. Implicit adaptation is measured by subtracting the aiming direction from the direction of the real hand path. **b:** In the invariant error method, participants are instructed to ignore an always-present, consistent task error while reaching their real hand to a visible target. All persistent performance changes are considered implicit. **c:** In the Process Dissociation Procedure, participants reach to visual targets without visual feedback of their hand position after adapting to a perturbation. Participants perform these no-feedback reaches while instructed to either using or not using strategies developed during learning. Implicit adaptation is the behaviour changes that cannot be suppressed when asked to exclude strategies.

A second measure of implicit adaptation is to observe how people adapt to consistent sensorimotor errors that are irrelevant to task goals (Fig 1.2 b). This method was adapted from Scheidt (2000) and Shmuelof et al. (2012) by Morehead et al. (R. J. Morehead et al., 2017). Here, participants are told to again reach for visual targets, but they experience an invariant error during the reach. The error is considered invariant because regardless of the real movement, the participants always experienced the visual representation of the hand deviate from the target by a predetermined amount. Crucially, participants were made aware of this fact and instructed to ignore the visual error and continue to move their real, but unseen, hand toward the targets. Due to these instructions, any persistent deviations of the real hand that arise due to the visual error can be deemed to be implicit in nature. Studies using these methods have repeatedly shown that implicit motor adaptation arises due to the discrepancy between the expected and actual visual consequences of the movements, regardless of the explicit goals of the task (Kim et al., 2018; R. J. Morehead et al., 2017).

A third method of measuring implicit adaptation is the “process dissociation procedure” (PDP), a methodology adapted from the cognitive psychology domain for motor learning by Werner et al., (2015) (Jacoby, 1991) (Fig 1.2 c). Here, after adapting to a visuomotor rotation, participants perform reaches to

visual targets without any visual representation of the hand. Before performing a reach, participants are instructed either use any cognitive strategy that they may have used during training, or to not use any strategy. If instructions are applied correctly, we can obtain an accurate measure of the implicit aftereffects of adaptation. This method does not interfere with the adaptation process since it is conducted post-adaptation. However, it is harder to determine the time course by which these sub-processes arise. Additionally, since this test may be conducted minutes after initial adaptation, there is some question of if participants can accurately recall all explicit strategies used during early adaptation (Hadjiosif & Krakauer, 2020).

For our studies, we primarily relied on the process dissociation procedure (PDP) to measure implicit components of adaptation, both to build on previous work by our research group, and to better answer the specific questions posed in this dissertation. Specifically, in our studies we aimed to explore the extent of implicit learning brought about by natural learning processes when participants were exposed to various visual stimuli over various learning schedules. Since the PDP is conducted post adaptation, it uniquely allows us to study learning processes in realistic contexts. By combining rigorous measures of implicit learning with advances in visual display technology, we aim to better the human motor system's ability to efficiently perform a large repertoire of highly adaptable movements.

Prior work suggests implicit adaptation to be constrained to a maximum of 15 degrees when adapting reaching movements to visuomotor rotations. This finding is robust and has been established in studies using all three methods of measuring implicit motor adaptation (Bond & Taylor, 2015; Kim et al., 2018; Modchalingam et al., 2019) (Fig 1.3). Larger perturbations necessitate explicit strategies to compensate for the limited implicit adaptation (Bond & Taylor, 2015; Kim et al., 2018; Modchalingam et al., 2019). Although implicit adaptation is often constrained to similar amounts within a given experimental setup, it may vary across studies and task conditions. While studies like Neville et al. (2018) suggest the limits may be lower, other studies like Morehead et al. (J. R. Morehead et al., 2015) indicate

the potential for a higher limit. Although the upper bounds of implicit adaptation can evidently be flexible, the factors affecting these limits are not clear. In recent work, people have looked at how limits of implicit learning relates to explicit components of learning, the reliability of visually and proprioceptively perceived locations of end effectors, and the introduction schedule of the perturbation (Albert et al., 2022; Tsay, Avraham, et al., 2021; Tsay, Kim, et al., 2021).

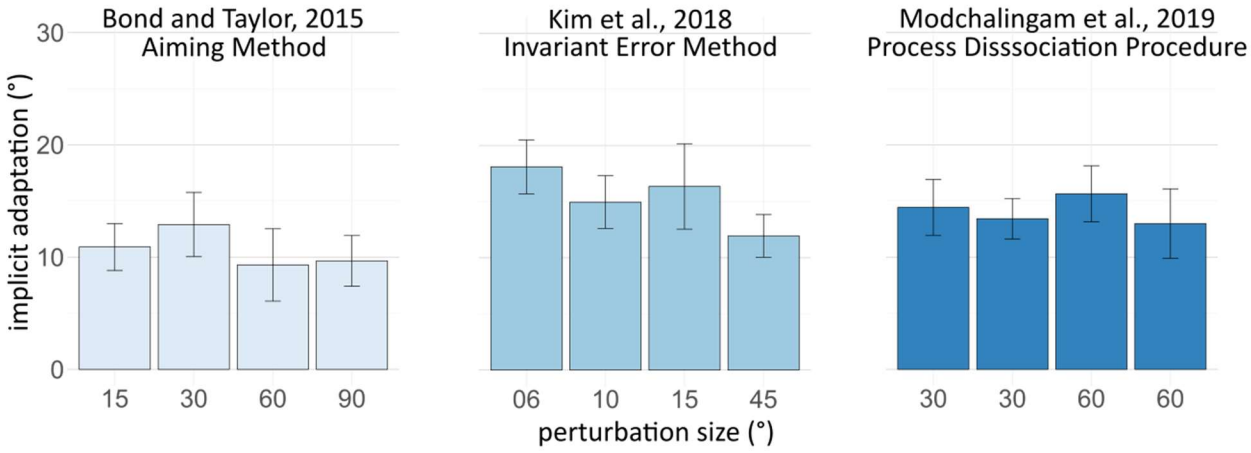

Figure 1.3: Limited extent of implicit motor adaptation.
Extent of implicit adaptation across multiple visuomotor perturbation sizes in prior work (Bond & Taylor, 2015; Kim et al., 2018; Modchalingam et al., 2019)

Perturbations can be introduced to participants abruptly, where participants may receive large error signals during early adaptation that can be explicitly corrected for, or gradually, where smaller errors are introduced sequentially, preventing explicit adaptation. In prior work, it is unclear if differences in perturbation onset affect the limits of implicit adaptation. While some studies suggest reducing explicit learning increases overall error-signals and lead to larger implicit adaptation (Kagerer et al., 1997; Michel et al., 2007; Salomonczyk et al., 2011), others do not (Buch et al., 2003; Kagerer et al., 2006; Werner et al., 2022). While discrepancies in implicit learning measures in past studies may explain some variation in findings, the way perturbations were introduced gradually may have also played a significant role. The methodologies for gradual perturbation onset differed between studies. Some

employed a ramped approach, where participants received minimal error signals during the perturbation increase (Butcher et al., 2017b). Other used a stepped approach where errors participants experienced perceptible errors during the trials in which the step increases occurred (Kagerer et al., 1997). In Chapter 2, we test if the schedule of perturbation introduction affects the limits of implicit motor adaptation using 2 distinct types of gradual perturbation introduction. One that limits the explicit components of adaptation, and one that allows for learning in multiple steps.

The observed exponential reduction of error during motor adaptation suggests that internal models specific to movement or task contexts are updated. Since people can concurrently adapt to perturbations without interfering with other movements (Ayala et al., 2015; Baldeo & Henriques, 2013; Galea & Miall, 2006; Gandolfo et al., 1996) there are likely multiple context-specific internal models used for movement. However, not all context changes reliably enable switching to context-specific motor memories, as evidenced by the need to wash out aftereffects of adaptation when returning to previously well-known, and sometimes well-cued contexts (Kluzik et al., 2008; Redding & Wallace, 1993; Taylor & Ivry, 2011). The factors contributing to the viability of a motor context to elicit switching from one context-specific internal model to another are not yet well understood. For example, performing an outward upper limb movement while maintaining different body postures or hand configurations may require drastically different muscle activation patterns. It follows that changes in body posture or hand configuration can enable the motor system to reliably switch to new context-specific internal models (Ayala et al., 2015; Gandolfo et al., 1996; Krakauer et al., 2006). Similarly, movements to distinct locations while maintaining a constant posture may also require different muscle activation patterns which, along with causing generalization of adaptation to be centered on learned movement directions, can lead to reliable motor context switching (Baldeo & Henriques, 2013; Baraduc & Wolpert, 2002; Cressman & Henriques, 2015). Finally, when both postures and movement directions are maintained, different perturbations that apply different forces on the moving end effector can again lead to context-

specific motor adaptation (Hirashima & Nozaki, 2012). Such properties of motor tasks that affect the dynamics of the motor behaviour are considered “intrinsic cues” and have been established to reliably inform context-specific motor memory creation.

The effects of cues that are “extrinsic” to the movement however, like sensed properties of the environment or objects with which we interact, are less well understood. Generally, extrinsic cues, even when they can reliably predict the presence of imposed perturbations, are not sufficient for preventing the updating of a single internal model and enabling context-specific learning (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Howard et al., 2013). However, some extrinsic cues, like the location of the interaction-point of a transported object, can lead to context-specific motor memory creation (Hegele & Heuer, 2010; Hinder, Tresilian, et al., 2008; McGarity-Shipley et al., 2020; Osu et al., 2004). Although it has been established that eliciting explicit awareness of the mapping between a cue and a perturbation can lead to context specific learning (Ayala & Henriques, 2020; Schween et al., 2020), it is not clear what property of extrinsic cues may determine if context-specific implicit motor memories are created or if existing internal models are updated. Two possibilities are the task-relevance of the cue, which may lead to increased saliency of the cue-perturbation mapping (Spotorno & Faure, 2011; Stirk & Underwood, 2007), and the explanatory power of a given cue, which may prevent model updating (Scarfe & Glennerste, 2014).

We can observe motor behaviour changes following detection of context changes to determine if context-specific motor memories are being employed during a motor task. During implicit adaptation, existing internal models are updated when motor errors arise. In the absence of context-specific motor learning, these same internal models are reupdated upon returning to previously experienced motor contexts. Updating and reupdating existing internal models leads to stereotypical learning curves every time a context switch occurs. This can be measured using either a dual adaptation paradigm, or a sequential adaptation paradigm. In dual adaptation paradigms participants are asked to concurrently

adapt to two perturbations that require distinct motor behaviour. If the perturbations oppose each other, like visuomotor rotations of the movement path in clockwise and counter-clockwise directions, and the motor contexts are not differentiated by the motor system, learning of one context interferes with learning of the other (Brashers-Krug et al., 1996; Karniel & Mussa-Ivaldi, 2002; Krakauer et al., 1999). In sequential adaptation paradigms, participants return to previously experienced contexts following adaptation to second motor context. If motor contexts weren't well differentiated, we expect stereotypical learning curves upon the return to the originally-experienced concepts. In both cases, if context-specific motor memories are created, we would expect step changes in performance when contexts change. In chapters 3 and 4, we use dual adaptation and return-to-baseline paradigms respectively to test if task relevant extrinsic cues and extrinsic cues that can explain perturbations may lead to context-specific adaptation.

Historically, we have used simple tasks to explore the mechanisms underlying motor learning in a well controlled manner. These paradigms often include diminished visual information and constraints to movements that are often required to have a desired level of experimental control over a visuomotor task. Examples include limiting a workspace to two dimensions and even mechanical constraints of joints which are not of interest. Although this approach to studying motor learning is important and has led to many important findings (e.g. constraint induced movement therapy), behaviour in the real world is often complex, and transfer of learning principles between the simple paradigms and real-world complex tasks can be poor (de Rooij et al., 2016; Saposnik & Levin, 2011; Wulf & Shea, 2002).

Ongoing advances in display technology can allow us to overcome some of these concerns. That is, using immersive virtual environments and well-tracked end effectors, we can have much richer tasks while still maintaining rigorous experimental control over the visual task environment. However, even when using virtual environments, a continued focus on simple tasks in motor learning paradigms have led to underwhelming transfer of learned simple tasks to real-world tasks (Palma et al., 2017; Saposnik &

Levin, 2011). To better understand learning in the context of complex tasks, we must study complex tasks in a laboratory setting.

An important property of complex tasks is the redundancy in possible solutions to the problem at hand. For example, when throwing a dart at a target at eye level, one can achieve the same goal with a hard throw and a low vertical release angle, or a softer throw but a higher vertical release angle. A key property of these complex tasks is that there are more execution variables (e.g. throw force and release angle of a dart) than there are variables that define performance on the task (e.g. distance from the target) (Sternad et al., 2014) (Fig 1.4a). In our standard reaching tasks for example, the execution variable (angle of heading) is directly coupled to the task outcome (distance from the target of the reach) (Fig 1.4b). The possible redundancy in solutions allows for variability and exploration in performance that would be inherently detrimental in simple tasks. To further explore complex tasks, we will use an immersive virtual environment to test a novel visuomotor task with redundancy in solutions.

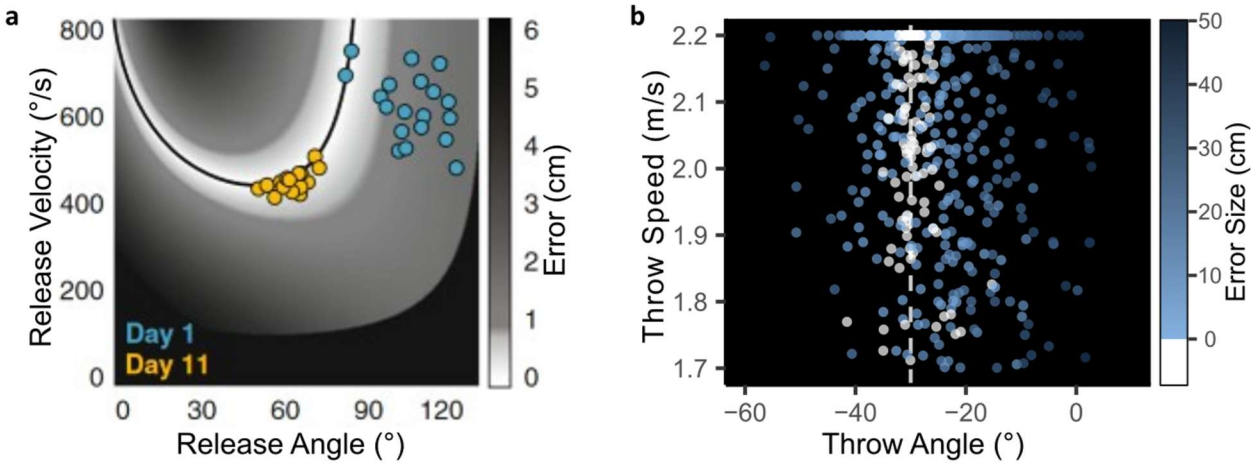

Figure 1.4: Complex motor tasks.
a: An example, from Sternad et al. (2014), of a solution subspace for a complex task. Here, any combination of Reach Velocity and Reach Angle that lies on the white-coloured region of the solution space results in a successful task completion. b: An example, from Chapter 4 of this dissertation, of a simple motor task, where performance in the task relies entirely on the throw angle, with added noise.

There have been recent efforts to study complex tasks using immersive environments. One such task, developed by Sternad et al. (2014) is termed “the skittles task”, and mimics the popular pub game of the same name. Here, participants throw a virtual ball on a string which is attached to a pole. Participants must swing the ball around the pole and hit “skittles” (wooden blocks) located on the other side. In this task, participants determine both the angle and the velocity of the ball at the point of release. Multiple combinations of the velocity and angle of release can lead to a successful trial. Figure 1.4 shows combinations of release angles and velocities and their resulting task outcome (measured as distance from the goal). Any solution that falls on the white-shaded area in the plot, known as a solution manifold, will result in a successful throw. Studies using this task have already proven fruitful, allowing us to study aspects of learning that in simple tasks would inherently result in detrimental performance. One important thing that these tasks can tell us, is how the brain deals with noise in motor performance during learning. It is difficult to entirely remove noise from our movements. Motor noise has a multitude of causes, including detrimental ones that must be overcome (e.g. feedback delays) as well as beneficial ones that may improve future performance (e.g. exploration). Noise due to exploration may be crucial when the source of our errors is unknown, but when the source is known, exploratory motor noise is less useful. In our studies, specifically in Chapter 4, we use both complex and simple tasks to ensure that our and past findings on implicit motor adaptation are not driven by the interplay between motor noise and complex task-success landscapes.

Overview of projects

Although motor learning is well studied, there is a lot we do not yet understand. For instance, we know that implicit learning plateaus at some limit regardless of the size of the perturbation being adapted to. However, it is not clear what causes this limitation. or where this limit lies for a given task

using a given set up prior to experimentation. Understanding this limit is important because we want to ideally overcome this; that is, we often want to maximize implicit learning. Promisingly, we know that the limit in implicit learning is not static. It is very much set-up and task- specific. This means if we do understand the mechanisms involved in limiting implicit learning, we can hope to account for them in learning plans.

Additionally, many motor learning paradigms are simplified compared to their real-life counterparts. For instance, we have many degrees of freedom and redundancy when performing a reach to a real object without any constraints. Reaching studies, however, are often simplified to point displays with movements constrained to a two-dimensional plane. There are viable reasons for this simplification; the data can be easily interpreted and modeled, and the environment can be well controlled. There are, however, important drawbacks that come with this amount of simplification. Although unconstrained real-world tasks may not be sufficiently controllable for rigorous scientific study, virtual reality technology gives us a middle ground where participants can perform unconstrained movements in three-dimensional space while allowing for great control over the visual environment. Using this technology, we can determine which motor learning principles derived from simplified tasks stand up to learning more complex tasks, and which do not. We can then determine the features of reality, whether internal or external to the actor, that contribute to these principles of learning.

This dissertation examines the nature of implicit motor adaptation and how it is influenced by different learning environments and task characteristics. Implicit motor adaptation is a cornerstone of both skill development and skill maintenance. Although the factors affecting implicit motor adaptation and its limits have been a focus of study for a long time, both new and more careful methods of measuring implicit motor adaptation have made it an important area to focus on. Using a process dissociation procedure designed to measure implicit components of motor adaptation following natural

learning time courses, we established that both the limits of implicit adaptation may be more flexible both in terms of its apparent limits and its response to visually changing task contexts.

In Chapter 2, we investigated whether the extent of implicit learning could overcome typical limitations observed in past work when visuomotor perturbations are introduced gradually. By testing the effect of gradually introducing perturbations in both stepped and ramped schedules, we demonstrated that a stepped introduction, where participants adapt to a large perturbation in small but noticeable increases in the perturbation size, led to significantly larger implicit adaptation than both abruptly introduced perturbations and those introduced in a ramped manner.

Building on this, in Chapters 3 and 4, we explored the role of visual contextual cues in driving implicit adaptation. In chapter 3, we focused on the potential for object specific motor memory formation, specifically testing if object-shape cues relevant to movement goals could enable this process. Results revealed a primary bias toward error assignment at the hand level, indicating that such cues, while influential for motor performance, play a limited role in context-specific implicit memory formation. In chapter 4, we expanded our exploration into visually cued movement contexts by introducing perturbations to either throw directions or ball accelerations in a virtual throwing task, paired with manipulations of the visual environment. This study revealed that acceleration-related perturbations triggered flexible adaptation independent of visual surface-slant cues, while throw direction-based perturbations led to internal model updating. Furthermore, we established that although it did not affect the propensity for the formation of new motor memories, the visual slant implicitly influenced motor performance, highlighting the multifaceted role of visual environmental properties in guiding motor learning processes.

Chapter 2: Adapting to visuomotor rotations in stepped increments increases implicit motor learning

Abstract

Human motor adaptation relies on both explicit conscious strategies and implicit unconscious updating of internal models to correct motor errors. Implicit adaptation is powerful, requiring less preparation time before executing adapted movements, but recent work suggests it is limited to some absolute magnitude regardless of the size of a visuomotor perturbation when the perturbation is introduced abruptly. It is commonly assumed that gradually introducing a perturbation should lead to improved implicit learning beyond this limit, but outcomes are conflicting. We tested whether introducing a perturbation in two distinct gradual methods can overcome the apparent limit and explain past conflicting findings. We found that gradually introducing a perturbation in a stepped manner, where participants were given time to adapt to each partial step before being introduced to a larger partial step, led to ~80% higher implicit aftereffects of learning, but introducing it in a ramped manner, where participants adapted larger rotations on each subsequent reach, did not. Our results clearly show that gradual introduction of a perturbation can lead to substantially larger implicit adaptation, as well as identify the type of introduction that is necessary to do so.

Introduction

The human motor system can quickly adapt to errors in our movements to improve future performance. Motor adaptation involves multiple learning processes including explicit conscious strategies that change our movement intent and implicit updates to internal models controlling the execution of our intended movements (Hegele & Heuer, 2010; Heuer & Hegele, 2015; McDougle et al., 2016; Taylor et al., 2014; Taylor & Ivry, 2011; Werner et al., 2015). Although the interaction between the

two processes is crucial to motor learning, studying them in isolation lets us glean how each may uniquely contribute to our ever-changing motor repertoire. In this study, we focus on implicit motor learning and its apparent limits. We show that our current understanding of implicit motor learning cannot fully explain its occasionally varying asymptotic limits in visuomotor rotation paradigms and provide a method of increasing implicit contributions to motor learning.

In many visuomotor adaptation paradigms, adapting reaching movements to consistent perturbations eventually leads to implicit learning reaching a steady-state below full compensation of the perturbation (Bond & Taylor, 2015; Kim et al., 2018; McDougle et al., 2015; Vaswani et al., 2015). When people adapt to relatively large perturbations, we repeatedly observe an upper bound to asymptotic implicit learning that is independent of the perturbation size (Bond & Taylor, 2015; Kim et al., 2018). This effect is observed when implicit learning is measured by subtracting planned strategy use (Bond & Taylor, 2015), by restricting strategy use after adaptation (Modchalingam et al., 2019; Neville & Cressman, 2018), or when people implicitly adapt to invariant motor errors (Kim et al., 2018, 2019). Thus, this cap in implicit adaptation appears robust.

The factors governing the upper limits of implicit learning are an area of active study (Albert et al., 2022; Kim et al., 2018; Tsay, Kim, et al., 2021). While other errors may influence implicit learning (Albert et al., 2022; Leow et al., 2018; Tsay, Haith, et al., 2022), it is considered largely driven by sensory prediction error (SPE) (Mazzoni & Krakauer, 2006; Tsay, Haith, et al., 2022; Tseng et al., 2007) – that is, the difference between the predicted sensory consequences of a planned movement and the perceived sensory consequences upon movement execution. When adapting to large perturbations that are introduced abruptly, participants may become aware of a perturbation and explicit re-aiming strategies may be formed to partially counter the perturbation. Since the magnitude of explicit strategies is flexible and scales to the size of the perturbation, larger perturbations can bring about additionally reduced

implicit motor adaptation (Bond & Taylor, 2015; Modchalingam et al., 2019; Neville & Cressman, 2018), resulting in apparent limits to implicit learning.

Conversely, it follows that limiting explicit strategy use should increase implicit learning. By introducing the perturbation gradually, we can limit any noticeable errors for participants to construct explicit strategies. This should increase implicit learning. Some studies support this postulation (Kagerer et al., 1997; Kluzik et al., 2008; Michel et al., 2007; Salomonczyk et al., 2011), but in other studies measures of implicit learning are similar regardless of whether the perturbation was introduced abruptly or gradually (Buch et al., 2003; Kagerer et al., 2006; Werner et al., 2022). While some of the discrepancies may be due to failure to exclude strategies sufficiently in measures of implicit adaptation in some studies, the primary and untested difference may be how gradual perturbations are introduced.

Perturbations are typically gradually introduced to participants in one of two ways: in a ramped manner where the magnitude of the perturbation is increased a small amount every trial, or in distinct steps where participants experience the same perturbation for multiple trials before the perturbation is further increased. For example, in the seminal study by Kagerer et al. (1997), participants adapted to perturbations in 10° incremental steps, each step consisting of 60 reaches. In other studies, participants adapted to perturbations in a ramped manner, where perturbations increased by small amounts on each subsequent reach (Butcher et al., 2017a; Salomonczyk et al., 2011).

The effects of the varying methods of perturbation introduction on the limits of implicit learning are not known. We were partly motivated by previous work by Salomonczyk et al. (Salomonczyk et al., 2011), who observed increases in aftereffects of adaptation above conventional implicit adaptation limits using gradually introduced visuomotor rotations. Participants were introduced to the perturbations in a hybrid manner with properties from both ramped and stepped methods of gradual perturbation introduction. In that study, participants adapted to a 70° perturbation over 3 blocks. At the start of each block the perturbation was introduced in a ramped manner – 0.75 degrees per trial – to 30°, 50° and 70°

in blocks 1, 2 and 3 respectively. In each block however, participants reached to targets with the total visuomotor rotation extensively before moving onto the next block, possibly allowing for consolidation of learning at each step of adaptation. Additionally, participants were not asked to exclude explicit strategies when tested for aftereffects of learning. Thus, although it is clear that we can elicit aftereffects of learning above levels elicited when adapting to abrupt perturbations, it is still unclear whether these are due to failure to exclude strategies sufficiently in measures of implicit adaptation, a trial-by-trial ramped increase in the size of the perturbation, or block-by-block stepped increases in the size of the perturbation.

To resolve these ambiguities, we first attempt to isolate implicit learning during classical visuomotor adaptation, as well as measure explicit strategy use in a comparable way, by using a strategy exclusion method known as the process dissociation procedure (Werner et al., 2015). We then tested whether introducing a perturbation gradually (in both a ramped and stepped manner) and thus purportedly reducing explicit strategy by providing smaller, less salient errors elicits higher asymptotic implicit motor learning. We show that it can, but only when perturbation is introduced in a stepped manner which suggests that not all gradual introductions are equal.

Methods

Participants

105 participants (75F, 29M, 1 chose not to identify, $mean_{age}$ = 20.56, sd_{age} = 5.15, $range_{age}$ = 17-63) participated in the study. All participants self-reported to be right-handed and had normal or corrected-to-normal vision. Participation was voluntary and all participants gave informed, written consent prior to data collection. The procedures used in this study were approved by York University's

Human Participants Review Committee and all experiments were performed in accordance with institutional and international guidelines.

Setup/Apparatus

Participants sat on a height-adjustable chair facing an experimental apparatus containing a downward-facing LCD screen (30Hz, 20”, 1680 × 1050, Dell E2009Wt) and mirror to display visual feedback, and a tablet and pen (30Hz, 1920 x 1080, Wacom Intuos Pro PTH860) to record the hand position (Fig. 2.1a). They individually adjusted the chair’s height and distance from the apparatus until the display was fully visible and they could comfortably make reaching movements across the tablet. Participants held the pen in a precision grip and maintained contact with the tablet throughout the experiment. A thick cloth draped over their right shoulder (not shown in Fig. 2.1) occluded vision of their arm movements. All visual feedback was presented through the downward-facing screen reflected by the mirror. Visual feedback was displayed via in-house software created for designing and conducting visuomotor reaching experiments (’t Hart, Henriques, et al., 2022). The position of the mirror projected the visual feedback to appear as if on the same horizontal plane as the participants’ hand movements.

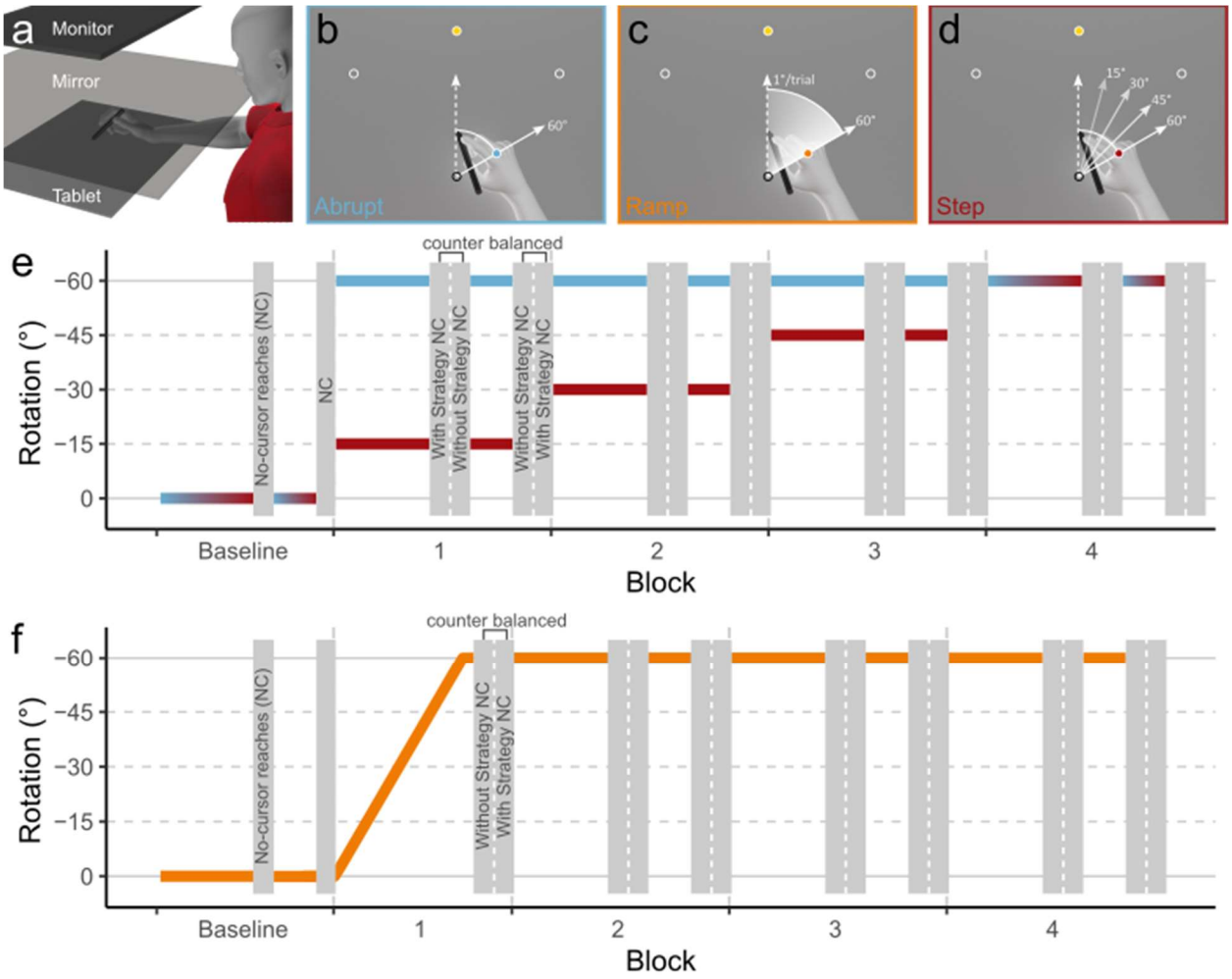

Figure 2.1: Experimental setup and perturbation introduction schedules
a: Experimental apparatus for task presentation (monitor and mirror) and data collection (tablet) **b-d**: Methods of perturbation introduction for the three groups of participants. **e**: The schedule of tasks in the Abrupt and Step groups over the course of the experiment. **f:** The schedule of tasks in the Ramp group. The baseline and the 4th block were identical for all groups. During each block, participants performed two bouts of Reach-with-cursor and two bouts of No-cursor tasks. Participants in the Ramped group performed one bout of the No-cursor task in Block 1.

Visuomotor rotation tasks

Participants made outward reaches towards 1 cm-diameter circular targets by smoothly gliding the pen held in their hand along the touchpad. The targets were located 10 cm away from the starting

position at one of 3 possible locations: 45, 90, or 135 degrees in polar coordinates (Fig. 2.1b-d). Participants were instructed to make quick, straight reaches towards the target but were not penalized for failing to do so. In tasks where participants received visual feedback of movements, called “Reach-with-cursor” tasks, a 1 cm-diameter circle represented their hand position. To complete a Reach-with-cursor task, the center of the hand cursor needed to be within 0.5 cm of the target’s center, while remaining still on the touchpad for 500ms. In other tasks, called “No-cursor” tasks, visual feedback of the hand was not provided during or after the movement. To complete No-cursor tasks, participants needed to indicate the completion of their movement by holding their hand still for 500ms following a reach. For these tasks, they were not required to acquire the target. After completion of either task, participants were instructed to return their hand to the starting position to begin the next trial. During return movements, participants were guided back to the starting position via a circle centered on the starting position which’s radius was equal to the participants’ distance from the starting position.

Experiment protocol

The participants were randomly assigned to 3 possible groups: “Abrupt” (n = 35, 22F, 12M, 1 chose not to identify), “Ramp” (n = 33, 23F, 10M), and “Step” (n = 37, 30F, 6M). Each group experienced a different method of perturbation introduction (Fig. 2.1e). Figure 2.1b-d shows the perturbation experienced in Reach-with-cursor tasks by each group throughout the experiment. In trials where the perturbation was 0°, the position of the hand-cursor was aligned with that of the participant’s real hand. When a non-zero perturbation was applied, any movement along the touchpad was rotated clockwise by the magnitude of the perturbation. Participants needed to rotate their hand path counterclockwise by the magnitude of the perturbation to make smooth and straight reaches to the targets.

All three experiments consisted of 5 blocks, divided into two phases: the "Baseline” phase and the "Rotated” phase. The Baseline phase consisted of one block and the rotated phase consisted of 4 blocks. A block began with the Reach-with-cursor task (45 trials), followed by the No-cursor task (9 trials

in the Baseline phase and 18 trials in the Training phase), followed then by the Reach-with-cursor task (21 trials), and finally by the No-cursor task (9 trials in the Baseline phase and 18 trials in the Training phase). All blocks in all groups followed this block structure with the exception of Block 1 in the Ramped group. To ensure that the perturbation ramped up to 60 degrees over 60 trials without interruption, Block 1 of the Ramped group did not include the first No-Cursor task. When transitioning between tasks, the words “Reach to Target” and “Reach with No Cursor” were displayed to participants to indicate the next trial belonging to the Reach-with-cursor task and No-cursor task respectively.

Participants took a short break before starting the Rotated phase. During the break, participants were told there may be changes in the behaviour of the hand cursor for the rest of the experiment. Participants were told to mentally note any strategy they may employ to counter the behaviour of the hand-cursor, as they may be asked to use or not use that strategy during No-cursor tasks. Detailed instructions can be found at https://osf.io/a7k6s/.

To isolate implicit aftereffects of learning, and to assess explicit strategy use following adaptation, we used a process dissociation procedure (PDP). During the Rotated phase of the experiment, in addition to the “Reach with No Cursor” instructions, the words “WITH strategy” or “WITHOUT strategy” cued participants to employ, or not employ any cognitive strategy they may have used for the next 9 No-cursor trials. Additionally, participants were verbally instructed “if you were using a strategy, please make use of the strategy you learned to correct for odd movement of the cursor” during With Strategy No-cursor tasks, and “do not make use of any strategies learned earlier and treat this as you did the original Reach-to-Target tasks (before the break)” during Without Strategy No-cursor tasks. After completing the 9 trials, participants received the alternate instruction for the next 9 No-cursor trials. The order of the With and Without Strategy instructions was counterbalanced to avoid order effects. We used deviations from baseline performance in Without-strategy-no-cursor tasks as our measure of implicit aftereffects of

learning. As our measure of explicit strategy use, we used any added deviation evoked by our instruction to use a remembered strategy.

Analysis

To measure performance during our reaching tasks, we calculated the angular deviation of a participant's hand path from a straight-line movement to the target at the point of maximum velocity – which we term "hand deviation". Similar measures of directional error are often calculated at a temporal or spatial cutoff from the starting point of a reaching movement (Bond & Taylor, 2015; Mazzoni & Krakauer, 2006; Neville & Cressman, 2018; Tsay, Kim, et al., 2021; Werner et al., 2015). Our measure of hand deviation, like other measures of initial directional error, reflects the direction of the planned reaching movement before the effects of feedback-based corrections. When reaching with a rotated cursor in the Rotated phase of the experiment, participants had to deviate their hand paths counterclockwise by the full amount of the visuomotor perturbation to make the cursor move directly to the target. We corrected for individual biases in reach behaviour by subtracting the mean hand deviations for each target in the Baseline phase of the experiment from hand deviations to the corresponding targets in the rotated phase. All subsequent calculations and data analysis were conducted on baseline-corrected data. To determine if participants adapted to the visuomotor rotation presented to them, we analyzed performance during key trial sets during Reach-with-cursor tasks in the Rotated phase of the experiment. The first trial set included the first 3 trials during learning, representing one reach to each of the three possible targets with the perturbation applied. Only the participants in the Abrupt group experienced the full 60° rotation during this trial set. Additional trial sets of interest included the final 6 Reach-with-cursor tasks in Block 4 for all groups.

To confirm that participants in all groups adapted to the 60° rotation, we conducted a 2x3 mixed analysis of variance (ANOVA) with the group which participants belonged to as a between-subject factor

and the Initial and Final block trial sets of interest (See Figure 2.2a: grey-shaded areas) as a within-subject factor.

To test whether the method of perturbation introduction affected implicit motor adaptation, we compared the aftereffects of learning as measured in Without Strategy No-cursor trials. We made two sets of comparisons. First, we compared hand deviations during these No-cursor tasks in the initial blocks in which each group first became exposed to the full 60° rotation: Block 4 for the Step group, and Block 1 for the Ramp and Abrupt groups. Additionally, to account for time spent adapting to a visuomotor perturbation, we compared Hand deviations during Without Strategy No-cursor tasks in Block 4 for all groups. For both comparisons, we first calculated mean hand deviations during each block for each participant. We then performed a one-way ANOVA to determine the effects of the method of perturbation introduction on hand deviations during these Without Strategy No-cursor tasks. For all comparisons, we computed Inclusion Bayes factors between models that include or do not include relevant effects (Clyde et al., 2011). To analyze strategy use following adaptation, we calculated the mean explicit strategy used during each block by each participant. We did this by subtracting mean hand deviations within a block during Without Strategy No-cursor tasks from mean hand deviations within a block during With Strategy No-cursor tasks. We repeated the analyses specified above for the explicit strategies participants employed.

We also explored if the method of perturbation introduction affected the temporal dynamics of implicit aftereffects of learning and explicit strategy use – both measured via the PDP. We expected implicit aftereffects to decay over time. We calculated mean rates of change in hand deviations during each block of No-cursor tasks for participants in the rotated phase of the experiment. For each participant, we fitted a simple linear model predicting hand deviation as a function of the trial number within a No-cursor block. To determine the effects of the method of perturbation introduction and the block number on decay rates of implicit and explicit motor adaptation processes, we conducted separate

two-way 3 (method of perturbation introduction) x 4 (block) mixed ANOVAs for implicit and explicit effects of learning, with the method of perturbation introduction as a between-subject factor and block as a within-subject factor.

Results

First, we confirmed that participants can adapt appropriately to all three methods of perturbation introduction – i.e., Abrupt, Ramp, and Step. Participants in all groups adapted to the presented perturbations over the 4 blocks of the rotated phase of the experiment by deviating their hand-paths in the opposite direction of the perturbation (main effect of trial set: $F_{(1,102)} = 1681.30$, $p < .001$, $\eta^2_G = .87$, $BF_{incl} > 10^6$) (Fig. 2.2a-b). The method of perturbation introduction affected the extent of learning in the Rotated phase (interaction between group and trial set: $F_{(2, 102)} = 15.48$, $p < .001$, $\eta^2_G = .11$, $BF_{incl} > 10^6$). This is likely driven by differences in the initial trials of the rotated phase of the experiment, as by the end of the final block, participants in all groups were able to adapt to ~86% of the 60° visuomotor rotation (Step group mean: 51.81°, 86.35%; Ramp group mean: 50.34°, 83.90%; Abrupt group mean: 53.02°, 88.37%). We find moderate evidence that all three groups adapted to a similar level by block 4 of the experiment ($BF_{incl} = 0.30$).

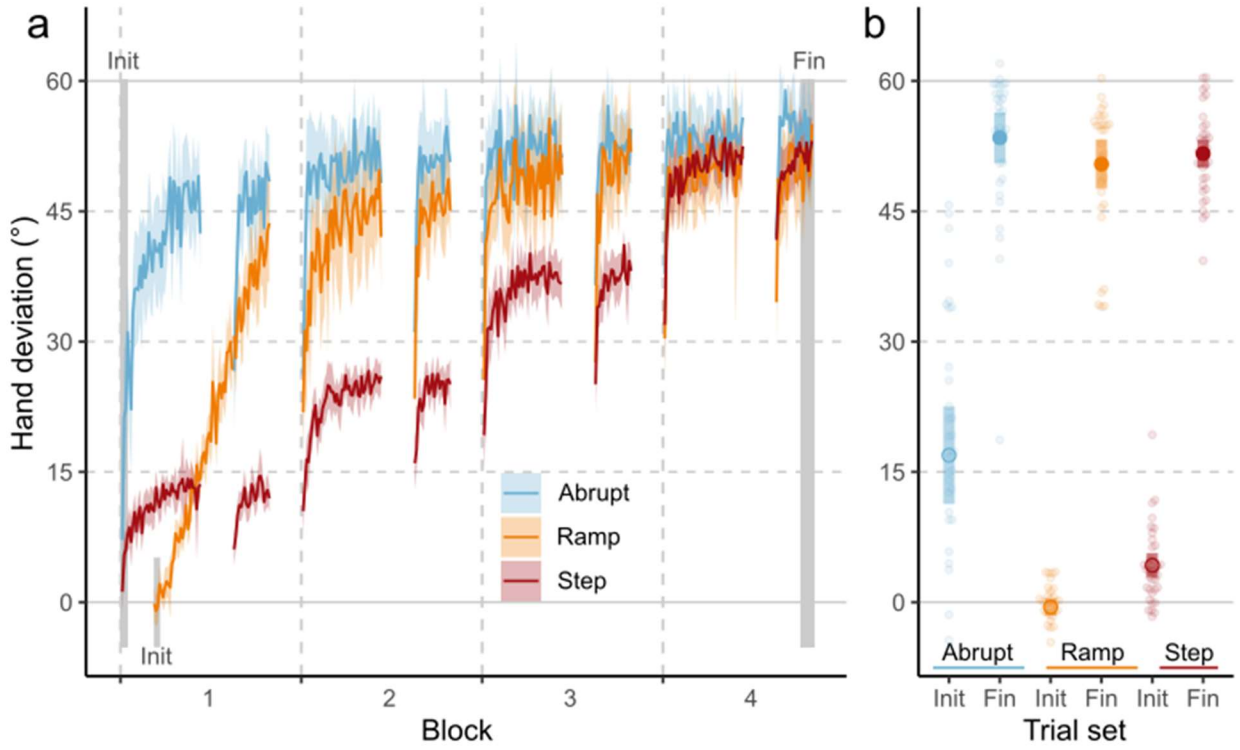

Figure 2.2: Hand deviations during training

a: Mean hand deviations from straight-to-target reaches for participants in each group during Reach-with-cursor trials. Shaded grey regions indicate trial sets if interest that were further analyzed. **b**: Mean and individual hand deviations in trial sets of interest. Coloured regions represent 95% CI.

To measure implicit aftereffects of adaptation, we asked participants to reach to targets without visual feedback of their hand position. Here, we asked participants to exclude any explicit strategies they used to compensate for the perturbation during training. During the first block of reaching with a 60° visuomotor rotation (Block 1 for the Abrupt and Ramp groups, Block 4 for the Step group), aftereffects of learning were affected by the method of perturbation introduction (Fig. 2.3a: main effect of group: $F_{(2, 102)} = 44.20$, $p < 0.001$, $\eta^2 = .46$, $BF_{incl} > 10^6$). Implicit learning was higher for participants in the Step group (mean = 21.96°, sd = 8.07°) than those in the Ramp group (mean = 10.74°, sd = 3.71°, Tukey's HSD: $p < .001$, $BF_{10} > 10^6$) and the Abrupt group (mean = 10.76°, sd = 4.50°, Tukey's HSD: $p < .001$, $BF_{10} > 10^6$). We found moderate evidence that participants in the Ramp and Abrupt groups have similar amounts of implicit learning ($BF_{10} = 0.249$) after one block of adaptation.

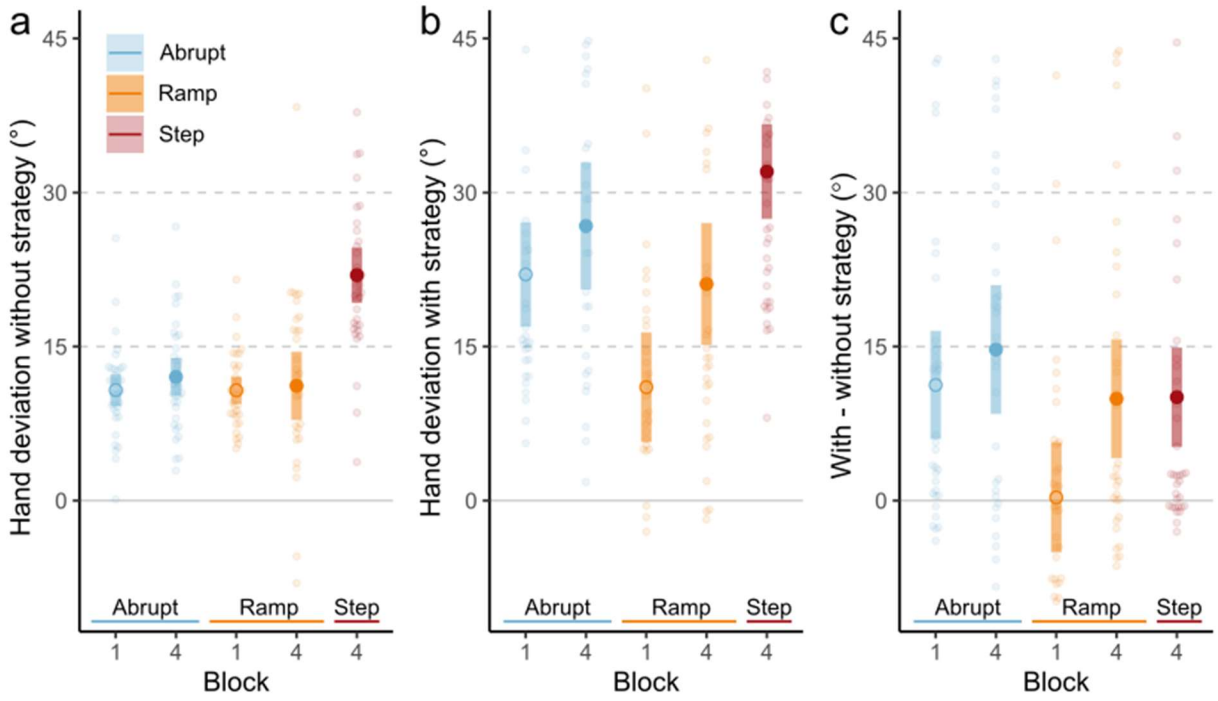

Figure 2.3: Implicit and explicit adaptation in all groups.
Mean and individual hand deviations from straight-to-target reaches during No-cursor tasks in blocks 1 and 4 without (**a**) and with (**b**) strategy use. **c**: Mean and individual explicit strategy use (calculated by subtracting Without-strategy hand deviations from With-strategy hand deviations) in blocks 1 and 4. Block 1 of the Step group was excluded due to not having adapted to a 60° rotation as in the plotted groups. Coloured regions represent 95% CI.

To account for time spent adapting to a visuomotor perturbation, we also repeated our analyses on the final block of each condition. The method of perturbation introduction affected the implicit aftereffects in the final block of the experiment (Fig. 2.3a: main effect of group: $F_{(2, 102)} = 21.43$, $p < 0.001$, $\eta^2 = .30$, $BF_{incl} = 7.33x10^5$). Post hoc tests revealed that after 4 blocks of adaptation, participants in the Step group exhibited ~80% higher implicit learning (mean = 21.96°, sd = 8.07°) than those in the Ramp group (mean = 11.18°, sd = 9.38°, Tukey's HSD: $p < .001$, $BF_{10} = 6.57x10^3$) and the Abrupt group (mean = 12.04°, sd = 5.34°, Tukey's HSD: $p < .001$, $BF_{10} = 2.20x10^5$). We find moderate evidence that participants

in the Ramp and Abrupt groups have similar amounts of implicit learning after being exposed to the perturbation for 4 blocks (BF_{10} = 0.27).

When initially experiencing a 60° perturbation – after 1 block in the Ramp and Abrupt groups, and after 4 blocks in the Step group – explicit strategy use was affected by the method of perturbation introduction (Fig. 2.3c: main effect of group: $F_{(2,102)}$ = 5.46, p = 0.005, η^2 = 0.10, BF_{incl} = 6.80). During these initial blocks of experiencing a 60° perturbation, there was moderate evidence that participants in the Step and Abrupt groups could evoke strategies to account for the same proportion of a 60° perturbation (BF_{10} = 0.26). Furthermore, after 4 blocks of training, we found moderate evidence of similar explicit strategy use when cued in all groups (Fig. 2.3b: BF_{incl} = 0.19)

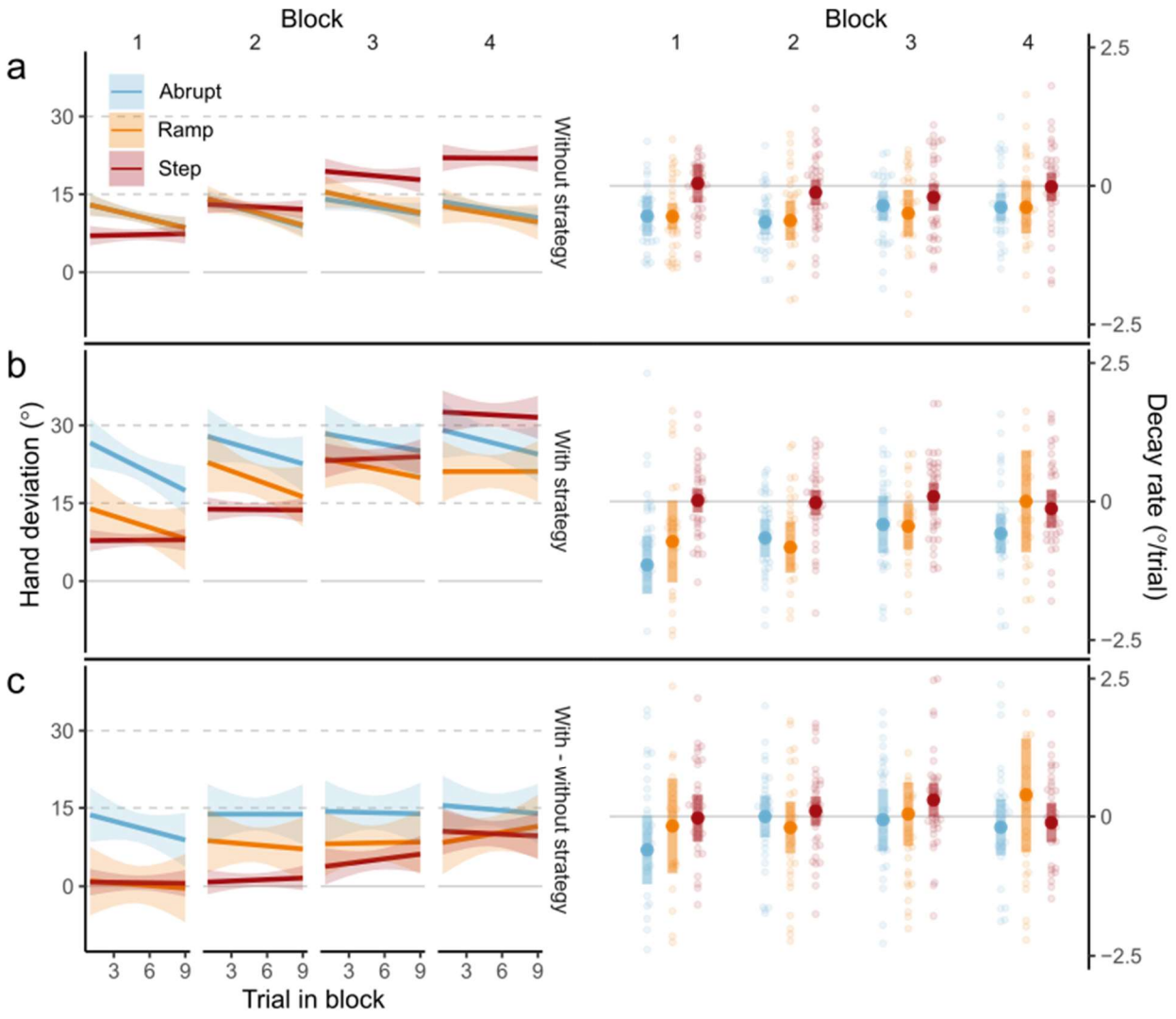

Figure 2.4: Trial-by-trial changes in hand deviations during PDP trials.
Left column: Mean hand deviations from straight-to-target reaches and calculated explicit strategies over 9 consecutive trials during No-cursor tasks without (**a**) and with strategy use (**b**) and calculated explicit strategy use (**c**). Right column: Mean and individual rates of change over 9 consecutive trials during each block of the Rotated phase. Coloured regions represent 99% CI.

Both implicit aftereffects of learning, measured via the exclusion of explicit strategies during No-cursor reaches, and explicit strategies may decay over time when repeatedly reaching without a cursor. To test whether these decay rates were affected by the method of perturbation introduction, we compared the rate of change in performance during 9-trial No-Cursor tasks. The method of perturbation

introduction affected the rate of change of implicit aftereffects during 9-trial set of No-Cursor reaches (Fig. 2.4a: main effect of group $F_{(2,102)} = 7.36$, $p = 0.001$, $\eta^2 = 0.05$, $BF_{incl} = 11.51$) but the block number did not ($F_{(3,306)} = 1.01$, $p = 0.387$, $BF_{incl} = 0.03$). The method of perturbation introduction but not the block number also affected the rate of change of hand deviations in Use-strategy no-cursor reaches (Fig. 2.4b: main effect of group $F_{(2,102)} = 6.84$, $p = 0.002$, $\eta^2 = 0.04$, $BF_{incl} = 7.13$, but not block $F_{(3,306)} = 2.09$, $p = 0.102$, $BF_{incl} = 0.13$), but the rate of change of calculated explicit strategies was not affected by either the method of perturbation of introduction (Fig. 2.4c: no effect of group $F_{(2,102)} = 0.95$, $p = 0.389$, $BF_{incl} = 0.06$) or the block number ($F_{(3,306)} = 1.08$, $p = 0.358$, $BF_{incl} = 0.03$). When collapsed among blocks participants in the Step group had lower rates of decay over 9 No-cursor reaches (mean = -0.07°/trial, sd = 0.53°/trial) than those in the Ramp group (mean = -0.51°/trial, sd = 0.62°/trial, Tukey's HSD: $p = .003$, $BF_{10} = 17.37$) and the Abrupt group (mean = -0.49°/trial, sd = 0.48°/trial, Tukey's HSD: $p = .005$, $BF_{10} = 31.83$). Our exploratory analysis on the rates of change of implicit and explicit components of learning suggests a possible mechanism by which stepped introduction of perturbations led to increased implicit aftereffects, but a more thorough examination of decay rates over a larger number of No-cursor reaches is necessary.

Discussion

The extent of asymptotic implicit adaptation in visuomotor rotation reaching paradigms is commonly held to have an upper limit independent of the size of the perturbation when a perturbation is abruptly introduced. It is also thought that this limit may be overcome by gradually introducing the perturbation. Here, we find that gradually introducing a perturbation in a stepped manner, but not in a ramped manner, led to ~80% larger implicit aftereffects of learning, compared to abruptly introducing the perturbation.

We reproduced the often observed ~15° limit to implicit motor adaptations when adapting to a large, abruptly introduced visuomotor rotation – measured with strategy exclusion trials. Whether this cap also applies to perturbations that are less salient, like those gradually introduced, is unsettled. Some previous studies that gradually introduced perturbations show possibly larger aftereffects (Butcher et al., 2017a; Kagerer et al., 1997; Salomonczyk et al., 2011). Furthermore, recent studies have proposed that implicit adaptation processes both compete with and compensate for explicit strategies (Albert et al., 2022; Miyamoto et al., 2020). There is consequently strong theoretical backing for increased implicit learning in response to gradually introduced perturbations. However, there are many methods of introducing a perturbation gradually, and although they are generally considered under the same umbrella, it is not clear whether all have similar effects on implicit, or even explicit, learning. Against our expectations, when we directly compare these two types of gradual learning, we found increased implicit aftereffects of learning only when perturbations were introduced in a stepped, but not a ramped manner. This despite the Step group experiencing the full 60° rotation for only one block as opposed to three blocks for the Ramp group. The lack of disambiguation between gradual learning paradigms may have partially contributed to the conflicting findings in previous studies on gradually introduced visuomotor perturbations.

Specifically, our results suggest that introduction of a gradual visuomotor rotation in either a stepped or ramped manner may differently affect asymptotic implicit learning and may explain discrepancies in past studies. In some studies that found higher implicit aftereffects when gradually introducing a perturbation, such as the seminal study by Kagerer et al., introduced the perturbation in a stepped manner (Kagerer et al., 1997; Michel et al., 2007). Likewise, some studies that found no differences had a ramped introduction (Werner et al., 2022). Our results also suggest that the high implicit learning seen in Salomonczyk et al. (Salomonczyk et al., 2011) was likely due to the block-wise changes in perturbation size and not the ramp up at the onset of each block. However, not all studies

neatly fit into this dichotomy (Buch et al., 2003; Butcher et al., 2017a; Kagerer et al., 2006; Kluzik et al., 2008). When we compare implicit aftereffects to perturbations introduced in abrupt and ramped manners in two experiments by Butcher et al. (Butcher et al., 2017a), we find higher implicit learning – comparable to our Step group – in a ramped group compared to an abrupt group. Notably, in Butcher et al. (Butcher et al., 2017a), participants experienced a ramped introduction over significantly more trials (320 trials) compared to those in their abrupt group (128 trials), and our own Ramp group (60 trials). These findings, along with our own, suggest that continued exposure to changing error signals may have additional effects on asymptotic implicit learning. Further work is needed to investigate these effects in depth.

In an interesting but exploratory finding, we see not only higher implicit aftereffects of learning, but also more robust implicit aftereffects of learning in our Step group. In the Abrupt and Ramp groups, we found typical decay of implicit aftereffects over the course of multiple reaches without any visual feedback of hand position (Bindra et al., 2021; Bond & Taylor, 2015; J. R. Morehead et al., 2015; R. J. Morehead et al., 2017; M. A. Smith et al., 2006; Taylor et al., 2011, 2014) – that is, our measures of implicit aftereffects decreased over time. In the Step group however, we find no such decay during nine No-cursor reaches (Fig. 2.4a). Introducing perturbations in a stepped manner may cause not only larger, but also more persistent, implicit learning. Taken together, the smaller increments followed by extended consolidation may be the necessary scaffolding for increased, robust implicit learning in stepped conditions.

Given that these different gradual methods of perturbation introduction led to clear differences in implicit aftereffects of learning, we also asked whether explicit strategy use was differently affected. To do this, we used a process dissociation procedure to calculate explicit strategy use. Although a process dissociation procedure (PDP) is one of many methods to measure explicit strategy use, and the choice of methodology may affect the contribution of explicit strategies to overall motor learning (Maresch et al.,

2021), the PDP has been reliable in consistently detecting changes in scenarios where explicit strategy use is expected to vary (Gastrock et al., 2020; Modchalingam et al., 2019; Werner et al., 2015) and it is consistent with measures of explicit strategies that ask participants to directly report aiming strategies (’t Hart, Taqvi, et al., 2022). In line with the theory of explicit and implicit processes of adaptation being in competition with, or compensating for one another, participants in the Step group should show diminished explicit strategies compared to the Ramp group. In our study however, although the Step group had larger reach aftereffects during block 4 when compared to the Ramp group (21.49° vs. 11.81° respectively), we do not see any clear evidence of consequently lower explicit strategies in the Step group – or for that matter, even the Abrupt group (Fig. 2.3c). Additionally, despite low explicit strategy use in block 1 in the Ramp group, we did not find evidence of increased implicit motor learning at that point in time when compared to the Abrupt group. This suggests that implicit adaptation may change in some way that is partially independent of explicit strategy use (’t Hart, Taqvi, et al., 2022). Our results also challenge the commonly held assumption that adapting to gradually introduced large rotations, as in the Ramp group, is less explicit over long time periods.

What features of the stepped introduction are crucial for eliciting larger, and possibly more stable implicit learning? We do not yet know. The two methods of gradually introducing a perturbation were different along two main features; the time spent ramping up to a 60° rotation, and the ability to consolidate implicit learning during adaptation. The Ramp group was introduced to a full 60° rotation in fewer trials and was not given time to consolidate learning for any given intermediate perturbation size. Although the Step group was given up to 66 trials to consolidate learning to an intermediate perturbation, is possible that shorter steps would have been sufficient to elicit more implicit learning given that saturation, and likely consolidation, of implicit components of learning can occur in far fewer than 66 trials (Ruttle et al., 2016, 2021). In learning paradigms with stepped introductions of perturbations, along with the number of trials spent on each step, the size and number of steps may also

matter. Unpublished results from our research group suggest smaller step sizes may elicit even more implicit learning than we find in our current study (’t Hart et al., 2019). Additionally, measuring decay in No-cursor trials following adaptation, and perhaps across even more trials than in this study, may be useful in gauging the resilience of implicit components of adaptation. Future studies should aim to identify key features of gradually introduced perturbations that affect implicit learning. Identifying these features will allow us to maximize implicit learning, a key outcome of rehabilitation and training paradigms.

DATA AVAILABILITY

Data and analysis are available on Open Science Framework (https://osf.io/a7k6s/)

Chapter 3: Movement-goal relevant object shape properties act as poor but viable cues for the attribution of motor errors to external objects

Abstract

When a context change is detected during motor learning, motor memories - internal models for executing movements within some context - may be created or existing motor memories may be activated and modified. Assigning credit to plausible causes of errors can allow for fast retrieval and activation of a motor memory, or a combination of motor memories, when the presence of such causes is detected. Features of the movement-context intrinsic to the movement dynamics, such as posture of the end effector, are often effective cues for detecting context change whereas features extrinsic to the movement dynamics, such as the colour of an object being moved, are often not. These extrinsic cues are typically not relevant to the motor task at hand and can be safely ignored by the motor system. We conducted two experiments testing if extrinsic but movement-goal relevant object-shape cues during an object-transport task can act as viable contextual cues for error assignment to the object, and the creation of new, object-shape-associated motor memories. In the first experiment we find that despite the object-shape cues, errors are primarily attributed to the hand transporting the object. In a second experiment, we find participants can execute differing movements cued by the object shape in a dual adaptation task, but the extent of adaptation is small, suggesting that movement-goal relevant object-shape properties are poor but viable cues for creating context specific motor memories.

Introduction

Contextual information about the environment, the objects we interact with, and our own body is crucial for reliable motor control. Different environments may require different muscle activations to perform similar motor tasks, and changes to our end effectors, such as injuries to a hand or modifications to a tool, may require different movement kinematics. It is well established that the motor system can select from multiple previously-learned internal models, termed motor memories, cued by internal or external contexts to execute movements (Berniker & Kording, 2008; Cothros et al., 2006; Kluzik et al., 2008; Krakauer et al., 1999; Oh & Schweighofer, 2019; Wolpert & Kawato, 1998). Along with features of the movement itself (Heald et al., 2021; Oh & Schweighofer, 2019), contextual cues can aid in reliably selecting the correct internal model (Ayala et al., 2015; Forano et al., 2021; Howard et al., 2013; Schween et al., 2018).

When the predicted consequences of a movement does not match the actual outcome, the difference, known as the sensory prediction error, can be used to update the internal models used to make the prediction (Mazzoni & Krakauer, 2006; Taylor & Ivry, 2012; Wolpert & Flanagan, 2001). Alternatively, if the sensory prediction error is sufficiently large, existing models that better predict the observed outcome given the intended movement may be activated. In the absence of any existing internal models that predict the observed outcome, new internal models may be created (Heald et al., 2021; Oh & Schweighofer, 2019).

The decision on whether to update an existing internal model or to create a new one can be informed by several factors. Features of the movement itself, as compared to predicted consequences of internal models, can be used to select an internal model for a given context (Oh & Schweighofer, 2019). Attributing errors to specific causes using available contextual cues can also allow for quick and reliable selection of internal models when those causes are detected (Berniker & Kording, 2008; Kluzik et al.,

2008). During tool use for example, errors can be attributed to external sources, such as the environment or the object being interacted with, and internal sources, such as the arm or hand used in the interaction. If the attribution of errors is accurate, models specific to the currently detected context can be accessed and updated. Additionally, accurate attribution of errors can allow for the switching of internal models before a movement needs to be initiated, and thus an error needs to be committed and perceived, allowing fast switching between multiple internal models and simultaneous adaptation to multiple contexts. In this study, we explore the types of cues that can lead to reliable attribution of errors to external sources and in turn facilitate fast switching of motor plans.

Cues that are "intrinsic" to a movement, i.e., cues that directly affect movement dynamics, such as movement direction, type, sequence, or posture, reliably facilitate fast context switching (Ayala et al., 2015; Ayala & Henriques, 2020, 2018; Baldeo & Henriques, 2013; Howard et al., 2012, 2013; Woolley et al., 2007). Findings on cues "extrinsic" to movement dynamics on the other hand, such as background colour and object identity are mixed (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Hegele & Heuer, 2010; Hinder, Woolley, et al., 2008; Osu et al., 2004; Woolley et al., 2007). In general, extrinsic cues are often not sufficient for accurate error attribution during motor learning (Hinder, Tresilian, et al., 2008; Hinder, Woolley, et al., 2008). Recent findings revealed that some extrinsic cues, such as colour (Forano et al., 2021), the action-effects of the effector (Schween et al., 2019a), and visual location of the movement (Schween et al., 2019a) can elicit dual adaptation if explicit adaptation processes (e.g., strategy formation) are engaged during adaptation, explaining some of the mixed findings and suggesting a critical role of cognitive strategy in dual adaptation (Forano et al., 2021). Furthermore, extrinsic cues that inform of the dynamics of the interaction-point of tools (Heald et al., 2018; McGarity-Shipley et al., 2020) can facilitate distinct motor memory formation. In these studies, the property of the tool that may cue the presence of a perturbation is task relevant. For example, in a study by McGarity-Shipley and colleagues (McGarity-Shipley et al., 2020), the location of the control point of a tool – the

point with which the object interacts with the world – both cued the presence of opposing perturbations to movements and was integral to completing the task. We test if task relevancy itself can be enough of a cue to facilitate multiple motor memory formation.

In this study, we increased relevancy of an extrinsic cue (the shape of an object) to task goals by having participants perform an object transport task in an immersive virtual-reality environment where they move a 3D object to one of two receptacles. The shape of the object determined the receptacle it must be transported to. To isolate the object-shape cue, we applied a visuomotor rotation (VMR) to movements only when transporting objects (VMR direction mapped to object shape) while ensuring that movement dynamics, object dynamics and interaction dynamics were the same between differently shaped objects. In one experiment, we tested whether such an extrinsic cue was sufficient to allow for associated motor errors to be attributed to the object itself, rather than the hand. In a second experiment, we tested whether further increasing task relevancy by forcing attention to the object-shape in a dual adaptation task allowed for the formation of distinct motor memories for differently shaped objects. We found that object-shape cues did not serve as sufficient contexts to elicit object-shape specific adaptation when adapting to a single visuomotor rotation, and were poor but viable cues for object-shape specific adaptation when adapting to multiple shape specific perturbations.

Methods

Participants

Sixty-two participants (47 Female, 19.87 ± 3.15 years of age, mean ± SD) participated in the study in one of two experiments: “Single Learning” (N=32, 24 Female, 20.03 ± 3.21 years of age) and “Dual Learning” (N=30, 23 Female, 19.69 ± 3.14 years of age). All participants were right-handed, had

normal or corrected-to-normal vision, and were naïve to visuomotor learning experiments. Participation was voluntary and all participants provided written, informed consent. All data for this study was collected at the Sensorimotor Control Lab at York University between October 16, 2019, and March 03, 2020. The procedures used in this this study were approved by York University's Human Participant Review Committee and all experiments were performed in accordance with institutional and international guidelines.

Apparatus

Participants sat on a height-adjustable chair facing a table placed at waist level. Participants donned a head-mounted display system (HMD: Oculus Rift Consumer Version 1; resolution 1080 by 1200 for each eye; refresh rate 90 Hz) and held an Oculus Touch controller in their right hand. Participants in the Single Learning experiments also held an Oculus Touch controller in their left hand. All visual feedback was provided via the HMD in an immersive virtual-reality experiment space developed in Unity 3D. We used the Unity Experiment Framework to handle trial and block schedules within the experiments (Brookes et al., 2020). Three Oculus Constellation sensors tracked the positions of the HMD and Oculus Touch controllers. To begin the experiments, participants placed their left hand on a magnetized docking apparatus (7.5 cm in diameter) attached to the table edge at body-midline. This apparatus acted as the starting position for each trial in the experiments and aided in returning the right hand to the starting position in the absence of visual feedback. The Oculus Touch controllers were equipped with magnets to aid attachment to the magnetized dock.

Object-transport task

All visual feedback during the task was provided in the immersive virtual reality (VR) environment. In all experiments, participants repeatedly performed the Object-transport task. Each trial

of the task began when participants returned the Oculus Touch controller held in their right hand to the magnetized dock. The dock was located near the starting position for each trial, termed the “Home” position. At the start of each trial, participants were shown an avatar-like representation of their hand (Fig 3.1A-B). An object in the shape of a cube (2 cm x 2 cm x 2 cm) or a sphere (2 cm diameter) appeared 10 cm away from the Home position, and two receptacles (box and cylinder shaped, depth of 2 cm) appeared 15 cm or 12 cm away from the object for the Single and Dual Learning experiments respectively. The opening of the box receptacle was 4 cm x 4cm x 4 cm and the opening of the cylinder was 4 cm in diameter. Participants were required to transport the object within 1 cm of the center of the receptacle in any orientation to complete the task. The target of the transport movement during a given Object-transport task was the receptacle with an opening matching the shape of the object.

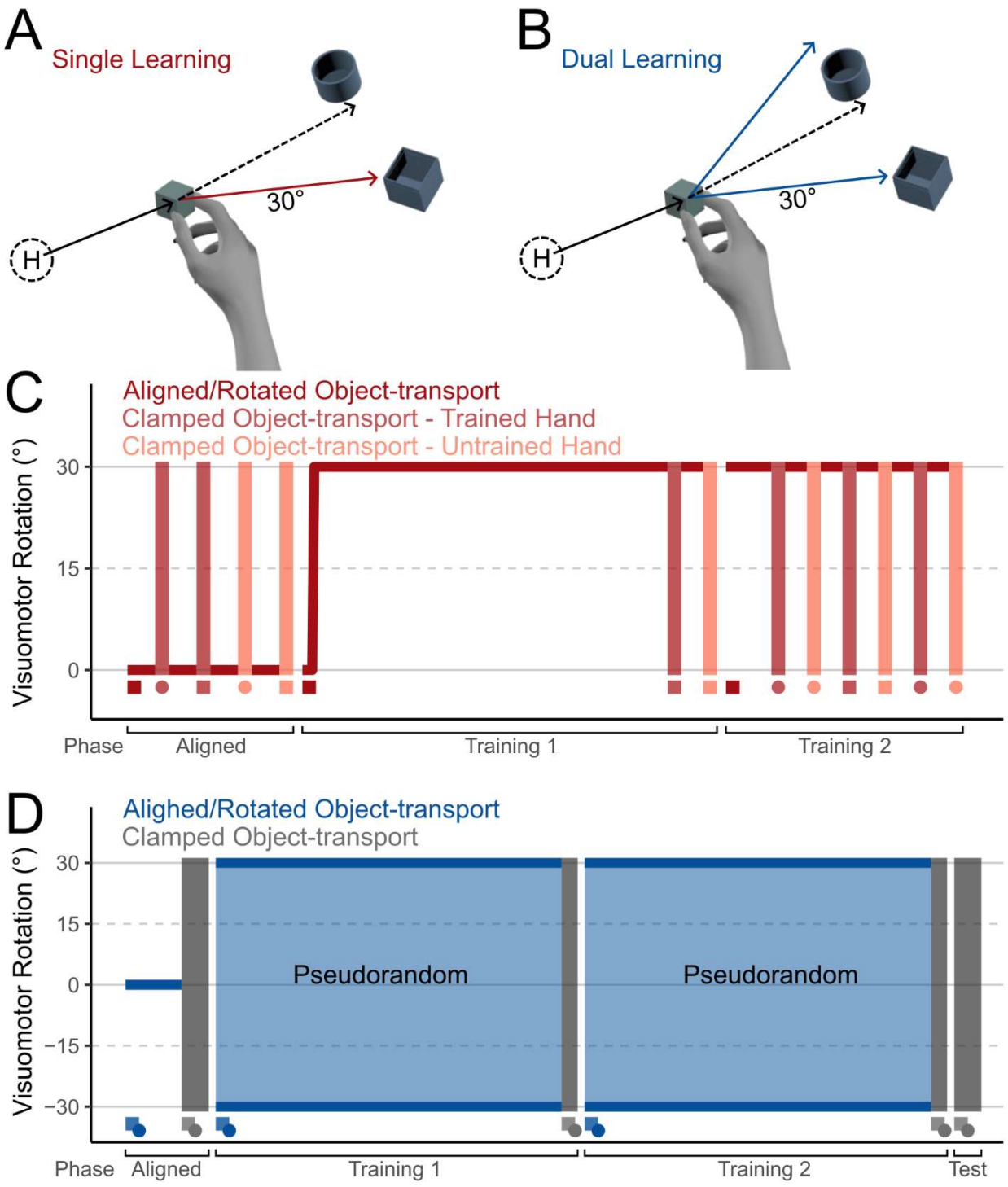

Figure 3.1. Experiment setup and procedure.

A-B: Trial protocol during a Rotated Object-transport task in the Single (A) and Dual (B) Learning experiments. In both experiments, participants began a trial at the Home Position (H) and made a

reaching movement toward an object. Each trial ended when participants transported the target to the corresponding receptacle. Solid lines represent visual movement direction and dashed lines represent real movement directions. C. The order of tasks during the Single Learning experiment. For each set of the Clamped Object-transport task, participants transported an object with the same or different shape as comparted to the object transported during the Rotated Object-transport tasks. D. The order of tasks during the Dual Learning experiment. All tasks in the Dual Learning experiment were performed using the right hand.

In the Single Learning experiment, participants transported objects of a single shape (counter-balanced between participants) during each block (Fig 3.1C). The trial-by-trial locations of the correct receptacles and the object's spawn locations were pseudorandomized, appearing at 45, 90, or 135 degrees in polar coordinates relative to the Home position. In the Dual Learning experiment, participants transported objects of both shapes during each block. Here, the object-shapes appeared in trial-sets of 3, providing participants multiple opportunities to learn a shape-perturbation mapping before experiencing different perturbations to their movements. The trial-set-by-trial-set order of the object-shapes was pseudorandomized, ensuring that each object-shape appeared an equal number of times within a block. The trial-by-trial locations of the correct receptacles were pseudorandomized, appearing at 45, 90, or 135 degrees in polar coordinates centered on the object's spawn location.

Each trial contained two steps: Reach and Transport. During the Reach step, participants moved directly towards the object and made a pinch gesture using the index finger and thumb to interact with it. Once the gesture was completed the Reach step ended and the Transport step began. To highlight the object identity, the hand representation disappeared, and participants transported the object to the

corresponding receptacle. A trial ended when participants moved the object to the centre of the corresponding receptacle.

In each experiment, participants performed three variations of the Object-transport task: Aligned, Rotated, and Clamped. The Reach step, during which the visual representation of the hand was spatially aligned with the participant's real hand, remained consistent across all variations. During the Transport step, the movement path of the object was aligned with the real movement path in the Aligned variation and a 30° visuomotor rotation (either clockwise or counterclockwise) was applied on the horizontal plane in the Rotated variation. In the Clamped variation, to prevent feedback-based corrections during a movement, the object's movement path was constrained to travel directly to the appropriate receptacle during the Transport step, with the object's distance from its starting position matched to the hand's distance from the object's initial location.

Experiment protocol

All participants began the experiment with their right-hand controller magnetically attached to the magnetized dock. They were instructed to make smooth, direct movements throughout the experiment. Although no strict time limits were imposed, participants were encouraged by the experimenter to move in a quick and uniform pace throughout the experiment and were warned if they moved too slowly. Before beginning the experiments, participants completed practice trials to familiarize themselves with the virtual environment and task. Following the practice trials, participants completed one of either the Single Learning or Dual Learning experiments. Both experiments involved an Aligned phase, used to measure individual baseline performances, and one or more Training phases (Fig 3.1). The Dual Learning experiment also included a short Test phase. In all phases, participants repeatedly performed the Object-transport task. Participants performed the Aligned Object-transport task during the Aligned phase of the experiments and the Rotated Object-transport task during the Training phase. Participants also performed Clamped Object-transport tasks in all phases.

In the Single Learning experiment, we investigated if adapting to a perturbation when transporting an object could be linked to the object's shape if the shape was relevant to the task goal. Participants completed 3 phases in the experiment during a single session: The Aligned phase, and two Training phases (Fig 3.1C). To prevent fatigue, each phase of the experiment was preceded by a short break lasting a minimum of 30 seconds. During the Aligned phase, participants performed 60 trials of the Aligned Object-transport task using their dominant hand. Four 6-trial blocks of the Clamped Object-transport tasks were interspersed within the Aligned phase following each set of 15 Aligned trials. During the first Training phase, following 6 trials of the Aligned Object-transport task, participants adapted to a 30° visuomotor rotation (clockwise or counterclockwise, counter-balanced across participants) using a designated object-shape (either cube or sphere, counter-balanced across participants) for 180 trials of the Object-transport task. Following the first set of Rotated Object-transport tasks, we tested if adaptation transferred to using either a differently shaped object or a different hand using Clamped Object-transport tasks where participants transported differently shaped objects, used a different hand to transport the object, or both. If adaptation was specific to the object shape, it would persist when participants switched hands, but diminish when they encountered a different object shape. Participants first performed two 6-trial blocks of the Clamped Object-transport task, with a 15-trial block of the Rotated Object-transport task in between. Then, in the second Training Phase, participants first performed 24 trials of the Rotated Object-transport task using the designated object-shape, then performed six 6-trial blocks of the Clamped Object-transport task, with 15-trial blocks of the Rotated Object-transport task in between.

In the Dual Learning experiment, we investigated whether participants could concurrently adapt to two distinct visuomotor rotations at the same time when the perturbations were matched to specific object-shapes. Here, participants completed 4 phases in the experiment during a single session: the Aligned phase, followed by two Training phases and a Test phase. Each phase was again preceded by a

short break lasting a minimum of 30 seconds. During the Aligned phase, participants performed 30 trials of the Aligned Object-transport task. During each trial, participants transported one of the two possible object-shapes (cube or sphere, order pseudorandomized using 3-trial sets to ensure each shape was transported an equal number of times). During both Training phases, participants adapted to two opposing 30° visuomotor rotations mapped to two distinct object-shapes (cube or sphere, object-shape-rotation mappings counterbalanced across participants, order pseudorandomized using 3-trial sets to ensure each shape was transported an equal number of times) for 180 trials. We tested whether participants dually adapted to both visuomotor perturbations during the Training phase and tested whether such adaptation relied on feedback-based corrections using Clamped Object-transport tasks. Following the 180-trial block of Rotated Object-transport tasks, participants performed 6 trials of the Clamped Object-transport task (object-shape order pseudo-randomized using 3-trial sets). Additionally, to ascertain if participants experienced implicit dual adaptation, we conducted a short Test phase using 12 trials of the Clamped Object-transport task (object-shape order pseudo-randomized using 3-trial sets). To determine if participants adapted implicitly, we used an altered version of a process dissociation procedure in which we instructed participants to refrain from using any strategies they may have developed during the training phase (Jacoby, 1991; Werner et al., 2015).

Data analysis

All position measures were recorded using Unity 3D (2020.1.17, Unity Technologies, San Francisco, CA). Data was analyzed offline using R and was accessed for analysis from the start of data collection (October of 2019) to January of 2024. All data and analysis scripts, along with supplementary analysis notebooks, can be found in this project's Open Science Framework repository (https://osf.io/twgc8/).

We assessed performance in the object-transport task by calculating the hand angle (HA) of a movement. We defined HA as the angular deviation from a straight-line movement to the target at 3 cm

from the object's starting position. HA is a measure of initial directional error, prior to effects of feedback-based corrections. We corrected for individual biases in transport behavior by subtracting individual baseline performances per Target location from the HA. Further, to compare across counterbalanced rotation directions, we normalized HA relative to the direction of the applied visuomotor rotation. We conducted all subsequent calculations and data analysis on the baseline corrected and normalized data.

To investigate performance changes over time, we compared mean HAs during the initial and final trial-sets of the first Training phase in each experiment, when participants were abruptly introduced to the visuomotor perturbations. The initial trial-set consisted of 3 trials: one reach to each of the 3 available targets. The final trial-set consisted of 9 trials.

To determine if participants in the Single Learning experiment adapted to the visuomotor rotation, we compared HA during the Reach and Transport step of the first and last trial-sets during the Training phase using separate paired sample t-tests. We then tested possible error attribution to either the object or the hand by comparing HA during the Clamped Object-transport task under various conditions. We performed a 2x2 repeated-measures analysis of variance (ANOVA) with the hand (same or different hand) and the object shape (same or different object shape) as within-subject factors. We used Tukey's HSD to conduct pairwise analysis when post-hoc tests were necessary. For all statistical tests, we additionally computed Inclusion Bayes factors between models that include or do not include relevant effects (Clyde et al., 2011).

To determine if participants in the Dual Learning experiment adapted to opposing rotations, we first determined if participants HAs changed over the course of the Training phase using paired sample t-tests. We separately compared the changes in HAs during the Reach and Transport steps. Additionally, to determine if participants performed differently without feedback-based corrections, we compared non-

normalized HAs during the Transport step of Clamped Object-transport tasks in the Dual Learning experiment, where participants transported objects associated with positive and negative rotations using a paired sample t-test. To determine if object-shape related changes in HA were implicit, we compared non-normalized HAs during the Transport step of the Clamped Object-transport tasks when participants were instructed to not employ any strategies they may have learned to compensate for the visuomotor perturbations during the Training phase.

Finally, we tested whether the time taken to initiate and execute the Reach step, the time taken to initiate the Transport step, or the time taken to execute the Transport step changed during the Training phase of both experiments. For all three measures, we conducted separate 2x2 mixed ANOVAs with the experiment as a between-subject factor and the trial-set as a within-subject factor. When post-hoc tests were necessary, we used Tukey's HSD to perform pairwise comparisons.

Results

We conducted two experiments to determine if goal-relevant visual properties of objects would suffice to enable error attribution to an object during Object-transport tasks. In the first experiment, participants transported an object with their right hand. A 30° visuomotor rotation was applied to their movement while transporting the object. To test for attribution of error, they were asked to transport a novel object, with either the trained hand or with their untrained, contralateral hand.

In the second experiment, to understand whether the goal-relevant extrinsic cues could facilitate dual adaptation, we mapped opposing visuomotor rotations (30° CCW or 30° CW) to distinct object shapes (sphere or cube). To test for dual adaptation, participants preformed Clamped Object-transport tasks where the direction of movement was clamped to head directly to the target. To test for possible implicit dual adaptation, participants also performed Clamped Object-transport tasks while disengaging any strategies they may have formed during the Training phase.

Experiment 1: single learning

Visuomotor adaptation

We compared normalized hand angles (HA) during the initial and final trial-sets of the Training phase (Fig 3.2A-C). We found no evidence of change in the HAs during the Reach step, where the location of the hand was aligned with the real hand, between the initial and final trial-sets of the Training phase ($t_{(31)}$ = -0.554, p = 0.583, BF_{10} = 0.22). During the Transport step of the Object-transport task, participants adapted their movements to counter the visuomotor perturbation over the course of the Training phase ($t_{(31)}$ = 17.987, p < 0.001, BF_{10} = $8.36x10^{14}$, Fig 3.2B). Over 180 trials (60 trial-sets), participants adapted to 79.0% of the rotation (23.7° hand angle during the final trial-set of the Training phase).

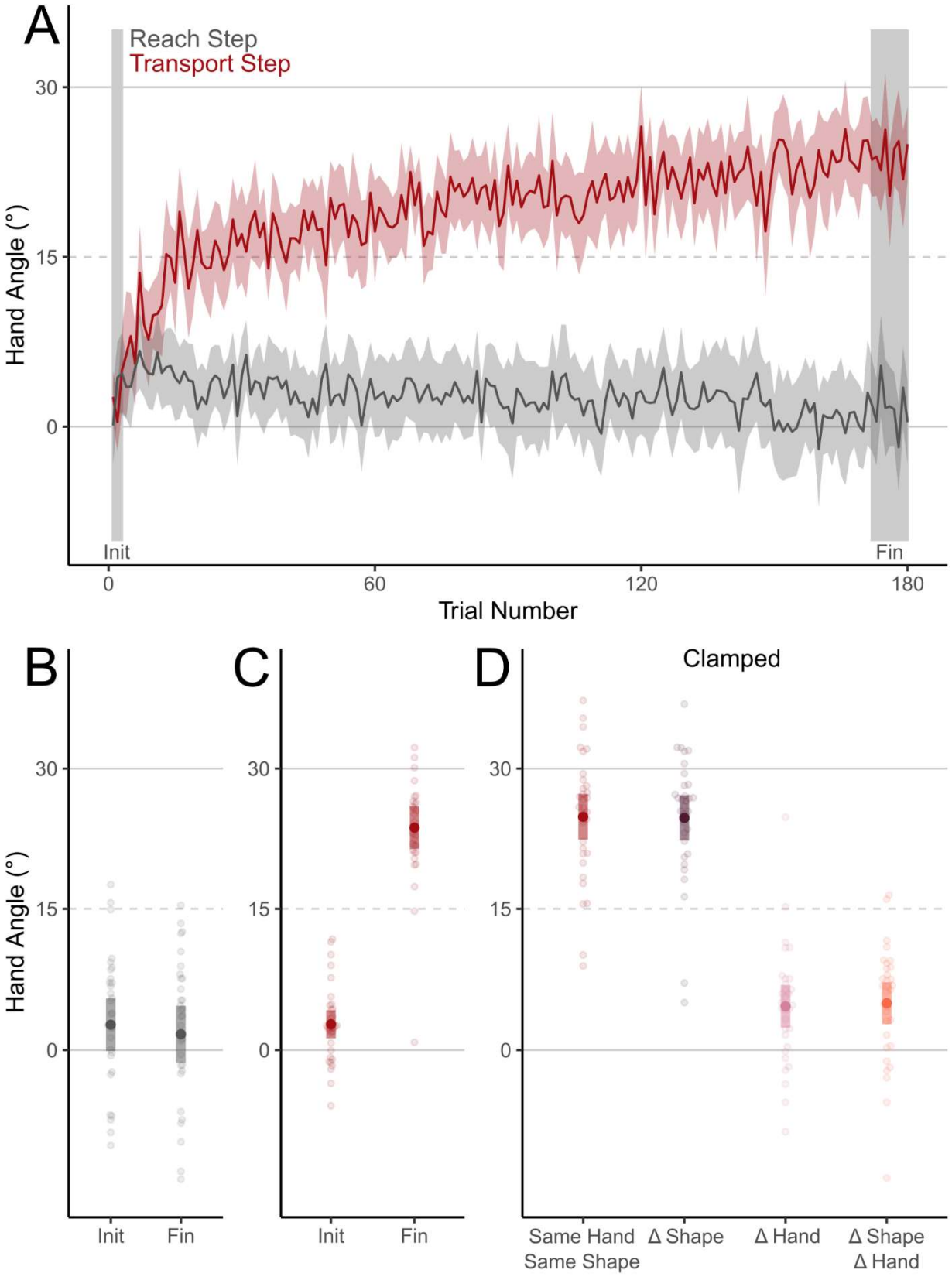
A
Reach Step
Transport Step
30
15
0
Hand Angle (°)
Init
Fin
0
60
120
180
Trial Number
B
C
D
Clamped
30
15
0
Hand Angle (°)
Init
Fin
Init
Fin
Same Hand
Same Shape
Δ Shape
Δ Hand
Δ Shape
Δ Hand

Figure 3.2. Hand Angles: Single Learning experiment.
Angular deviations from a straight-to-target movements (Hand Angle) during the Training phase in the Single Learning experiment. A. Hand Angles over the first 180 trials in the Training phase. B. Hand Angles during the Reach step of the initial and final trial-sets during the Training phase. C. Hand Angles during the Transport step of the initial and final trial-sets during the Training phase. D. Hand Angles during Clamped Object-transport tasks while participants transported objects of a different shape from the Rotated Object-transport task (Δ Shape), with a different hand from the one used in the Rotated Object-transport task (Δ Hand), and both. Shaded areas represent 95% CIs.

Error attribution

We first determined if retrieval of the adapted motor memory was cued by the object-shape. After adapting to a 30° visuomotor rotation, we tested HAs during the Transport step of Clamped Object-transport tasks. (Fig 3.2D: main effect of hand: $F_{(1, 31)} = 174.588$, $p < 0.001$, $\eta^2 = 0.70$, $BF_{incl} = 3.10x10^{36}$). We found moderate evidence that the object shape did not affect HA ($F_{(1, 31)} = 0.030$, $p = 0.863$, $\eta^2 = 0.00007$, $BF_{incl} = 0.152$).

After collapsing across object shape, we found moderate evidence that participants performed the same as during the Rotated Object-transport tasks when transporting objects with the trained hand ($t_{(31)} = -0.588$, $p = 0.560$, $BF_{10} = 0.22$). Participants also retained a small but significant portion (~19%) of the change in HA developed during the Transport step of the Object-transport task when performing with the untrained hand ($t_{(31)} = 4.7836$, $p < 0.001$, $BF_{10} = 589.64$).

Experiment 2: dual learning

Visuomotor adaptation

Participants in the Dual Learning experiment completed a typical dual adaptation paradigm with object identity distinguishing the perturbation experienced on a given training trial. Overall, when collapsing across rotations, we found moderate evidence of no change in HA across the Training phase during the Reach step of the Object-transport task, where the location of the hand was aligned with the real hand ($t_{(29)} = 0.702$, $p = 0.488$, $BF_{10} = 0.24$). During the Transport step, participants were able to successfully counter 11.9% (3.59°) of the 30° visuomotor rotation by the final 3 trial-sets of the Training phase relative to their HAs during the Baseline phase ($t_{(29)} = 3.68$, $p < 0.001$, $BF_{10} = 35.0$). We failed to find any evidence for changes in HAs during the Transport step across the Training phase ($t_{(29)} = 1.90$, $p = 0.067$, $BF_{10} = 0.95$), suggesting learning was approaching saturation within the first three trials of experiencing a perturbation (Fig 3.3A-C).

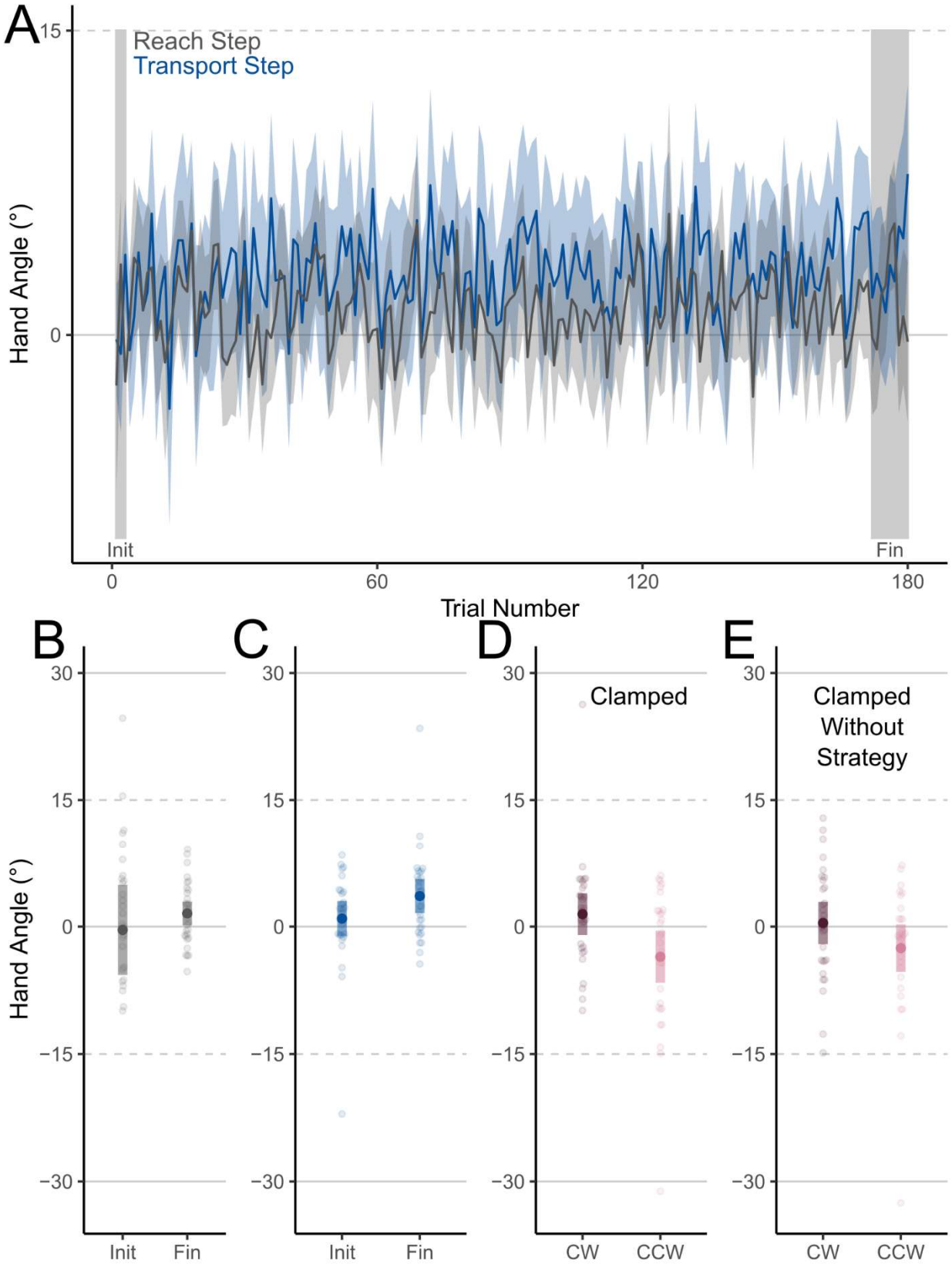
A
Reach Step
Transport Step
Hand Angle (°)
15
0
Init
Fin
0
60
120
180
Trial Number
B
C
D
E
30
15
0
−15
−30
Clamped
Clamped Without Strategy
Init
Fin
CW
CCW

Figure 3.3. Hand Angles: Dual Learning experiment.
Angular deviations from a straight-to-target movements (Hand Angle) during the Training phase in the Dual Learning experiment. A. Hand Angles over the first 180 trials in the Training phase. B. Hand Angles during the Reach step of the initial and final trial-sets during the Training phase. C. Hand Angles during the Transport step of the initial and final trial-sets during the Training phase. D. Non-normalized Hand Angles during the Transport step of Clamped Object-transport tasks while transporting the object associated with clockwise (CW) and counterclockwise (CCW) perturbations. E. Non-normalized Hand Angles during the Transport step of Clamped Object-transport tasks while transporting the object associated with clockwise (CW) and counterclockwise (CCW) perturbations when participants were instructed to exclude strategies that may have formed during the Training phase. Shaded areas represent 95% CIs.

For the Dual Learning experiment, we observed small changes in non-normalized HAs in the expected directions for each distinctive object during the Clamped Object-transport trials (Fig 3.3D). Participants' HAs differed between the two object shapes ($t_{(29)} = -2.58$, $p = 0.0153$, $BF_{10} = 3.14$). The magnitudes of the changes when compared to baseline performance were small: 1.47° and 3. 56° when transporting the shape associated with the clockwise and counter-clockwise visuomotor rotation respectively (Fig 3.3C). These changes in non-normalized HA further decreased when participants were instructed not to employ a strategy, resulting in a lack of statistical reliability (Fig 3.3E: $t_{(29)} = -1.89$, $p = 0.069$, $BF_{10} = 0.93$). Given the large inter-subject variability and small magnitude of error, we do not make strong conclusions about implicit and explicit subprocesses underlying the observed dual adaptation.

Reaction and execution times

We also tested if the time taken to initiate and execute the Reach step, the time taken to initiate the Transport step, or the time taken to execute the Transport step changed during the Training phase of both experiments (Fig 3.4). Although there was an interaction between the trial-set and experiment in time taken to complete the Reach step ($F_{(1, 60)} = 8.18$, $p = 0.006$, $\eta^2 = 0.062$, $BF_{incl} = 21.76$), this was driven by higher step-completion times in only the initial trial-set of Dual Learning experiment when compared to the final trial-sets of both the Single Learning (Tukey's HSD: $t_{(60)} = 3.62$, $p = 0.003$), and Dual Learning (Tukey's HSD: $t_{(60)} = 4.29$, $p < 0.001$) experiments (Fig 3.4A). By the end of the Training phase, participants in both experiments took a similar amount of time to complete the Reach step (Tukey's HSD: $t_{(60)} = -2.05$, $p = 0.182$). This may be due to the confusing nature of abruptly experiencing opposing perturbations.

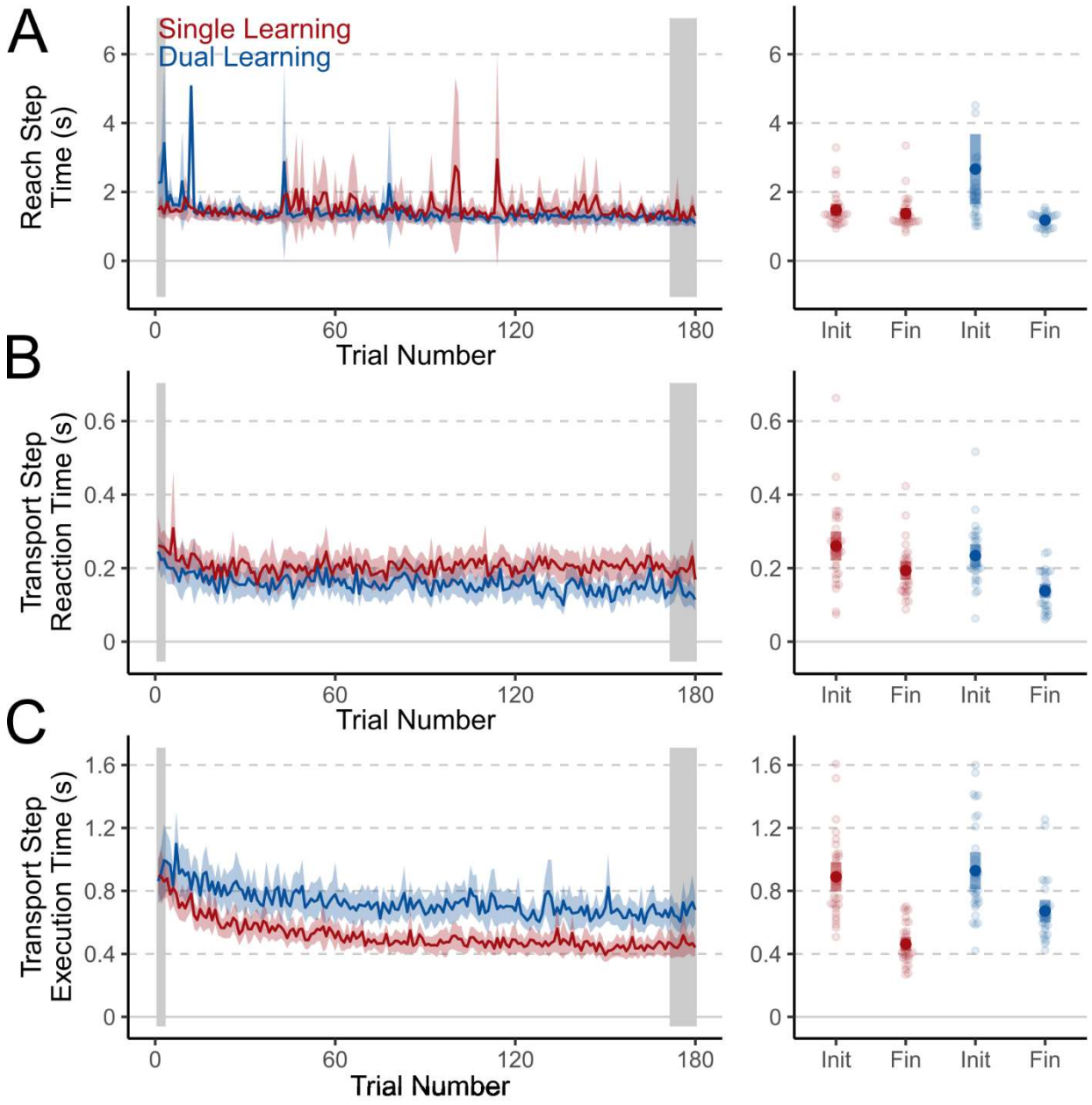

Fig 3.4. Reach and Transport step movement times and reaction times.

Changes in movement initiation and execution times during Object-transport tasks during the Training phase of the Single Learning (red) and Dual Learning (blue) experiments. A. Time required to initiate and execute the Reach Step (Step 1) of the Object-transport task during the Training phase. B. Time to initiate movements during the Transport Step (Step 2) of the Object-transport task during the Training phase. C.

Time required to execute the Transport Step (Step 2) once a movement had been initiated. Shaded areas represent 95% CIs.

Both experiment ($F_{(1, 60)} = 6.45$, $p = 0.014$, $\eta^2 = 0.060$, $BF_{incl} = 2.74$) and trial-set ($F_{(1, 60)} = 38.47$, $p < 0.001$, $\eta^2 = 0.205$, $BF_{incl} = 1.12x10^6$) affected reaction times during the Transport step across the Training phase (Fig 3.4B). Surprisingly, participants in the Dual Learning group were faster to start executing their transport movements by the end of training when compared to both the final trial-set of the Single Learning experiment (Tukey's HSD: $t_{(60)} = -3.52$, $p = 0.005$) and the initial trial-set of the Dual Learning experiment (Tukey's HSD: $t_{(60)} = 5.08$, $p < 0.001$). This may indicate low cognitive strategy use, leading to the small behavioural changes seen in the Rotated Object-transport task analysis.

Finally, the experiments differently affected execution time changes between initial and final trial-sets (Fig 3.4C: $F_{(1, 60)} = 4.95$, $p = 0.030$, $\eta^2 = 0.033$, $BF_{incl} = 7.42$). Despite similar execution times for the Transport step in both groups during the initial trial-set (Tukey's HSD: $t_{(60)} = 0.543$, $p = 0.948$), and participants in the Dual Learning group having to transport objects a shorter distance than those in the Single Learning group, execution times were higher in the Dual Learning group in the final trial-set (Tukey's HSD: $t_{(60)} = 5.154$, $p < 0.001$). This is likely due to additional correction times needed by participants making larger errors in the final trial-set of the Dual Learning experiment.

Discussion

The formation of new motor memories associated with detectable contexts enables quick switching between motor contexts by activating associated motor plans when a specific context is detected. Assigning errors from movements to plausible causes is crucial for associating motor

memories with specific contexts, as these causes serve as contextual cues for future retrieval of motor commands. Properties of movement end effectors, such as human body parts or external objects, that are intrinsic to movement dynamics reliably aid in forming motor memories tied to specific contexts. The role of properties extrinsic to movement dynamics, like visual properties of the object of interaction, is less well understood. Our findings show that visual object-shape cues linked to a visuomotor perturbation are insufficient for creating distinct motor memories when adapting to a single visuomotor rotation, even when the object-shape was relevant to task goals. When the mapping between two distinct object-shapes and two distinct perturbations were repeatedly experienced in a dual-learning paradigm, participants' performance differed between object-shapes, but expressed only partial adaptation.

In the Single Learning experiment, we directly tested if motor control changes to a visuomotor perturbation were linked to an object's shape. Participants adapted to a visuomotor perturbation with a single object-shape, and we assessed if the adaptation persisted when the objectshape or the hand used was changed. In our experiment learning was entirely attributed to the hand and environment, not the object-shape. When using the same hand for differently shaped objects, the adaptation effects transferred fully to the new object. This result suggests that object shape was not a strong enough contextual cue to facilitate assignment of motor error. This is a common finding for cues extrinsic to movement dynamics (Hinder, Tresilian, et al., 2008; Hinder, Woolley, et al., 2008). While some studies show that purely visual properties of a task, such as colour (Osu et al., 2004), or additional movement of a visual end-effector (McGarity-Shipley et al., 2020) can facilitate distinct motor memory formation, our findings indicate that movement-goal relevant object-shape properties alone are likely insufficient.

When using the non-adapted hand to move objects, both familiar and unfamiliar, ~19% of the total adaptation was retained. This component of learning is consistent with previous findings (Kong et

al., 2017), and may reflect learning to perform the task itself or updates to a baseline internal model for performing object-transport movements (Oh & Schweighofer, 2019).

When using the adapted hand, performance during clamped trials in the Single Learning experiment, where participants were not asked to exclude strategies, was similar to performance during late training. Although decay of adaptation is minimized in reaching tasks with clamped feedback, we did not expect complete retention from the rotated-feedback Object-transport tasks (Brennan & Smith, 2015; Kitago et al., 2013; Krakauer et al., 2019; Vaswani et al., 2015). In our experiments, trials with clamped feedback and preceding trials with rotated feedback shared the same target locations requiring similar movement vectors to complete the task. In addition to model-based motor learning, model free mechanisms such as reinforcement learning to favour movement directions towards the learned target directions may have resulted in the apparent high retention and low decay of adaptation in our tasks with clamped feedback (Diedrichsen et al., 2010; Haith & Krakauer, 2013).

Adaptation to errors attributed to objects has been observed in the past (Kong et al., 2017). In a study testing the assignment of credit to errors during Object-transport tasks, Kong et al. (Kong et al., 2017) trained participants to transport familiar objects (cups). The researchers observed a reduction in measured adaptation when participants transported a different object while still using the trained hand. Since transporting cups is a common task, participants likely employed pre-existing internal models for this category of interactions that could be flexibly switched to given changes in object identity. Unlike previous studies, our study's virtual reality environment, and the dynamics of interactions within that environment, was unfamiliar to most participants. Since participants transported objects with both the left and the right hand during the Aligned phase of the experiment, and since posture, perspective, and the used hand can lead to the formation of distinct motor memories and enable dual adaptation (Ayala et al., 2015; Schween et al., 2019a; Verhulst et al., 2022), new hand-specific internal models for object transport may have been created, leading to low transfer across hands. The additional haptic feedback

from transported real-world objects could further facilitate the development of motor memories specific to the movements involved in transporting these objects. Cues intrinsic to movements such as the altered forces or postures required when transporting real-world objects can reliably facilitate object-specific adaptation (Ayala & Henriques, 2020; Ghahramani & Wolpert, 1997; Seidler et al., 2001). In contrast, our virtual task required the same forces to move the hand with and without the objects. Indeed, participants expressed hand-specific adaptation despite participants not experiencing any perturbation during the Reach step of the Transport tasks. The two steps of the Transport task may have been poorly differentiated due to the absence of additional, non-visual cues.

In the Dual Learning experiment, participants could perform the object-transport movements differently when transporting objects with two distinct shapes matched to two distinct perturbations by the end of the Training phase. Using an altered process dissociation procedure, we attempted to qualify if these learning effects were due to the development of explicit strategies or implicit motor memories. We did not find conclusive evidence to suggest either subprocess of adaptation drove the overall learning effects. Studies exploring dual adaptation in conventional upper-limb motor learning tasks suggest a strong contribution of explicit processes (Forano et al., 2021; Schween et al., 2019b). Although patterns of adaptation are similar in immersive virtual environments (Anglin et al., 2017; Ballester et al., 2015; Groen & Werkhoven, 1998; Verhulst et al., 2022), the effects of interactions within a new environments on the subprocesses of motor learning are not yet well explored. Early work suggests that adaptation in immersive environments may rely more heavily on explicit learning (Anglin et al., 2017). Further, when performing reaching tasks in immersive virtual environments, stable viewpoints while parallelly adapting to two perturbations, like in our study, may also lead to more explicit learning (Verhulst et al., 2022). Furthermore, interacting in the virtual environment may have affected the outcome of the Dual Learning experiment due to the “newness” of the environment. Newly created internal models for new environmental contexts likely initially allow for high variability in predicted

movements (Oh & Schweighofer, 2019). In immersive virtual environments where object interactions are unfamiliar to participants, new internal models of object transport may be flexible enough to encompass the variance of visual movements ascribable to opposing visuomotor perturbations. In future work, long-term exposure to virtual environments, or recruitment of participants with immersive-virtual-reality exposure, may mitigate such “newness” effects.

Considering people's ability to switch between different tools and the strong reliance on the visual system in motor adaptation, we predicted that visual shape properties of objects relevant to the performed movement could viably cue activating context-dependent motor memories. However, in this study, we find they are not sufficient for motor memory formation and switching in object-transport tasks. It is possible that in our tasks, the object-shape, although relevant to the task of choosing the target of the reach, was not sufficiently relevant to the lower-level task of transporting an object. That is, despite our task requiring explicit attention to the object-shape to determine the movement goal, it was not relevant to the execution of the movement. Additionally, motor adaptation, and interference from opposing perturbations, can often occur independently of explicit attention [46]. Visual properties of objects that affect the execution of the movement may sufficiently cue motor memory formation and switching. Conversely, it is possible that shape properties are simply not sufficient and different properties of tools, such as visual endpoints or tactile/proprioceptive factors, are needed to create and switch to object-specific motor memories. Overall, our findings suggest that movement-goal relevant object-shape cues may not be sufficient to create new context-dependent internal models for motor control when adapting to a single object-specific perturbation, and may act as weak but viable cues when adapting to multiple object-specific perturbations.

Chapter 4: Motor adaptation to environment changes predicting interactable object behaviour can be flexible and implicit

Abstract

The human motor system can adapt to perturbations by updating existing models of motor control or by creating context-specific motor memories or strategies. We investigate if motor adaptation is context-informed when a perturbation is applied to either the throw direction of a ball, or the acceleration of the ball post-release during a virtual throw-to-target task. Using the visual slant of the task surface in an immersive virtual environment, we determine if the tendency for model updating is influenced by informative visual cues that predict perturbations to intended actions. Our findings reveal that perturbations resembling accelerations enabled flexible motor adaptation regardless of the presence of the slant cue. Perturbations in the throw direction conversely led to internal model updating. Additionally, visual slant properties of the task surface elicited implicit, slant-specific changes in performance. Our findings underscore the role of visual properties of both perturbations and environments in flexible motor learning.

Introduction

The ability to flexibly adapt to changing environments is crucial for successful performance in many real-world motor tasks. Upper limb motor adaptation has been extensively studied in the past by perturbing the hand movement or representations of the hand, leading to errors in predictions of sensory consequences of movements and eliciting an updating of internal models governing actions. Although such motor adaptation paradigms well represent internal changes to the body, such as injury or fatigue, a significant portion of motor learning in daily activities involves the motor system adapting to changes in objects and the surrounding environments. When adapting to these externally localized perturbations, there may be clear visual indicators that predict the behaviour of objects of interaction, such as the movement of grass on a golf course that predicts the strength of a sidewind. In such situations, rather than updating current model for the task, motor adaption may rely on forming context-specific motor memories or cognitive strategies, allowing for effective and rapid task switching when environments change.

Understanding how the brain adapts to real-world perturbations is essential for developing effective interventions and training programs for individuals with motor impairments or those seeking to improve their motor skills. In this study, we tested if adaptation to perturbations that affect the acceleration of a thrown object, suggesting external sources of errors, leads to more flexible motor adaptation than the internal-model updating expected when adapting to visuomotor rotations, which suggest internal sources of error. Although participants adapted to both types of perturbations, those adapting to accelerations in ball paths and even perturbations visually resembling accelerations did not show evidence for model updating. Instead, these perturbations facilitated more flexible motor learning. We additionally tested if immersive visual cues that could plausibly explain errors or aid in strategy-formation could supress model updating. We find informative changes in the visual environment did not

affect model updating characteristics but could cue immediate and implicit changes in task performance during learning and de-adaptation.

In prior work, systematic differences between predicted and actual consequences of planned upper limb movements reliably lead to the updating of internal models of motor control that map goals to actions (Krakauer et al., 1999; Miall & Wolpert, 1996; Shadmehr et al., 2010; Shadmehr & Krakauer, 2008). Updating existing models avoids switching costs associated with motor memory selection and retrieval, allowing for efficient and timely movements (Haith et al., 2015; Leow et al., 2017). Motor errors can be reduced exponentially via one or more learning processes (Baddeley et al., 2003; M. A. Smith et al., 2006; van Beers, 2012; Wei & Körding, 2010). However, this approach is not ideal when motor contexts change rapidly as these models must be re-updated to previously experienced contexts through the same learning processes, and errors must again be decreased exponentially over time. More flexible motor learning, either through the creation of new implicit motor memories or through strategy formation, may improve task-success when movement types, objects of interaction or environments change rapidly (Kunavar et al., 2023). Although behaviour patterns indicating model updating have been observed when adapting to errors predicting a movement or hand-object interactions (Ahmed et al., 2008; Ingram et al., 2010; Kong et al., 2017; McGarity-Shipley et al., 2020), the relative contributions of model-updating or more flexible motor learning when adapting to errors in predicting object-environment remains unclear. In this study, we use a target-directed ball throwing task to test if motor adaptation patterns differ when adapting to perturbations that are likely due to environment interactions, like accelerations added to the movement paths of thrown objects, or hand-object interactions, like rotations of intended throwing directions.

Localizing the source of a given error during a motor task can be crucial for determining if existing internal models should be updated or if an alternative model or strategy should be created.

Perceptual cues the suggest a change in movement type, like changes in hand or body posture, reliably lead to flexible motor adaptation through the formation of new motor memories that can be switched to when returning to previously experienced conditions (Ayala et al., 2015; Ghahramani & Wolpert, 1997; Howard et al., 2013; Seidler et al., 2001). When the movement type remains consistent, findings on the efficacy of interactable object or environment-based cues to facilitate flexible motor adaptation are mixed (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Hegele & Heuer, 2010; Hinder, Woolley, et al., 2008; Osu et al., 2004; Woolley et al., 2007). Generally, properties extrinsic to movements, such as the colour of objects in the environment or object identity do not facilitate the creation of new motor memories (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Howard et al., 2013). In some cases however, visual properties of the environment may serve to explain errors in outcomes under a given predictive model and render model updating less useful (Scarfe & Glennerste, 2014), allowing for flexible motor learning, possibly through the use of explicit strategies (Forano et al., 2021; Hegele & Heuer, 2010; Hinder, Tresilian, et al., 2008; Kong et al., 2017; McGarity-Shipley et al., 2020; Osu et al., 2004). Both saliency and task relevance are crucial for detecting changes in context and may explain these conflicting findings (Spotorno & Faure, 2011; Stirk & Underwood, 2007). Although cues like environment colour are salient, they may not facilitate context-change detection to the same degree as task-relevant cues (Heald et al., 2018; McGarity-Shipley et al., 2020; Stirk & Underwood, 2007). In dual-adaptation paradigms for example, although the colour of the target of reaching movements may fully indicate the presence of a target-colour-specific perturbation, the creation of target-colour-specific motor memories is not likely since the colour of external objects is usually irrelevant to internal models of upper limb movements. It is not clear however, if this holds when visible environmental changes fully predict changes in object-environment interactions. In studies where motor learning intrinsically involves learning the interaction between movement and the environment, properties of the object being interacted with are essential, as learning is often optimized to account for object or environment

properties even when errors are low (Levac et al., 2019; Sternad et al., 2014). Here, we examined whether adaptation patterns differ from those in upper-limb motor adaptation tasks when errors could be explained by object-environment-interactions in an immersive virtual environment. Specifically, we investigate if changes in internal model updating caused by our prescribed internally and externally attributed perturbation types is influenced by visual cues in the environment that reliably predict the behaviour of thrown objects, such as the slope of a surface on which thrown objects travel.

In a series of experiments, participants made realistic throwing movements to hit targets in a virtual task where the thrown object rolled on a flat surface. During the experiments participants adapted to two perturbation types: visuomotor rotations at the moment of release, often internally attributed, and perturbations resembling real-world accelerations, acting on the object after the release. We test if acceleration-like perturbations lead to flexible motor adaptation allowing for fast changes in performance in new or repeated motor contexts. We further test if immersive and informative visual cues, which may prompt faster motor adaptation, can also lead to more flexible motor learning for both internally and externally attributed perturbation types. We find that accelerations, and even perturbations that are visually acceleration-like, can lead to more flexible motor learning than model updating. In all cases, immersive visual changes to the slant of the task surface prompted immediate behaviour change but did not facilitate the creation of new motor memories or strategies required for flexible motor learning. In a subsequent experiment, these visual environment-cued behaviour changes persisted even while participants supressed cognitive strategies during throwing movements. We conclude that behavior changes triggered by informative and task relevant changes in the environment can occur implicitly. This implies that the updated models in these instances include models of ball-environment interactions, rather than models specifically of the arm or release dynamics.

Methods

Participants

169 participants (103 female, 20.75 ± 4.55 years of age, mean ± SD) participated in the study and were divided into one of 8 groups within 4 experiments. All participants had normal or corrected-to-normal vision and were naïve to visuomotor learning experiments. All participants voluntarily participated in the study and provided written and informed consent. The procedures used in this study were approved by York University's Human Participant Review Committee and all experiments were performed in accordance with institutional and international guidelines.

Apparatus/Setup

Participants sat on a height-adjustable chair with a table at waist height. Armrests were adjusted to match the table height and participants rested their elbows on the armrests for comfort between trials. Participants were then verbally instructed on the details of the task. The instructions used can be found at this project's Open Science Framework repository (osf.io/a5nv3/). After receiving the verbal instructions, participants donned a head-mounted display system (HMD: Oculus Rift Consumer Version 1; resolution 1080 by 1200 for each eye; refresh rate 90 Hz) and grasped Oculus Touch controllers in both hands. Three Oculus Constellation sensors tracked the positions of the HMD and Oculus Touch controllers. Participants received all visual feedback via the HMD. The virtual-reality environment was developed in Unity 3D, using the Unity Experiment Framework to handle trial and block schedules during the experiment (Brookes et al., 2020). Before starting the experiments, participants performed practice trials where they were encouraged to explore the tasks involved in the experiment. Participants could repeat the practice trials if required. Once all practice trials were completed, further instructions were provided by the experimenter and participants began the experiment.

Roll-to-Target Task

In all experiments, participants repeatedly performed the Roll-to-Target task. The goal of the task was to roll a ball such that it travelled as close as possible to a target location (Fig 4.1a). Participants received a score from 0-10 for each roll based on the minimum distance between the ball path and the target. Participants also received +5 bonus points for accurately hitting the target.

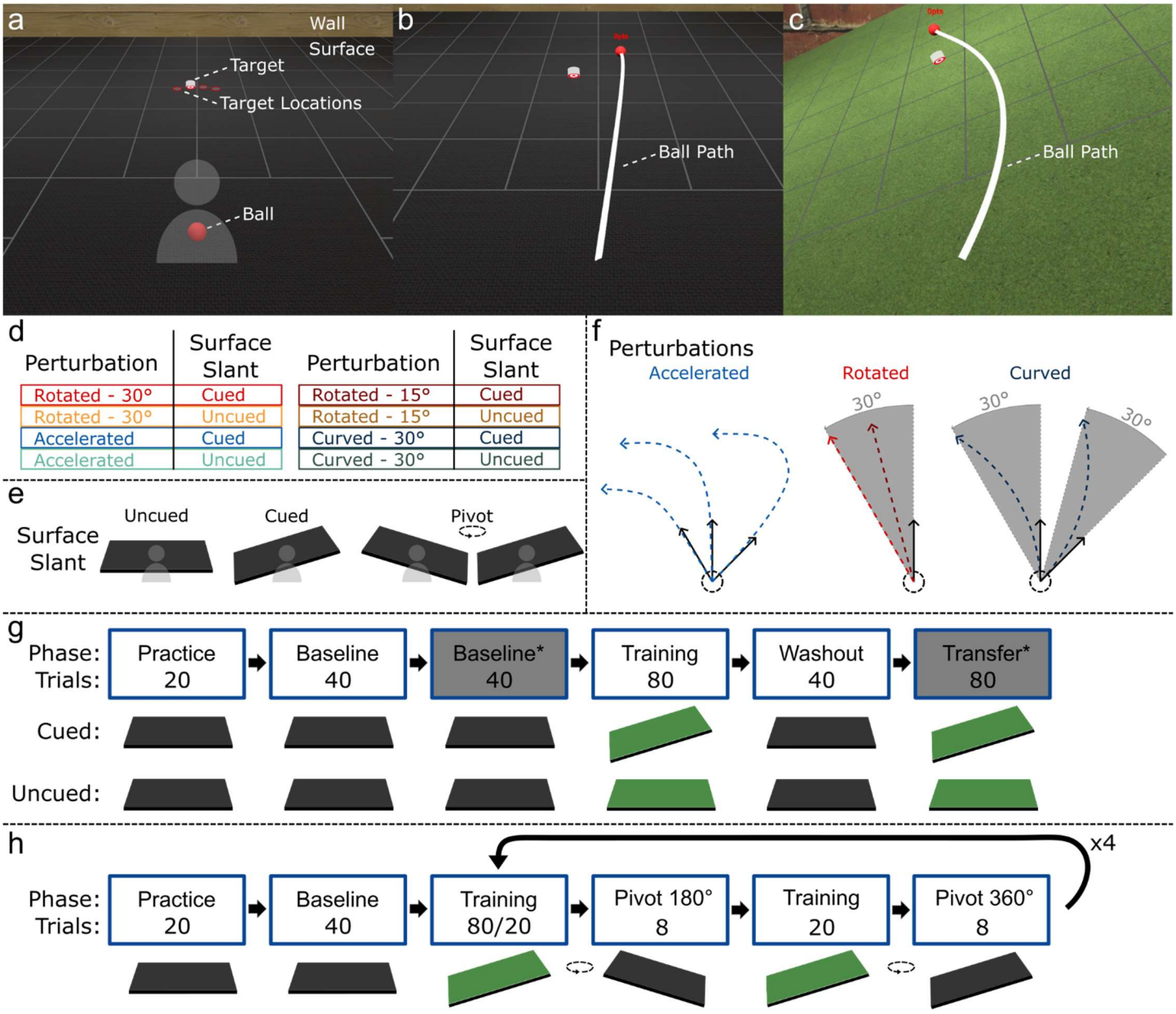

Figure 4.1: Experiment setup, perturbation types and visual cues.
a: Visual display in HMD at the start of each trial in the Roll-to-Target task. The target appeared at one of 4 possible target locations. **b**: Visual display at the end of the Feedback phase of a Roll-To-Target task with the task surface aligned with the real-world floor and Baseline-accelerations. **c**: Visual display at the end of the Feedback phase of a Cued-Curved Roll-to-Target task. **d**: Possible perturbation/cue combinations during the Training and Transfer phases of Experiment 1. **e**: Possible immersive visual slants of the task surface. During Cued Roll-to-Target tasks in Experiment 1, the task surface was slanted 25°**.** In Experiment 2, a 25° visual slant acted as the cue during the Training phase and the animation prior to each Washout phase resulted in a -25° or 25° visual slant for 180° and 360° animations respectively. **f**: Possible perturbations during the Feedback step of Roll-To-Target tasks. **g**: Phases and trials in Experiment 1. Surface Baseline* and Transfer* phases were not analyzed in this study. Participants used their non-dominant hands during Baseline* and Transfer* phases. **h**: Phases and trials in Experiment 2.

Each trial of the task began by participants holding their right hand near the midline of their body below the chin. In the virtual environment, they were situated over a large horizontal plane (4 m x 4 m) located at waist height, termed the Surface (Fig 4.1a). A wall with a horizontal wood plank or brick texture at the far end of the Surface, along with grid-lines along the task surface, provided an accurate visual representation of the orientation of the Surface. A virtual 10-cm diameter ball was placed in front of the participant at the “starting position”. A target was placed 1 meter away from the starting position of the ball in one of 4 possible locations on the Surface (84°, 88°, 92° and 96° in polar coordinates: Fig 4.1a). Target locations were pseudorandomized so that in every 4-trial set, participants threw to each target at least once.

The goal of the Roll-to-Target task was to make a throwing movement to roll a ball and hit targets as accurately as possible. Each trial contained an Action step and a Feedback step. Each trial began with an Action step, where participants made a throwing movement to the target by holding down the trigger button on the Oculus Touch controller with their index finger and making a quick, outward motion with their dominant hand. The ball was released when the hand moved 15 cm from the starting position of the throw, or when the trigger button was released, whichever event occurred first. To ensure consistent rolling motions, participants needed to complete the Action step within 1.5 seconds from the start of the trial to receive a score for the trial. Although participants did not receive a score under this time-out condition, we included these trials in our analysis. The Feedback step began immediately upon the release of the ball.

During the Feedback step, participants observed the ball roll and were given feedback on the ball path. The speed and direction of the throwing movement at the point of release in the Action step determined the speed and travel path of the ball in the Feedback step. The speed of the ball was capped at a maximum of 3.96 m/s. The feedback step ended either after hitting the target or after 2 seconds had elapsed from the start of the Feedback step. At the end of the Feedback step participants were shown a visual representation of the ball path and received a score for the trial based on the minimum distance between the ball path and the target (Fig 4.1b-c).

Task Variations

We used 4 variations of the Roll-To-Target task that modified the relationship between the throwing movement in the Action step and the ball path in the Feedback step: Aligned, Rotated, Accelerated, and Curved (Fig 4.1d). While all participants performed Aligned Roll-To-Target tasks, the Rotated, Accelerated, and Curved variations were considered perturbations and each participant only experienced one of the 3, dependent on their group (see Experiment Protocol).

In Aligned variations of the task, the visual Surface was aligned to the real-world floor-plane. In all other variations, the Surface was either in the same visual alignment as the Aligned variation, or displayed with a 25° CCW visual slant (Fig 4.1c) in groups termed “Uncued” and “Cued” respectively (Fig 4.1d-e).

In Aligned Roll-to-Target tasks, the direction and speed of the throw in the Action step determined the initial heading direction and speed of the ball in the Feedback step. In Aligned tasks, we continuously applied ‘Baseline Accelerations’ to the ball path (-0.31, -0.15, 0.15, 0.31 m/s^2, pseudorandomized). Baseline Accelerations were used so that all Roll-to-Target trials involved changes in the ball’s direction of travel. Baseline accelerations were small, centered around zero and had an unpredictable order to have little to no effect on task performance.

In Accelerated Roll-to-Target tasks, the initial direction of the ball movement during the Feedback step matched the throw direction in the Action step, while a constant leftward acceleration of 2.49 m/s^2 was applied to the ball as it rolled during the Feedback step (Fig 4.1f). The movement path of the ball during this task variation resembled a plausible movement path on a surface with a 25° surface slant. Although all Roll-to-Target tasks included accelerations in the ball path during the Feedback step, only the acceleration in Accelerated tasks could be reliably countered.

In Rotated Roll-to-Target tasks, the speed of the throw in the Action step determined the initial speed of the ball, but the initial heading direction of the ball in the Feedback step was rotated by 30° or 15° counter-clockwise relative to the throw direction along the Surface plane (Fig 4.1f). We applied Baseline Accelerations to all Rotated Roll-to-Target tasks. We used a rotation size of 30° and an acceleration of 2.49 m/s^2 in the experimental groups to match the changes in throw angles required to reliably hit targets with Rotated and Accelerated perturbations. In a follow up experiment, we used a rotation size of 15° to match the error sizes participants observed in the Accelerated perturbations.

In Curved Roll-to-Target tasks, the initial speed and direction of the ball movement during the Feedback step matched the throw speed and direction during the Action step. During this task variation, the path of the ball curled in a counter-clockwise direction so that the ball passed through a point 30° counter-clockwise to the throw direction when at the target distance (Fig 4.1f). The magnitude of the angular offset of the ball path was scaled to the distance from the starting position of the ball. Curved perturbations required the participants to match the throw speeds and throw angles required to reliably hit targets in the 30° Rotated Roll-to-Target tasks.

Experiment Protocol

Experiment 1: Effects of visual cues and perturbation types on context-based flexibility of motor learning.

Participants in Experiment 1 were divided into one of 4 experiment groups: Cued Rotated (n = 20, 11 female, 20.10 ± 2.17 years of age), Uncued Rotated (n = 21, 11 female, 20.05 ± 2.56 years of age), Cued Accelerated (n = 20, 14 female, 20.85 ± 5.89 years of age), or Uncued Accelerated (n = 19, 13 female, 21.05 ± 6.65 years of age); or one of 4 follow-up groups: Cued Rotated-15° (n = 15, 10 female, 19.80 ± 1.08 years of age), Uncued Rotated-15° (n = 14, 7 female, 21.00 ± 4.61 years of age), Cued Curved (n = 20, 12 female, 21.05 ± 4.31 years of age), or Uncued Curved (n = 20, 11 female, 20.35 ± 4.60 years of age) (Fig 4.1d).

After completing practice trials, an experimenter reiterated the task objectives. These instructions were also displayed within the virtual reality environment and participants were encouraged to mentally follow along (instructions found at osf.io/a5nv3/). The experiments were divided into multiple phases (Fig 4.1g). All experiments began with a Baseline phase where participants performed 40 Aligned Roll-to-Target tasks. These tasks were performed in trial-sets of 4 trials within which participants rolled the ball to each of the 4 possible targets and experienced each of the 4 possible Baseline

Accelerations. The order of the target locations and Baseline Accelerations were randomized independently of each other within the trial-sets. The visual task surface was always aligned with the floor plane during the Baseline phase. Participants in the Cued and Uncued Aligned and Rotated groups performed an additional 40-trial Baseline phase using their non-dominant hands. This data was not analyzed for this study but is included in the data repository (osf.io/a5nv3/).

Following the Baseline phase, participants were asked to take a short break for a minimum of 1 minute. The experimenter then read further instructions informing the participants that although the environment may change, their goal was to always hit the target with the ball as accurately as possible. Participants in all groups then completed the Training phase (80 trials) where they performed one of 4 variations of the Roll-to-Target tasks, determined by their assigned group. The visual task surface was slanted by 25° (CCW roll) in all Cued groups and was aligned with the real-world floor plane in all Uncued groups. During the Training phase, the colour of the task surface was changed from black to green in the Cued groups in the four initial experiment groups, while the colour of the surface was changed to green for all groups in the follow-up groups.

To test the decay of learned behaviour when returning to baseline-like conditions, participants completed a Washout phase consisting of 40 trials of the Roll-to-Target task immediately following the Training phase. For all groups, the visual task surface was aligned with the floor plane during the Washout phase.

Participants in the Cued and Uncued Aligned and Rotated groups performed an additional 40-trial Transfer phase with their non-dominant hands. The Transfer phase was identical to the Training phase. This data was not analyzed for this study but is included in the data repository (osf.io/a5nv3/).

Experiment 2: Effects of visual surface-slant cues on implicit motor learning.

In a second experiment (1 group: n=20, 14 female, 22.40 ± 5.88 years of age), we tested whether internal model-updating during motor adaptation relies on visual environmental cues – namely the visual slant of the surface in the Roll-To-Target tasks.

In this experiment we introduced Pivots: animations of the virtual task-surface played between phases of the experiment (Fig 4.1e, right side). Each Pivot lasted 2 seconds and involved a counter-clockwise (CCW) rotation of task surface on the yaw axis, either by 180° or 360°. During the Pivot animations, participants were verbally instructed via a recording played in the head mounted display system to disengage any cognitive strategies they may have used during the Training phase. Pivots were always followed by 8 Aligned Roll-to-Target trials to test the effect of the Pivot on performance (Fig 4.1h).

Participants first completed a Baseline phase, performing 2 sets Aligned Roll-to-Target tasks (16 trials, then 8 trials) separated by a 180° Pivot. Participants then repeated the 2 sets of Aligned Roll-to-Target task, separated by a 360° Pivot.

During the Training phase, participants performed 80 Rotated Roll-to-Target trials with a rotation magnitude of 30°, and the visual task surface was slanted by 25° (CCW roll), as in the Cued groups in Experiment 1. The colour of the task surface was changed to green during the Training phase.

During Test phases, we used 8-trial blocks to test the effect of a 180° or a 360° pivot of the task surface. We repeated the test blocks so that participants performed 4 test blocks following a 180° pivot, and 4 test blocks following a 360° pivot. Participants performed top-up Training blocks (20 trials of the Cued Rotated Roll-to-Target task) in between each set of test blocks (Fig 4.1h).

Data Analysis

For each trial, we calculated the angle of the throwing motion in the Action step relative to a straight-line to the target along the task surface plane (termed "Throw Angle"), the speed of the throw, and the minimum distance to the target along the ball's travel path. The Throw Angle was our primary measure of interest as participants were required to modify it to successfully hit targets in all our perturbed conditions. During Rotated and Curved Roll-to-Target tasks, changes in Throw Angles alone determined task success, while the speed of the throw also impacted task success in Accelerated Roll-to-Target tasks. We also calculated Minimum Errors for each trial: the smallest distance from any point on the ball path during the Feedback step to the centre of the target.

To account for individual differences in baseline throwing characteristics, we calculated the median Throw Angles of each participant when throwing to each of the 4 possible target locations during the Baseline Phase. We subtracted these target-specific baseline Throw Angles from the calculated Throw Angles in the Training and Washout phases. We similarly determined baseline errors for each target by calculating the median magnitude of error experienced during the Feedback step of the Roll-to-Target task. To obtain a measure of additional error due to our imposed perturbations, we subtracted these target-specific errors from the errors experienced during the Training and Washout phase.

To compare across groups, we normalized each participant's Throw Angles relative to their median Throw Angles during the middle of the Training phase (trials 33-40). We then fit exponential decay functions to the change in each participant's normalized Throw Angles during the first 40 trials of the Training and Washout phases.

$$p_{learn} = a - a(1 - r)^{t-1} \quad (1)$$

Equation 1 represents the change in performance over trials (t) in the Training phase (p_{learn}) given a participant's learning (r) and the asymptote of adaptation (a).

$$p_{decay} = s(1 - r)^{t-1} \quad (2)$$

Equation 2 represents the decay in learned behaviour over trials (t) in the Washout phase (p_{decay}) given a participant's start point of decay (s) and decay rate (r). We assumed all participants started at baseline-like performance at the start of the Training Phase and returned to baseline-like performance at the end of the Washout phase. To visualize the reduction in errors over time during the Training phase, we also fit the exponential decay formula (Eq 2) to the changes in Minimum Errors over time in the Training phase.

We analysed the fit parameters for the start points and decay rates during the Washout phase (Eq 2) to determine if adaptation to our imposed perturbations led to the updating of existing models of motor control or the creation of new models. In instances of model-creation, we expected performance to return to baseline conditions quickly once a context change was detected during the Washout phase, signalled by low initial start points or fast decay rates. Alternatively, in instances of model updating, we expected high start points and relatively slower decay of learned behaviour during the Washout phase.

In Experiment 1, we tested whether a visual environmental cue or the perturbation type affected if internal models of motor control were updated. We used a 2x2 between-subject design where each participant experienced one of the 4 possible permutations of Visual Cue (Cued or Uncued) and Perturbation type (Accelerated or Rotated) combinations during the Training phase.

In Experiment 1, we first determined if the presence of the visual cue or perturbation type affected the characteristics of participants' learning curves. We compared learning rates and asymptotes in the Training phase by conducting two 2x2 between-subject Analysis of Variance (ANOVA) tests with the presence of the visual cue and perturbation type as between-subject factors. When effects were found we also calculated and reported an effect size (generalized η^2) and computed and reported

inclusion bayes factors between models that included and did not include relevant effects (Clyde et al., 2011). We used Tukey's HSD for post hoc pairwise analyses when necessary.

To determine if participants could flexibly change motor behaviour when experiencing previously seen contexts, we then compared start points and decay rates during the Washout phase with two additional 2x2 between-subject ANOVAs with the presence of the visual cue and perturbation type as between-subject factors. We again calculated generalized η^2, inclusion bayes factors and Tukey's HSDs when effects were found.

We repeated these 4 2x2 between-subject ANOVAs for Follow-up Experiment 1 and 2. In Follow-up Experiment 1, we compared Cued and Uncued Rotated-15 groups with the original Cued and Uncued Accelerated groups. In Follow-up Experiment 2, we compared the original Cued and Uncued Rotated groups with Cued and Uncued Curved groups.

In Follow-up experiment 1, we conducted additional 2x2 ANOVAs, with visual cue and perturbation type as between subject factors, comparing start points and error reduction rates fit to the reduction in Minimum Error during the Training Phase. We conducted two sets of 2x2 ANOVAs, first comparing the start points and error reduction rates of Minimum Error in the Accelerated groups to those in the Rotated groups, and second comparing the start points and decay rates of Minimum Error in the Accelerated groups to those in the Rotated-15 groups.

In Experiment 2, we tested whether environmental changes affected model updating. To elicit the updating of existing internal models, the Training phase was identical to the Cued Rotated group. We fit exponential decay functions (Eq 2) to the decay of learned behaviour during the 8-trial test phases. To determine if environment changes led to implicit performance changes, we then compared changes in Throw Angles during Test blocks following 180° pivots against those after 360° pivots using two paired t-tests. For all tests, we reported Bayes factors and Cohen's d when effects were found.

Results

Experiment 1: Effects of visual cues and perturbation types on context-based flexibility of motor learning.

We first compared Learning Rates and Asymptotes of Learning during the Training phase for all groups. When adapting to the imposed perturbations during the Training phase, participants in all groups altered their Throw Angles in a clockwise direction (Fig 4.2a-b). The presence of a visual environmental cue led to faster learning ($mean_{learning\ rate(cued)}$ = 0.486, $mean_{learning\ rate(uncued)}$ = 0.210; main effect of cue: $F(1, 76) = 27.06$, $p < 0.001$, $\eta^2 = 0.26$, BFincl = $7.99x10^3$; Tukey HSD < 0.001, d = 1.16; Fig 4.2c-e). Adapting to Accelerated perturbations led to slightly higher asymptotes of adaptation (main effect of perturbation: $F_{(1, 76)} = 4.09$, $p = 0.047$, $\eta^2 = 0.051$, BFincl = 0.996; $mean_{asymptote(accelerated)}$ = 1.10, $mean_{asymptote(rotated)}$ = 1.03. This effect however was weak and did not survive multiplicity correction (Tukey HSD =0.050, d = 0.452; Fig 4.2e: right plot). Although weak, we controlled for this effect in a follow-up experiment using Curved perturbations (see Follow-up experiment 2). Overall, the slant of the task surface acted as an informative visual cue when adapting to both Accelerated and Rotated perturbations, allowing for more rapid motor adaptation.

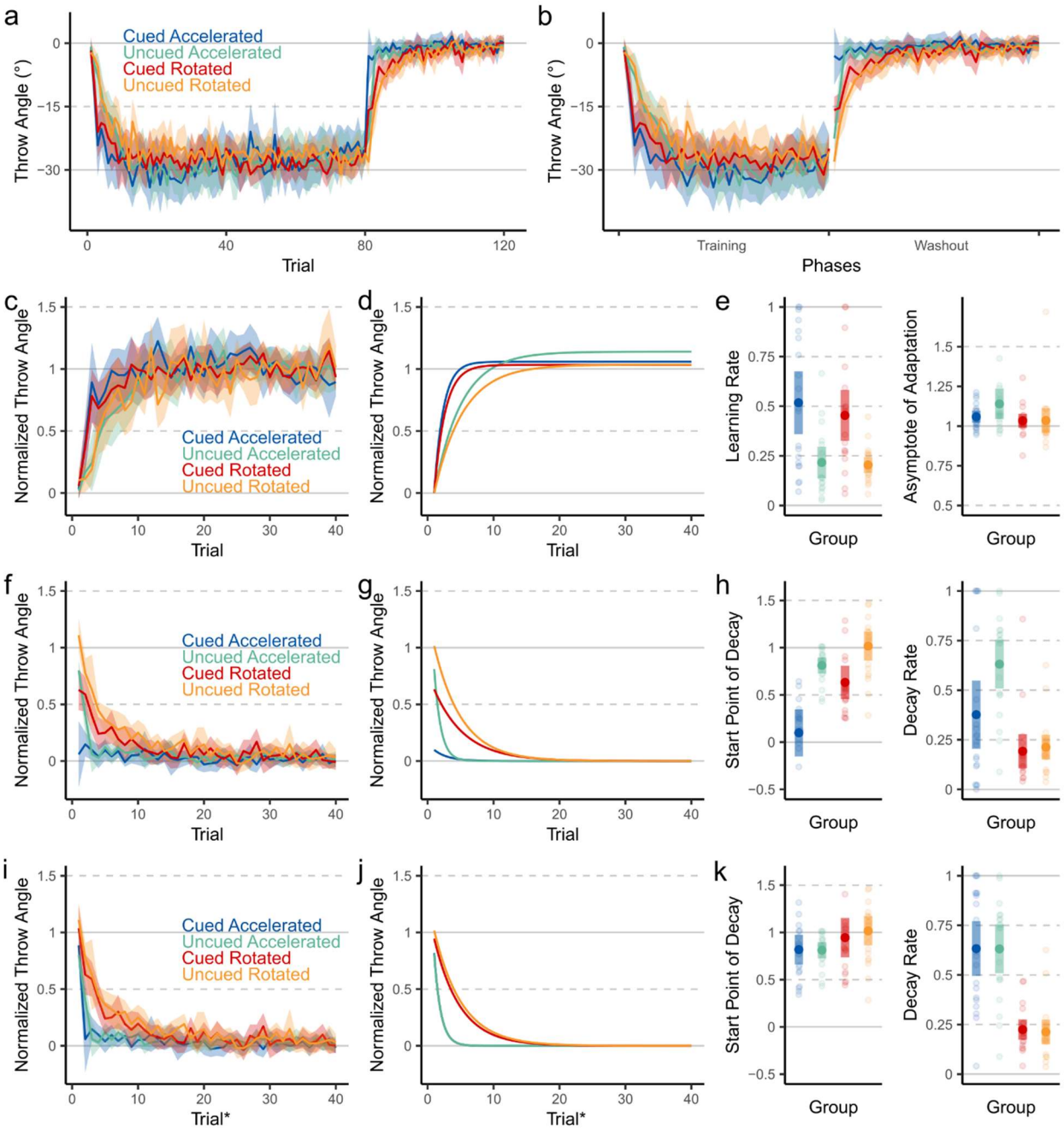

Figure 4.2: Changes in Throw Angles in Accelerated and Rotated groups.

a: Throw angle deviations from straight-to-target throws ("Throw Angle"), relative to individual baseline Throw Angles, over the Training and Washout phases in Experiment 1. **b**: Throw Angles during the first 40 trials of Training and Washout phases. These trials were used for fitting exponential decay models. **c**: Normalized Throw Angles during the first 40 trials of the Training phase. **d**: Exponential decay functions

fit to the changes in Normalized Throw Angles over trials in the Training phase. **e**: Learning rates and asymptotes of adaptation of fit Normalized Throw Angles of participants. **f**: Normalized Throw Angles during the Washout phase. **g**: Exponential decay functions fit to the changes in Normalized Throw Angles over trials in the Washout phase. **h**: Start points of decay and decay rates of Normalized Throw Angles of participants in the Washout phase. **i**: Normalized Throw Angles during the Washout phase including trials prior to cue detection (Trials+) in all Cued groups. **j**: Exponential decay functions fit to the changes in Normalized Throw Angles over Trials+ in the Washout phase **k**: Start points of decay and decay rates of Normalized Throw Angles of participants over Trials+ in the Washout phase. Shaded areas represent 95% confidence intervals.

To test the effects of the visual cues and perturbation types on model updating behaviour, we tested the speed at which participants could return to baseline-like performance levels during a Washout Phase, where all feedback was as in the Baseline Phase. We fit exponential decay functions to the decay of learned behaviour, i.e., the change in Normalized Throw Angles, when returning to unperturbed conditions. The Start Points were affected by both the presence of the visual cue (main effect of cue: $F(1, 76) = 29.87$, $p < 0.001$, $\eta^2 = 0.282$, $BF_{incl} = 2.16x10^4$) and the perturbation type (main effect of perturbation: $F(1, 76) = 9.83$, $p = 0.002$, $\eta^2 = 0.115$, $BF_{incl} = 21.69$; Fig 4.2h: left plot). Uncued perturbations ($mean_{start\ point(cued)} = 0.328$, $mean_{start\ point(uncued)} = 0.936$; Tukey HSD < 0.001, d = -1.22) and Rotated perturbations ($mean_{start\ point(accelerated)} = 0.458$, $mean_{start\ point(rotated)} = 0.807$; Tukey HSD = 0.002, d = -0.702) both led to higher retained deviations in Throw Angles at the start of the Washout phase. The low amounts of retained Throw Angle deviation in the Cued Accelerated group was notably different from all other groups (Tukey HSD < 0.001 when compared pairwise to all other groups) and likely drove a significant interaction between the effects of perturbation type and the presence of the visual cue ($F(1, 76) = 4.35$, $p = 0.040$, $\eta^2 = 0.054$, BFincl = 6.34).

The decay rates of learned behaviour during the Washout phase were also affected by both the presence of the visual cue (main effect of cue: $F(1, 76) = 6.03$, $p = 0.016$, $\eta^2 = 0.074$, $BF_{incl} = 4.18$) and the perturbation type (main effect of perturbation: $F(1, 76) = 29.01$, $p < 0.001$, $\eta_2 = 0.276$, $BF_{incl} = 1.29*10^4$) (Fig 4.2h: right plot). Cued perturbations ($mean_{decay\ rate(cued)} = 0.284$, $mean_{decay\ rate(uncued)} = 0.422$; Tukey HSD = 0.016, d = -0.55) and Rotated perturbations ($mean_{decay\ rate(accelerated)} = 0.504$, $mean_{decay\ rate(rotated)} = 0.203$; Tukey HSD < 0.001, d = 1.21) led to lower decay rates of the learned change in Throw Angles during the Washout phase. Additionally, we found an interaction ($F(1, 76) = 4.39$, $p = 0.040$, $\eta^2 = 0.055$, BFincl = 4.84) that was likely driven by the fast decay rates found in the Uncued Accelerated groups (Tukey HSD < 0.05 when compared pairwise to all other groups).

The surface slant cue affected both the Start Points and Decay Rates during the washout of learned behaviour. To determine if this cue served to initiate a context switch, we reanalyzed washout dynamics when including plausible context-switch detection in all groups. That is, we assumed that for the "Cued" groups, the change in surface slant during the first trial of the Washout phase would be sufficient to cue a context change, whereas, for the "Uncued" groups, the visual errors experienced during the first trial of the Washout condition would be necessary. To better compare the two groups, we included performance during the last trial of the Training phase for the "Cued" groups, ensuring our modelled Washout behaviour included context changes in all groups. We define Trials+ to be the relabelled trial numbers used for plotting and model-fitting. For all subsequent analyses, we used Trials+ to analyse the decay of motor adaptation during the Washout phase. Analyses of the uncorrected decay behaviour can be found in this project's Open Science Framework repository (osf.io/a5nv3/).

When corrected for the detection of context changes, only the perturbation type affected the Start Points of decay functions fit to washout behaviour (main effect: $F_{(1, 76)} = 4.76$, $p = 0.032$, $\eta^2 = 0.059$, $BF_{incl} = 1.34$; Fig 4.2i-k). Accelerated perturbations led to lower Start Points of decay ($mean_{start\ points\ (accelerated)} = 0.815$) than Rotated perturbations ($mean_{start\ points\ (rotated)} = 0.981$, Tukey HSD = 0.0323, d = -

0.488; Fig 4.2k: left plot). Differences in the solution space between the perturbation types may have led to the differences in the Start points of decay. We explore this possibility in Follow-up Experiment 2. Perturbation type alone determined the decay rates of learned deviations of Throw Angle (main effect of perturbation type: $F_{(1, 76)} = 75.59$, $p < .001$, $\eta^2 = 0.499$, $BF_{incl} = 1.49*10^{10}$; Fig 4.2k: right plot). Adaptation to accelerated perturbations decayed more rapidly than adaptation to rotated perturbations ($mean_{decay\ rate\ (accelerated)} = 0.632$, $mean_{decay\ rate\ (rotated)} = 0.219$; Tukey HSD < 0.001, d = 1.95.). The decay of adaptation to accelerated perturbations was fast, taking on average 2 trials to return to baseline-like performance, suggesting motor learning that is flexible when context changes are detected. Following adaptation to rotated perturbations, the lower decay rates suggest existing internal models were updated.

Follow up experiment 1: Rotated 15° perturbations.

For each trial, we defined Minimum Errors as the shortest distance between any point on the ball's travel-path during the Feedback phase and centre of the target. Although we designed our task to match the adaptation rates of Throw Angles during the Training phase for both Accelerated and Rotated groups, participants in the Accelerated groups experienced smaller Minimum Errors during the Training phase (Fig 4.3a-b). When fitting Eq 2 to Minimum Errors experienced in the Training phase, participants in the Accelerated groups experienced lower initial Minimum Errors (main effect of perturbation on starting points: $F(1, 76) = 57.00$, $p < 0.001$, $\eta^2 = 0.429$, $BF_{incl} = 9.52*10^7$; $mean_{initial\ minimum\ error(accelerated)} = 1.67$, $mean_{initial\ minimum\ error(rotated)} = 3.37$; Tukey HSD < 0.001, d = -1.69) and reduced Minimum Error more quickly (main effect of perturbation on learning rate: $F_{(1, 76)} = 7.05$, $p = 0.010$, $\eta^2 = 0.085$, BFincl = 3.75; $mean_{decay\ rate(accelerated)} = 0.244$, $mean_{decay\ rate(rotated)} = 0.125$; Tukey HSD = 0.010, d = 0.594; Fig 4.3b-c). To determine if differences in Minimum Error reduction led to the choice between model updating or flexible motor learning, we conducted a follow-up experiment matching the Minimum Error experienced between the two perturbation types. To do so, we repeated the Cued and Uncued Rotated conditions

with a second pair of Rotated conditions using a 15° rotation to the Throw Angle: the "Rotated-15" groups (Fig 4.1d-e: dark red and dark yellow).

To ensure both the Accelerated groups and the Rotated-15 groups experienced a similar evolution of Minimum Errors over time, we again fit Eq 2 to Minimum Error over the first 20 trials of the Training phase (Fig 4.3d-e). When adapting to 15° rotations, initial Minimum Errors were more likely under models that did not include effects of perturbation type, cue, or interactions between the two (BF_{incl} = 0.258, 0.539, 0.147, respectively; Fig 4.3f: left plot). Similarly, the rates of Minimum Error reduction between the Accelerated groups and the Rotated-15 groups were more likely under models that did not include effects of perturbation type, cue, or interactions between the two (BF_{incl} = 0.190, 0.265, 0.076, respectively; Fig 4.3f: right plot). After confirming that error reduction rates and starting errors were similar across all groups, we repeated the analyses in Experiment 1 using normalized Throw Angles.

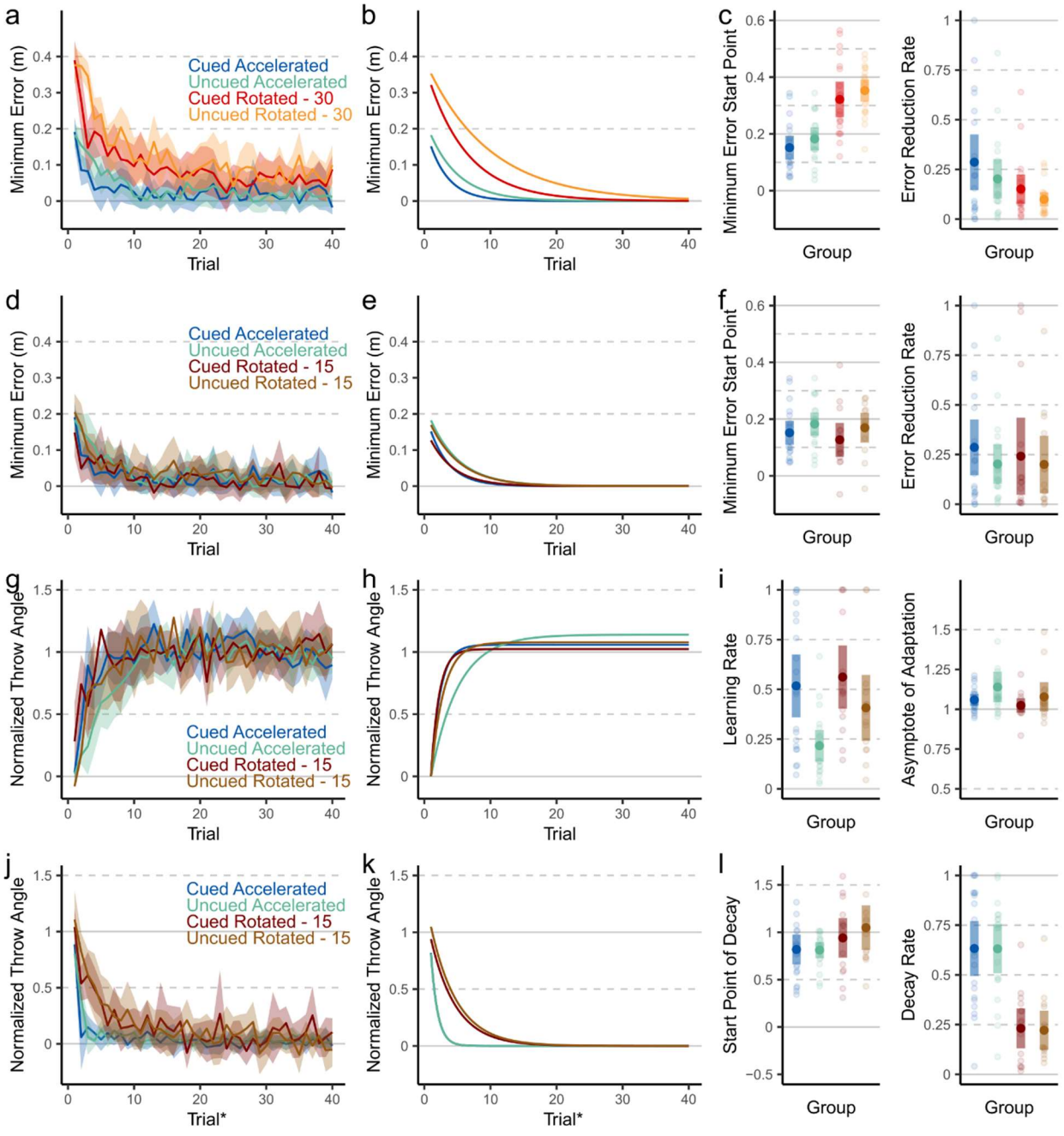

Figure 4.3: Changes in Minimum Error in Accelerated, Rotated-30, and Rotated-15 groups.
Minimum Errors during Training phases and Throw Angles during Training and Washout phases. **a**: Error experienced during the Training phase in Accelerated and Rotated groups. **b**: Exponential decay functions fit to the reduction of error over trials in the Training phase in Accelerated and Rotated groups. **c**: Start points and decay rates of fit Minimum Errors experienced by participants in Accelerated and Rotated

groups. **d**: Error experienced during the Training phase in Accelerated and Rotated-15 groups. **e**: Exponential decay functions fit to the reduction of experienced error over trials in the Training phase in Accelerated and Rotated-15 groups. **f**: Start points and decay rates of fit Minimum Errors experienced by participants in Accelerated and Rotated-15 groups. **g**: Normalized Throw Angles during the Training phase in Accelerated and Rotated-15 groups. **h**: Exponential decay functions fit to the changes in Normalized Throw Angles over trials in the Training phase in Accelerated and Rotated-15 groups. **i**: Learning rates and asymptotes of adaptation of fit Normalized Throw Angles of participants in Accelerated and Rotated-15 groups. **j**: Normalized Throw Angles during Trials+ in the Washout phase in Accelerated and Rotated-15 groups. **k**: Exponential decay functions fit to the changes in Normalized Throw Angles over Trials+ in the Washout phase in Accelerated and Rotated-15 groups. **l**: Start points of decay and decay rates of Normalized Throw Angles of participants during Trials+ in Accelerated and Rotated-15 groups. Shaded areas represent 95% confidence intervals.

During the Training phase, learning rates were affected by the presence of the visual cues (main effect of cue: $F(1, 64) = 11.30$, $p < 0.001$, $\eta^2 = 0.150$, BFincl = 32.84; Fig 4.3h-i). Cued perturbations led to a faster learning rate ($mean_{learning\ rate(cued)} = 0.540$, $mean_{learning\ rate(uncued)} = 0.312$; Tukey HSD = 0.001, d = 0.824; Fig 4.3i: left plot). This was driven by participants in the Uncued Accelerated group learning slower than both the Cued Accelerated and Cued Rotated-15 groups (Fig 4.3i: left plot). We found large individual differences in the learning rates of the Uncued Rotated-15 group, which was not reliably different from any other groups during post-hoc comparisons. The Asymptotes of Adaptation were similar across all groups; the observed asymptotes were more likely under models that did not include an effect of perturbation type, or an interaction effect between perturbation type and the presence of a surface slant cue ($BF_{incl} = 0.474, 0.303$, respectively; the effects of the presence of the surface slant cue were inconclusive ($BF_{incl} = 1.140$); Fig 4.3i: right plot).

We used Trials+ to analyze the decay behaviour of learned Throw Angle deviations during the Washout phase of this follow-up experiment (Fig 4.3j-k), accounting for when participants detected a context change. The Start Points of the decay functions were weakly affected by the perturbation type (main effect: $F_{(1, 64)} = 4.98$, $p = .029$, $\eta^2 = 0.072$, $BF_{incl} = 1.44$; Fig 4.3i: left plot). Accelerated perturbations led to lower Start Points compared to Rotated perturbations ($mean_{start\ points\ (accelerated)} = 0.815$, $mean_{start\ points\ (rotated\text{-}15)} = 0.994$; Tukey HSD = 0.029, d = -0.547). In line with our initial results, only the perturbation type affected the rates of decay (main effect: $F_{(1, 64)} = 47.66$, $p < .001$, $\eta^2 = 0.427$, $BF_{incl} = 3.74*10^6$), with Accelerated perturbations leading to faster decay of adaptation ($mean_{decay\ rate\ (accelerated)} = 0.632$, $mean_{decay\ rate\ (rotated\text{-}15)} = 0.227$; Tukey HSD < 0.001, d = 1.69: Fig 4.3i: right plot). Our primary findings from Experiment 1 remained consistent when adjusting for the sizes of experienced errors during the Training phase. This suggests that the differences in the propensity for model updating was not influenced by the observed differences in error sizes, but the types of the perturbation experienced.

Follow-up experiment 2: Curved perturbations.

When adapting to Accelerated perturbations, participants could hit the target with the thrown ball through specific combinations of Throw Angles and Throw Speeds. Figure 4.4a shows the solution space, the combinations of Throw Angle and Throw Speed used during the Training phase of the experiments and their associated Minimum Error sizes, for each target when adapting to Accelerated perturbations. The solution manifold is the sub-space within the solution space that led to direct target hits, indicated by white-coloured data points. The solution manifolds for Accelerated perturbations were a function of both Throw Angle and Throw Speed (Fig 4.4a), whereas the solution manifolds for Rotated perturbations was a function of only the Throw Angle, with some added noise due to the Baseline Accelerations (Fig 4.4b). Additionally, a larger range of Throw Angles could lead to task success when adapting to Accelerated perturbations (Fig 4.4a). To determine if these solution space differences during the Training phase affected our findings, we conducted a second follow-up experiment where the ball-

path during the Feedback step of the Roll-to-Target task was curved (see Fig 4.1f). The ball path was deviated from a straight-to-target path by an amount proportional to the distance from the starting position, so that when at the target distance, the angular deviation relative to the starting position is always 30°. Curved perturbations resulted in solution manifolds like Rotated perturbations (Fig 4.4b-c) while retaining visual feedback properties of Accelerated perturbations (Fig 4.1f). Once we ensured similar solution manifolds for both perturbation types, we compared changes in Throw Angles in the Curved groups with those in the Rotated groups to determine if our findings from Experiment 1 were driven by the different solution manifolds.

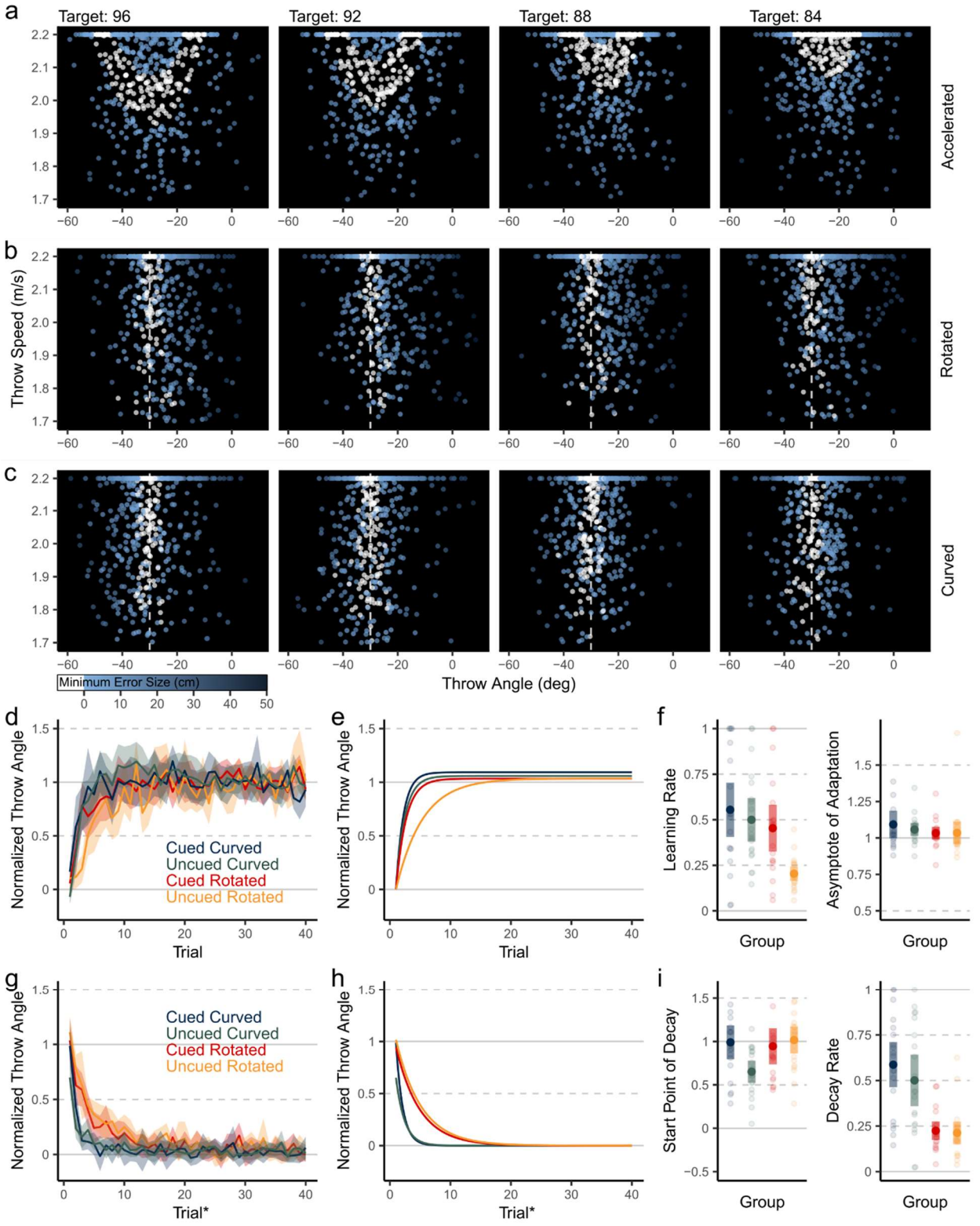

Figure 4.4: Minimum Error Sizes and Throw Angles in Curved and Rotated groups.

Minimum error sizes experienced (where white data points indicate a direct target hit) during throws in the Feedback step during the Training phase in Accelerated (**a**), Rotated (**b**), and Curved (**c**) groups as a function of Throw Angles and throw speeds in the Action step. **d**: Normalized Throw Angles during the Training phase in Curved and Rotated groups. **e**: Exponential decay functions fit to the changes in Normalized Throw Angles over trials in the Training phase in Curved and Rotated groups. **f**: Learning rates and asymptotes of adaptation of fit Normalized Throw Angles of participants in Curved and Rotated groups. **g**: Normalized Throw Angles during Trials+ in the Washout phase in Curved and Rotated groups. **h**: Exponential decay functions fit to the changes in Normalized Throw Angles over Trials+ in the Washout phase in Curved and Rotated groups. **i**: Start points of decay and decay rates of Normalized Throw Angles of participants during Trials+ in Curved and Rotated groups. Shaded areas represent 95% confidence intervals.

During the Training phase, learning rates were affected by both the perturbation type (main effect: $F_{(1, 77)} = 12.88$, $p < .001$, $\eta^2 = 0.143$, $BF_{incl} = 55.74$) and the presence of the visual cue (main effect: $F_{(1, 77)} = 7.60$, $p = .007$, $\eta^2 = 0.090$, $BF_{incl} = 7.61$; Fig 4.4e, f: left plot). Participants in the Uncued Rotated groups learned notably slower than all other groups (Tukey HSD < 0.010, pairwise against all groups), likely driving the observed effects (Fig 4.3f: left plot, orange data). The asymptotes of adaptation were similar across all groups ($BF_{incl} = 0.329, 0.191, 0.090$ for perturbation type, presence of visual cue, and an interaction, respectively; Fig 4.4f: right plot).

We again analysed the decay of learned behaviour with respect to the detection of context changes using Trials+. Participants in the Uncued Curved group had lower Throw Angles prior to the induced decay of adaptation during the Washout phase when compared to those in the Cued Curved group (Tukey HSD = 0.027) and the Uncued Rotated group (Tukey HSD = 0.013), driving an interaction effect between the perturbation type and the presence of a visual cue (interaction: $F_{(1, 77)} = 6.10$, $p =$

.016, $\eta^2 = 0.073$, $BF_{incl} = 2.82$; Fig 4.4i: left plot). Like our findings in Experiment 1 and Follow-up Experiment 1, only the perturbation type affected the decay rates (main effect of perturbation type: $F_{(1, 77)} = 44.94$, $p < .001$, $\eta^2 = 0.369$, $BF_{incl} = 2.63*10^6$; Fig 4.4i: right plot). The performance changes of adaptation to Curved perturbations decayed at a faster rate than those to Rotated perturbations ($mean_{decay\ rate\ (curved)} = 0.544$, $mean_{decay\ rate\ (rotated)} = 0.219$; Tukey HSD < 0.001, d = 1.49.). The visual perturbation type, that is, acceleration-like perturbations, and not the differences in solution spaces during the Training phase in Experiment 1, determined the propensity for internal model updating.

Experiment 2: Effects of visual surface slant cues on implicit motor learning.

Once we understood that Rotated perturbations likely led to model updating, we tested whether information about the environment informed the internal models being updated. In a second experiment, participants adapted again to a 30° rotation perturbation to Throw Angles, cued by a visual slant of the task surface as in the Rotated-Cued group in Experiment 1. Whereas the Washout phase in the Cued-Rotated group was cued by a visually flat surface on which to roll the ball, in this experiment, multiple Test phases were cued by an animation that pivoted the task surface either 180°, leading to a surface slant opposite that in the Training phase, or 360°, leading to the same surface slant as in the Training phase (Fig 4.1h). As expected, since internal models must be reupdated during the Test phases, the pivot angle did not have an effect on decay rates during the Test phases ($t_{(19)} = 09.59$, $p = 0.564$, $BF_{10} = 0.27$; Fig 4.5b: right plot). However, 180° animations led to less negative start points of decay ($mean_{180°} = -10.90$, $mean_{360°} = -19.70$; $t_{(19)} = -4.16$, $p < 0.001$, $d = 1.23$, $BF_{10} = 63.44$) than 360° animations (Fig 4.5b: left plot). Crucially, participants were asked to not use cognitive strategies during the Washout phases in Experiment 2. These findings suggest that the internal models updated when adapting to Rotated perturbations include environment characteristics like the slant of the surface that can lead to flexible motor behaviour.

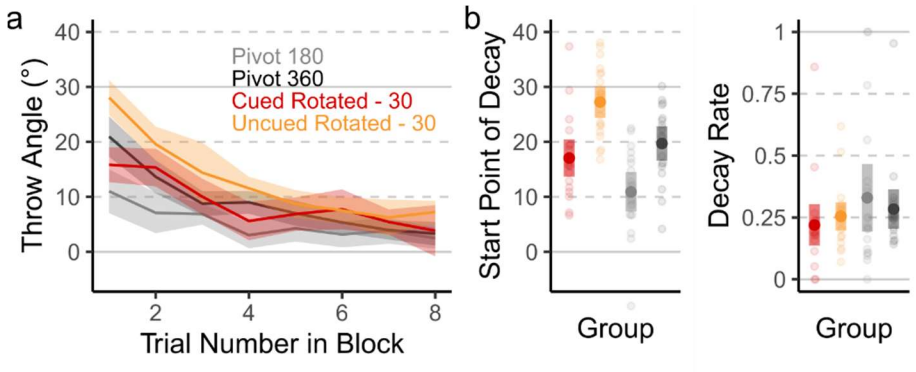

Figure 4.5: Changes in Throw Angles in the Pivot Experiment and Rotated groups.
a: Changes in Throw Angles over 8-trial Test phases in the Pivot Experiment, along with the first 8 trials in the Washout phase of the Cued and Uncued Rotated 30° groups from Experiment 1. **b**. Start points of decay and decay rates during 8-trial Pivot 180 and Pivot 360 Washout phases, along with start points of decay and decay rates during the first 8 trials of the Washout phase of the Cued and Uncued Rotated 30° groups from Experiment 1. Shaded areas represent 95% confidence intervals.

Discussion

In our virtual ball-throwing task, the tendency for model updating during motor adaptation was entirely determined by the type of perturbation experienced. When errors could be plausibly attributed to object-environment interactions, as in real-world-like accelerations of ball paths, motor learning was flexible, and performance could quickly switch between recently learned and previously experienced contexts. When the visual feedback of the hand-ball interactions at the moment of release were misaligned instead, suggesting internal sources of error, we observed evidence for the updating of internal models of motor control. Immersive visual cues about the task environment that reliably predicted motor-context switches enabled faster initial learning and fast switching to existing internal models but did not facilitate the creation of new motor memories. Although changes in the immersive virtual environment during perturbations did not determine if models were updating during motor

learning, properties of the virtual environment, like the surface slant, did inform the implicit internal models involved in executing a target-directed ball-rolling action.

In our study, Accelerated perturbations led to motor adaptation that could be flexibly changed when previously experienced contexts were detected. Accelerated perturbations can plausibly be explained by physical processes acting on the rolling ball, such as the effects of gravity when rolling on a slanted surface or the effects of sidewinds when rolling on a flat surface. Participants may have intuitively simulated physics properties that govern interactions in the environment (Battaglia et al., 2013; K. A. Smith & Vul, 2013) to explain away unpredicted behavior and supress model updating (Scarfe & Glennerste, 2014). Alternatively, recent findings suggest that people fail to accurately estimate accelerations while still compensating for acceleration-based errors over time (Brenner et al., 2016). It would then follow that acceleration-like errors, like the Curved perturbations in our follow up experiment that could not be explained by Newtonian mechanics, should also lead to learning similar to acceleration-based perturbations. That is indeed what we observed. Surprisingly, visual explanations for the acceleration perturbation, that is, the slant of the surface, did not have any additional effects on the tendency for model updating, suggesting visual information did not provide any additional information for the assignment of error to an external source.

Although motor changes during adaptation were matched across Accelerated and Rotated groups, participants in the Rotated groups experienced larger errors during trials in the early Training phase. Larger errors may also lead to slower decay, both due to higher amounts of implicit adaptation, and models being re-updated taking longer to return to baseline. Learning rates should be similar across learning rates when errors are similarly reliable (Baddeley et al., 2003; van Beers, 2012; Wei & Körding, 2010), but large error sizes could lead to large explicit changes in performance (Bond & Taylor, 2015). Findings in our follow-up study using 15° visuomotor rotations suggest the perturbation type, and not experienced error sizes, determined if internal models were updated. Although experienced errors in the

30° Rotated group were large, they may not have been large enough to elicit the use of large strategies that could be suppressed or changed in response to a changes in the external environment (Bond & Taylor, 2015; Modchalingam et al., 2019).

A successful real-world, target-directed throw can be achieved by various combinations of throwing speeds and throwing directions due to redundancies in the task. The solution subspace for our Accelerated tasks, i.e., a manifold along the solution space that led to successful task outcomes, allowed for higher variability in throwing directions than the Rotated conditions. When task solutions allow for redundancy, variability is only reduced to a limited degree (R. G. Cohen & Sternad, 2009; Huber et al., 2016). A wide solution subspace may allow for both increased motor exploration along the throwing angle dimension as well as reduced reinforcement learning to throwing directions specific to the perturbation, allowing for faster return to baseline-like performance (Haith & Krakauer, 2013; Uehara et al., 2019; Zhang et al., 2018). However, since adaptation to Curved perturbations where the solution space was identical to the Rotated perturbations was flexible, our findings suggest that visually observed properties of the perturbation, and not the solution space determine if models are updated.

In our follow-up experiments, although the colour of the task surface changed during the training phase, only the visual change in the task-surface slant reliably cued an immediate change in motor performance. Our findings support previous work suggesting colour changes in the environment are ineffective at eliciting dual learning, where the a creation of multiple context specific motor memories is necessary (Baldeo & Henriques, 2013; Forano et al., 2021; Howard et al., 2013). Generally, properties of the task environment that do not directly affect movement dynamics, termed “indirect cues”, do not reliably lead to the creation of new context-specific motor memories (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Howard et al., 2013). In our study however, both the visual slant and colour of the task surface were indirect cues containing no direct information about dynamic body states during a throwing movement. Our findings from Experiment 1 and Experiment 2 suggest that environment

properties serving as indirect cues that explain the behaviour of interactable objects, as opposed to less task-relevant cues, are effective at prompting the development of both explicit and implicit changes in behaviour.

Although prior works suggest likely strong contributions of explicit learning processes to visual slant-related learning (Forano et al., 2021), in this study, we do not distinguish whether a lack of model updating was due to the creation of cognitive strategies to counter the perturbation, or the creation of new implicit motor memories. Indeed, neither the use of explicit strategies during motor learning nor implicit motor learning processes prevent the parallel development of either class of adaptation (Albert et al., 2022; Bond & Taylor, 2015; Miyamoto et al., 2020; Modchalingam et al., 2019). In Experiment 2, we directly tested for implicit components of surface-slant specific adaptation. When participants were asked to exclude any strategies while throwing to targets on a slanted surface, we observed implicit slant-specific motor learning. Since we relied on verbal instructions, there is a chance that participants did not disengage explicit slant-specific aiming strategies. However, in such cases, we expect throws to the opposite direction when the task surface was pivoted 180°. Instead, all but one participant reduced their trained throwing angles in response to 180° pivots while maintaining the learned deviation direction, suggesting that the observed slant-specific behaviour changes were indeed implicit.

Overall, our results suggest that adaptation to acceleration-like perturbations to the path of a thrown object is flexible and does not rely on updating internal models of motor control. Additionally, informative task relevant environment cues may facilitate immediate and implicit behaviour changes but do not affect the propensity for internal model updating during motor learning.

Chapter 5: General Discussion

This dissertation explores the mechanisms of implicit motor learning processes, defining its boundaries, demonstrating its sensitivity to visual context changes, and evaluating its relevance to learning complex motor skills. Implicit adaptation, the unconscious updating or creation of internal models of motor control, plays a vital role in maintaining accurate and efficient movements in changing environments. By cleanly and reliably measuring implicit motor adaptation processes when learning rich, complex motor tasks, we demonstrate: 1) implicit adaptation boundaries are more flexible than previously established, modulated by how motor errors are introduced during a training paradigm; 2) when adapting to visually-driven errors, the motor system prioritizes updating existing internal models over forming context-specific memories, even with task-relevant object cues; 3) perturbations that are sufficiently explained by environmental changes, or errors that can be reliably attributed to external sources, can trigger context-dependent adaptation. These findings emphasize the adaptability of the motor system and the need for nuanced learning paradigms that account for task-specific goals and complexities.

In recent motor learning work, implicit mechanisms of sensorimotor adaptation were thought to be relatively inflexible; both in the extent of their contribution to overall adaptation to large errors, and in their response to visual stimuli about their environment. Prior research on the limits of implicit adaptation of upper limb movements to visuomotor rotations, including my Masters work (Modchalingam et al., 2019), suggest an upper bound between 15 and 25 degrees (Bond & Taylor, 2015). However, although these limits had been repeatedly observed within a study or motor adaptation paradigm, they were not consistent across works within the field (J. R. Morehead et al., 2015; Neville & Cressman, 2018; Salomonczyk et al., 2011). By cleanly measuring implicit components of uninterrupted sensorimotor adaptation using a process dissociation procedure (PDP), we clarified that these

differences in the limits of implicit adaptation can arise from differences in the methods by which perturbations were introduced to learners.

Despite our reliance on visual information for many tasks, visually distinct environments are often not sufficient for the creation of distinct context-specific motor memories (Baldeo & Henriques, 2013; Gandolfo et al., 1996). Motor contexts with differentiable dynamics of upper limb movements are generally required for context-specific motor learning. Different perturbations mapped to different arm postures or different target positions, for example, reliably lead to implicit behaviour changes between conditions, whereas mappings with visual information of the environment or objects of interaction did not (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Howard et al., 2013). In cases where extrinsic cues led to context-specific learning, it was through explicit mechanisms like the creation of aiming strategies. In this dissertation, along with confirming that visual shape of transported objects and visual environment properties could not lead to implicit context-specific learning, we established that visual environment cues can elicit context-specific learning that could be implicitly cued. Specifically, visual cues that plausibly explain task behaviour under perturbations that traditionally lead to implicit motor learning could implicitly modulate the amount of implicit adaptation. Additionally, we established that visual cues that may assign external sources to observed errors can lead to flexible adaptation, although not necessarily implicitly.

Extent of implicit motor adaptation

The limited contributions of implicit adaptation to overall motor learning are well established. Bond & Taylor (Bond & Taylor, 2015), using aim-subtraction methods to measure implicit adaptation, showed that when the number of target locations were kept consistent, implicit learning tended to remain consistent at around 15° even for perturbations as large as 90° visuomotor rotations. Further work by Kim et al. (Kim et al., 2018), using invariant-error based methods to measure implicit adaptation, confirmed that implicit adaptation to never-diminishing sensory prediction errors also saturated at levels

between 20° and 30°. Previous work by our lab, using the PDP to measure implicit adaptation, also established an extent of implicit visuomotor adaptation limited to about 15°. As the limitations of implicit adaptations are conserved across a variety of paradigms, this measure is likely robust when common task conditions, like the number of targets and the size of visuomotor rotations are within typically used ranges.

Prior work on the limits of implicit adaptation processes suggest that implicit learning can be small when the sensory prediction errors are consistent and small (1.75° to 6°) (Kim et al., 2018), or large when participants adapt repetitive movements to one target location (Bond & Taylor, 2015). However, measures of lasting implicit aftereffects of adaptation after long periods of adaptation suggest that even for small perturbations, implicit learning may saturate at levels similar to those observed when learning larger perturbations (Kim et al., 2018; Modchalingam et al., 2019). Additionally, in a set of experiments done by Neville & Cressman (2018), implicit learning was consistent across perturbation sizes but overall smaller than in previous studies suggesting there are properties of motor tasks that affect the extent of implicit learning. Knowing what causes such drastic changes in the extent of implicit learning can allow us to create better training programs and may inform the development of artificial learning models.

We suggest the schedule of perturbation introduction contributes to the observed discrepancies. Specifically, the extent of implicit learning can be improved above previously established limits by introducing large perturbations in parts, where participants adapt to a small but noticeable partial perturbation-step before being introduced to the next step. In prior work, there is mixed evidence for gradually introduced perturbations leading to improved extents of implicit adaptation processes. For example, Salomonzyk et al. (2011) found that aftereffects of adaptation, a traditional method of measuring implicit learning, scaled with perturbation sizes up to 70°, accounting for ~50% of learned behaviour in all cases. Seminal work for Kagerer et al. also suggested increased implicit learning when perturbations were introduced gradually. In many such studies however, implicit learning was not always

cleanly measured. Crucially, in many past studies, participants were assumed to not use cognitive strategies when performing non-perturbed reaching movements following motor adaptation. In recent work however, it is clear that people can adapt to multiple contexts using explicit strategies (Forano et al., 2021). Additionally, when perturbations were introduced gradually, it was both through a ramped manner where perturbations were introduced to the full amount gradually without allowing for full adaptation to previous steps, or through a stepped manner where full adaptation to intermediate perturbations were allowed. In Chapter 2, we tackled both possibilities by cleanly measuring implicit learning using a process dissociation procedure (PDP) where participants were required to exclude strategies during trials that tested for implicit learning and by directly comparing ramped and stepped introductions of perturbations to abrupt introductions. We established that the previously observed discrepancies were not solely due to discrepancies in measurement of implicit learning, and that stepped introductions of perturbations likely lead to a larger contribution of implicit learning mechanisms than either ramped or gradually introduced perturbations.

Future work should try and determine what about the introduction of errors in a stepped manner cause implicit learning to be higher. In work where limits of implicit learning are not rigid, it was previously suggested that any change in the extent of implicit learning was driven by reducing or increasing explicit processes that occur parallelly. Although this explanation is theoretically sound and we do not argue against the interaction between implicit and explicit learning processes (Albert et al., 2022; Miyamoto et al., 2020), we showed in Chapter 2 that limits of implicit motor adaptations could be different even when initial explicit learning is kept consistent. Therefore, it is worth looking for mechanisms beyond the interplay between implicit and explicit learning to explain our findings. Since we did not delve into the mechanisms that drive our observations, future work should delve into how stepped perturbations might affect implicit learning in other ways, such as how implicit learning evolves

over time, either using invariant error techniques or by measuring implicit learning often during adaptation (Ruttle et al., 2021).

Proprioceptive feedback, specifically changes in the perceived location of the hand during motor learning, may also influence implicit adaptation. Recent work by Tsay et al. (2022) suggests that limits of implicit learning may be driven by limits to proprioceptive realignment of the hand and arm during upper limb motor adaptation. As compared to the extent of implicit adaptation, changes in perceived hand positions as a consequence of learning are even smaller; accounting for a maximum ~5°, and are also inflexible, occurring even when visual information of the real hand is available during visuomotor adaptation tasks (Gastrock et al., 2020; Modchalingam et al., 2019). If shifts in felt hand position drive implicit adaptation (Tsay, Kim, et al., 2022), stepped perturbations could enhance implicit adaptation by amplifying shifts in felt hand position. Indeed, when perturbations were introduced in a combined ramped and stepped manner, Salomonszyk et al. (2011) revealed that proprioceptive recalibration increased relative to visuomotor perturbation sizes up to 70°. Future work should determine if stepped increases in error sizes themselves can lead to increased proprioceptive recalibration, and if this increase in turn drives increased implicit sensorimotor adaptation.

Motor learning and model updating

In Chapter 2 we established that implicit learning could be extended past previously established limits. In Chapters 3 and 4, we explore the mechanisms by which such adaptation occurs. Changes to internal models determining our motor output given movement goals drive persistent changes in motor behaviour. Such changes can occur via model updating, where internal models mapping intended movement goals to motor commands are – often implicitly – recalibrated to counter experienced errors, or through model-free learning mechanisms, such as the development of explicit strategies or through the creation of new context-specific implicit internal models. The implicit updating of internal models is efficient and is useful for reducing the time required to initiate actions but is less flexible in changing

environments. That is, when internal models governing certain movements are updated to experienced perturbations, we should expect these models to reupdate when we return to known movement contexts after adaptation. These updating processes lead to stereotypical learning curves where errors are reduced exponentially over repetitions of the movement. When environments change rapidly, the reliance on repeated movements to update internal models is detrimental, and it is beneficial to use some model-free mechanisms of learning as they allow for greater context-based flexibility. An active area of study is determining what contextual cues lead to model updating and what contextual cues can plausibly lead to more flexible, context-specific learning. Studying this is crucial because when training individuals on motor skills, we might want the skills to transfer to many tasks, like during rehabilitation, or be specific to certain context, such as when simultaneously learning to use multiple tools. By understanding the contextual cues that can push learning one way or the other, we hope to allow for training paradigms that better fit training goals.

In prior work, flexible, model-free learning was often driven by changes in contexts that affect the dynamics of updated movements, such as posture, or the location of targets. Some extrinsic cues however, like the visual interaction-points of manipulated objects, have been established to lead to model free learning (McGarity-Shipley et al., 2020). In Chapter 3, we asked if object-shape properties of transported objects could allow for simultaneous learning of visuomotor perturbations associated with two shapes. We established that object shape properties, even when task relevant are likely not reliable for implicit dual adaptation. Although we found some evidence for dual adaptation, the extent of adaptation was small.

Previous work has established that extrinsic cues can promote model-free motor adaptation via the development of explicit strategies (Forano et al., 2021). In Chapter 3, we found evidence supporting object-shape specific explicit strategy development when perturbations were mapped to differently shaped transported objects. However, the developed strategies were small, and the minimal object-

specific learning fails to explain people's ability to switch between multiple tools reliably and efficiently. Our findings suggest that visual shape properties of manipulated objects may not be sufficient for the development of context-specific motor memories and that visually distinguishable tools should be further differentiated to allow for simultaneous learning.

In prior work, McGarity-Shipley et al. (2020) revealed that different visual behaviours of the interaction-points of held objects may enable simultaneous motor adaptation. Here, the tools dynamically changed orientations while being transported across a virtual workspace, which led to different ends of the tool being the final interaction point in the task. These endpoints, when mapped to different perturbations, allowed for simultaneous adaptation (McGarity-Shipley et al., 2020). In Chapter 3, the base of the transported objects was the interaction point for all motor tasks and by differentiating the object-shapes during different perturbations, the interaction-points were also different. However, we did not find strong evidence for simultaneous adaptation, suggesting interaction-points alone are likely not sufficient for driving simultaneous context-specific motor adaptation. Non-visual properties, like the implied changes to mass and torque dynamics along a movement path as a tool moves, may have played a crucial role in past findings. Held objects, even when visually similar, may have different masses or mass distributions. Prior work suggest that changing masses of objects can lead to mass-specific adaptation, especially when these changes are visually cued such as with the fill level of some liquid in a container (Kong et al., 2017). Work on implied dynamic changes to consistent movements via follow-through movements suggest that implied differences to the dynamics of planned movements can elicit dual adaptation, even when actual dynamics remain the same (Ayala & Henriques, 2020; Sheahan et al., 2016).

In the studies in this dissertation, participants were required to make the same movements across all presented visual contexts. When manipulating multiple objects in real-world tasks however, distinct movement profiles may be associated with different objects, even when the objects are visually

similar. A spoon and fork for example may be held via similar postures and require similar movements to reach their interaction-points to targets but may be differentiated by their associated movement profiles. This is a topic worth studying in future research. Some recent work from our lab has started looking into it.

Aside from predicting the presence of a perturbation by association, in real-world motor tasks, visual cues may allow participants to predict perturbations or required movement corrections. In prior work, visual cues matched to perturbations are often associative; things like background colour, or even shapes of transported objects do not provide any information that can be acted upon prior to movement onset. The direction of blowing grass on a golf course on the other hand, when performing a putting task, may inform the motor system about the changes to movements that need to be made. In Chapter 4, we used the slant of a surface on which participants performed target directed ball rolling tasks as an informative visual environment cue. Prior work on ball-surface interactions suggest the motor system can use assumed physical object-interaction behaviour to better predict the behaviour of manipulated objects (Scarfe & Glennerste, 2014). Although, some prior work suggest that participants may simulate the behaviour of objects in a given environment over time (K. A. Smith et al., 2013), in Chapter 4, we established that such cues lead to faster adaptation even when they do not realistically predict the resulting perturbation. However, even though they lead to faster adaptation, they do not lead to the formation of context specific motor memories.

Real-world perturbations often provide visual cues about the source of errors in the task. For example, the swaying of grass on a golf course may indicate that a strong wind, and not muscle fatigue, led to a missed putt. As mentioned above, model-free learning is most beneficial in rapidly changing environments, notably when these changes in environment necessitate changes in motor commands. It then follows that cues indicating the source of experienced errors are essential for whether internal models are updated. In Chapter 4, we established that externally attributable errors could lead to flexible

motor adaptation. The plausible source of motor errors can provide crucial information on the relevance of the error, which has been established to be useful for motor learning (Wei & Körding, 2009). It has also been established, by measuring remaining learning effects when switching out the adapted end effector, that context-linked motor adaptation does occur when clearly established to be attributed to external objects (Kong et al., 2017). Notably, perturbations applied to the ball path after release in Chapter 4 reliably led to model free learning, suggesting that such perturbations may also lead to the assignment of external sources to experienced errors.

In Chapter 4, we did not differentiate between model-free learning via the development of explicit strategies or via the creation of multiple internal models of motor control. When feedback of motor error is delayed, as might have occurred when perturbations occur after the execution of motor actions in Chapter 4, explicit learning processes tend to dominate (Leow et al., 2017). However, by having participants adapt to visuomotor perturbations well-established to lead to implicit learning and by instructing participants to refrain from using cognitive strategies to change behaviour when environments change, we established that model-based implicit learning could be implicitly modulated by visual environment contexts. As with many recent studies, our findings further highlight the role of the interplay between learning mechanisms in shaping overall behavioral outcomes.

Conclusion

Overall, the work in this dissertation expanded our understanding of the limits of implicit upper-limb motor adaptation, and the effects of visual properties of the environment on implicit learning mechanisms. We clarified discrepancies in past studies and clearly established that increased limits of implicit upper-limb adaptation are driven by a stepped introduction of perturbations and not simply by reducing explicit components of learning. We also determined that decisions of updating existing internal models or creating context-specific motor memories are largely insensitive to visual

environmental changes. Although task-relevant contextual cues may enable changes in conscious, explicit motor behaviour using the cued feature, they do not substantially improve context-specific motor learning. Lastly, we established that visual changes that predict the behaviour changes of objects and assign errors to external sources can lead to context-specific adaptation. We underscore the flexibility of implicit motor learning processes that were previously held to be rigid.

The findings in this dissertation have several implications for the design of rehabilitation tasks, training programs and artificial learning systems. The improvements in implicit learning limits established in Chapter 2 suggest that learning schedules play a crucial role in the outcome of a motor learning program. Our findings suggest that to maximize changes in implicit, non-conscious motor behaviour, it is crucial to consider the methods by which errors are introduced to learners. Our work on the effects of visual context cues on the expression of learned behaviour in Chapters 3 and 4 suggest that visual environments used in training paradigms must strongly assign sources to errors to produce environment-specific motor learning. This research informs the design of error visualizations when learning to use novel tools, both when training with the tool and in everyday tool use, emphasizing considering the ability for visual cues to reliably assign motor errors. Conversely, our findings lend credence to the transferability of learned behaviour from visually distinct training to post-training environments, such as when using virtual reality or simulation-based training programs. Finally, these insights can be applied to the development of artificial learning systems, enabling more efficient adaptation in complex environments by mimicking human error attribution and context-based adaptation mechanisms. Overall, our findings offer insights for improving efficient, unconscious motor control by altering training schedules and visual contextual cues, and we hope our work lays a foundation for further research that can be applied widely to rehabilitation and training design.

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