DE NOVO LEARNING OF MOTOR SKILLS

by

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Abstract

From playing the piano to driving a car, humans acquire a wide range of motor skills throughout their lifetimes. How are people capable of learning such a wide repertoire of skills? Studies in motor learning have attempted to address this question by examining "adaptation", a trial-by-trial learning mechanism where movements are updated via the reduction of sensory prediction errors. However, a growing body of literature suggests that adaptation alone cannot account for how people learn many real-world skills. It has instead been hypothesized that the brain acquires many new skills by building a new motor controller "*de novo*". Currently, little is understood about *de novo* learning as most prior studies of motor learning have focused on investigating adaptation. In this dissertation, we performed a series of experiments to characterize the nature of *de novo* learned controllers. First, we devised a novel frequency-domain system identification approach to characterize how people learn to compensate for visuomotor perturbations. We used this approach to demonstrate that people learn skills which require continuous movement output—such as riding a bike or juggling—via *de novo* learning. We then designed a challenging *de novo* learning task which involved controlling an on-screen cursor using a bimanual mapping. In contrast to many laboratory-based motor learning tasks which can be learned on the timescale of minutes, participants required multiple days of practice to learn the bimanual mapping. In this task, we found that participants' responses to mid-movement perturbations remained limited after four days of practice, suggesting that limitations in one's ability to select appropriate actions may contribute to performance plateaus during learning. Finally, we used the same bimanual mapping to understand how *de novo* learned skills become habitual. We found that participants' behavior could continue to become more skillful despite the fact that it had already become habitual, suggesting that the emergence of skill and habit are dissociable during learning. Collectively, our results illustrate the behavioral phenomenology associated with *de novo* learned controllers and highlight the critical role that *de novo* learning plays when people learn real-world skills.

Thesis advisor: John W. Krakauer

Reader: Adrian M. Haith

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Chapter 1

Introduction

1.1 Non-technical overview

Humans learn many motor tasks throughout their lives. Some are essential life skills, such as the ability to walk or talk. Others we spend decades of our life committed to learning and pursuing as a career, such as performing as a concert violinist or professional basketball player. Still others might be odd skills found in circuses, from juggling on a unicycle to contortionism. These examples highlight the fact that people are capable of learning a wide variety of motor tasks, and the range of tasks that the human race learns only continues to expand with time.

How are we capable of learning virtually any motor task that we can imagine? Movement of any body part requires the contraction and relaxation of muscles. Muscle contraction is in turn controlled by signals (“motor commands”) generated by the motor cortex (Donoghue and Sanes, 1994). To perform any motor task successfully, the motor cortex must be able to appropriately coordinate the motor commands it sends to the muscles. However, when we are faced with performing an unfamiliar task, the cortex may not be immediately capable of such coordination. Thus, the above question can be rephrased as follows: how does the brain learn to generate the requisite motor commands for performing a novel motor task?

Intuitively, we may imagine there are different solutions to this problem. Sometimes, the new task we want to learn may be similar to a task we already know how to perform. For instance, we may want to learn to play the ukulele after having learned the guitar, or we may want to learn to play table tennis after having learned tennis. Here, learning is relatively easy because we are able to take the motor commands we already know how to perform (guitar or tennis) and retune them to perform slightly different motor commands (ukulele or table tennis). This learning mechanism is commonly referred to as “adaptation” (Shadmehr et al., 2010; Krakauer and Mazzoni, 2011). But in other instances, the new task we want to learn may be unlike any other skill in our existing motor repertoire. For instance, knowing how to play the guitar doesn’t do much for us if we want to use a pair of chopsticks or drive a car. In these cases, the brain may need to learn how to generate new patterns of motor commands. This learning process has been dubbed “*de novo* learning” (Telgen et al., 2014; Sternad, 2018).

Despite the fact that many of the skills we learn throughout our lives are likely learned *de novo*, very few studies have rigorously examined this learning process. Instead, many studies of motor learning have focused on examining adaptation tasks. Although adaptation is undoubtedly an important component of real-world motor learning, previous studies have shown that this mechanism alone is insufficient for explaining all motor learning phenomena that humans exhibit (Taylor et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011; Bond and Taylor, 2015). Therefore, a more complete understanding of real-world motor learning will require a closer empirical investigation of *de novo* learning. To this end, I performed a series of studies to characterize people's motor control capabilities as they learned new skills *de novo*. These studies will be described in subsequent chapters. For the rest of this chapter, I will expand on some of the background concepts introduced here in more technical detail.

1.2 Conceptual overview of *de novo* learning

The problem of motor learning can be more formally conceptualized as a process for learning a "controller". At an abstract level, a controller is a function, f, represented within the brain which outputs motor commands, u, based one's current state, x, the current time, t, and one's goal:

$$u = f(x, t, g). \tag{1.1}$$

The parameters of a controller are tuned such that it will produce appropriate motor commands for a specific task. In order to perform different tasks, the brain may possess multiple controllers, each with its own task-specific tuning. However, when learning a new motor task, the brain may not yet possess a controller that can generate appropriate motor commands based on the inputs it is provided. Thus, the brain's goal during motor learning should be to acquire a controller that can do so.

One way the brain might acquire the right controller is by leveraging the motor controllers it already possesses in service of performing a new task (e.g., one's controller for playing the guitar might serve as a useful foundation for acquiring a ukulele controller), an example of which is adaptation. Adaptation is conceptualized as a gradual, parametric change to a movement policy driven by sensory errors (Shadmehr et al., 2010; Krakauer and Mazzoni, 2011). On a mechanistic level, it has been hypothesized that the cerebellum possesses a "forward model" which simulates how the body will move in response to upcoming motor commands and generates a prediction of the movement's sensory consequences based on this simulation. The motor system uses this prediction to judge how close the body is to achieving its movement goal and plan subsequent movements accordingly. Through adaptation, the motor system can learn to generate more accurate predictions, thereby reducing future movement errors. (Though, this particular forward model-based mechanism for adaptation has been disputed; see Hadjiosif et al., 2021).

However, the motor system cannot take advantage of this if one's forward model is not producing accurate predictions. In such cases, the cerebellum can compute the error between the actual and predicted sensory feedback (i.e., sensory prediction error) and use this error to update the forward model, improving predictions about future movements. This is the proposed mechanism underlying adaptation. Within our framework of controllers, adaptation can more simply be conceptualized as changing an adaptation parameter, θ, which is input to the controller:

$$u = f(x, t, g, \theta). \tag{1.2}$$

Adaptation likely serves a critical role in our ability to perform tasks similar to ones which we already know how to perform. However, this mechanism alone cannot explain how people learn all motor behaviors. For instance, adaptation has been commonly invoked as an explanation for how people learn to perform reaching movements while compensating for rotations of their visual feedback ("visuomotor rotation"; Mazzoni and Krakauer, 2006; Shabbott and Sainburg, 2010; Morehead et al., 2015). But previous studies have shown that adaptation can only account for roughly 15–25° of compensation, beyond which other learning processes must contribute (Taylor et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011; Bond and Taylor, 2015). Furthermore, under more drastic perturbations, such as a mirror-reversal of visual feedback, adaptation seems to act in the wrong direction and can worsen performance rather than improve it (Abdelghani et al., 2008; Hadjiosif et al., 2021). This demonstrates that the scope of tasks which can be learned via adaptation is quite limited.

How can one learn a task that that cannot be solved via adaptation? In these situations, it is useful for the brain to generate a new controller from scratch. In other words, instead of continuing to use controller f, the brain will instead construct a new controller g with parameters specifically tuned for the task at hand. Parameter tuning occurs through practice, and once properly tuned, the new controller should allow one to appropriately select and execute movements at low latency. This learning process has been dubbed *de novo* learning (Telgen et al., 2014; Sternad, 2018). As mentioned previously, it is speculated that many of the real-world skills that we learn are acquired *de novo*, given that humans must learn a large diversity of motor tasks throughout our lives. However, very little is understood about this learning process as most prior work in motor learning has centered around adaptation.

Several hypotheses have been posited regarding the mechanism and neural bases underlying *de novo* learning. But due to their highly speculative nature (and because one need not understand them to read the studies contained in this thesis), I will reserve my survey of these hypotheses for the Discussion in Section 6.2. The curious reader can skip ahead to this section if so inclined. For now, it will suffice to say that the mechanistic underpinnings of *de novo* learning are unknown. In fact, it is unclear whether the term "*de novo* learning" should single out a specific learning mechanism in the first place; it is entirely possible that building a new controller from scratch engages multiple learning mechanisms and that *de novo* learning is really an umbrella term which we use to refer to this collection of mechanisms. For the purposes of this thesis, I will define *de novo* learning to mean any learning mechanism that is engaged to build a new controller *aside* from adaptation (and cognitive re-aiming, which I will discuss further in Chapter 3).

At this point, it is worth clarifying the distinction between *de novo* learning and the broader concept of motor skill learning. I will define skill learning to be any process that allows people to acquire new skills (this definition excludes adaptation, which recalibrates existing skills). While *de novo* learning is certainly a large part of skill learning, building and tuning a new controller is not the only way in which one can learn a skill. For instance, if one wants to improve the precision with which they execute a particular movement, the brain may dedicate more neurons to the movement, increasing the movements' signal-to-noise ratio and thereby reduce movement variability. Thus, although *de novo* learning and skill learning may seem like they are synonymous, they should be treated as separate concepts.

The distinction that I draw between adaptation and *de novo* learning is not merely a conceptual one but one that is supported by empirical evidence. In particular, people appear to exhibit different behavioral phenomenology when learning to counter mirror reversals of visual feedback, a putative *de novo* learning task (Telgen et al., 2014), versus rotations of visual feedback or force fields (i.e., adaptation tasks). For one, countering a mirror reversal takes much longer to learn than adaptation tasks (Telgen et al., 2014), aligning with the general notion that learning real-world skills often requires hours, days, or even years of practice (Sternad, 2018; Krakauer et al., 2019). Learning to counter a mirror reversal also does not appear to generalize to online corrective movements (Gritsenko and Kalaska, 2010; Telgen et al., 2014; Kasuga et al., 2015), in contrast to adaptation (Ahmadi-Pajouh et al., 2012; Cluff and Scott, 2013; Telgen et al., 2014).

Moreover, mirror-reversal learning appears to have a dissociable neural basis from adaptation tasks. Studies in patient populations have revealed that people with impairments in cerebellar function have difficulty learning adaptation tasks like countering visuomotor rotations (Rabe et al., 2009; Schlerf et al., 2013) or split-belt treadmill walking (Morton and Bastian, 2006) but are no different from healthy controls in their ability to counter mirror reversals (Schugens et al., 1998). On the other hand, patients with impaired basal ganglia function have difficulty countering mirror reversals (Schugens et al., 1998; Gutierrez-Garralda et al., 2013) but are otherwise fine with adaptation tasks (Gutierrez-Garralda et al., 2013). This suggests that the neural basis for *de novo* learning, at least in part, lies in the basal ganglia.

In summary, these studies show that *de novo* learning is distinct from adaptation and is deserving of separate empirical investigation. Furthermore, I believe that understanding how *de novo* learning occurs will play a major role in our understanding of how people acquire new motor skills in the real world. While I do not claim that I have solved the riddle of *de novo* learning in this thesis, my work has focused on a more specific question: what are the characteristics of the controllers that people learn *de novo*? At any given time point during learning, people employ some controller to generate movements, and this controller is updated through practice. The studies in this thesis do not focus on the question of how these updates occur, but rather on how the updates affect a controller's ability to generate movements.

As with all studies in experimental psychology, an effective investigation of *de novo* learning requires the use of an appropriate learning task. In the past, several different types of tasks have been used to study *de novo* learning. One type of task involves learning to execute movement patterns that one has never executed before. These tasks often involve learning some arbitrary mapping between the body and an on-screen cursor, using equipment such as body-machine interfaces (Wang et al., 2014) or the "cyberglove" (Mosier et al., 2005; Ranganathan et al., 2014). Similar to tasks like figure skating and gymnastics, here, the act of performing the required movements is difficult in and of itself, and learning thus entails practicing these difficult movements. Another type of task involves learning to use information from new sensory modalities for control (Bach-y-Rita and Kercel, 2003; van Vugt and Ostry, 2018), such as learning to make arm movements towards auditory targets. This is not unlike playing the cello where one must learn how to adjust their fingers' positions based on auditory feedback of the notes they create.

Although one could imagine other kinds of *de novo* learning tasks, my thesis work has been primarily focused on a third kind of task, that of selecting movements one already knows how to execute. For instance, driving a car or playing video games are both tasks which require years of practice for people to master. However, the reason these tasks are difficult to master is not because the requisite movements are difficult to execute; an inexperienced driver can just as skillfully turn a steering wheel as an experienced driver. Instead, the difficulty lies in selecting which actions to perform in a given context (i.e., learning a controller which can appropriately generate motor commands). There are two main benefits to examining these kinds of *de novo* learning tasks in the laboratory. From a scientific standpoint, learning to select appropriate actions is a fundamental component of real-world skill learning. And from a practical standpoint, these tasks isolate the learning problem to action selection, whereas other types of tasks confound learning action selection with other types of learning (e.g., learning action selection and action execution are confounded when learning to control an on-screen cursor with a body-machine interface). Each of the studies presented in this dissertation will examine learning in a *de novo* learning task that primarily challenges action selection.

1.3 Chapter preview

In Chapter 3, I will present a study that examines how people learn continuous skills like riding a bike or juggling. Skills like these require people to respond quickly and continuously to the state of the environment; when riding a bike, if one does not quickly rotate the handlebars when their bike is tilting, they will topple off the bike. Currently, little is understood about how people learn continuous skills. Previous work has shown that the scope of tasks which can be learned via adaptation is quite limited, and other more cognitive learning processes—such as strategic re-aiming—require too much time to deploy when performing tasks under time pressure. As such, we hypothesized that people may learn these skills *de novo*.

To investigate this question, we examined how people learn to compensate for a rotation (a canonical adaptation task) or a mirror reversal (a proposed *de novo* learning task) of visual feedback while tracking a target moving in a sum-of-sinusoids trajectory. The quick, pseudorandom motion of the target prevented people from compensating for each visuomotor perturbation using a series of re-aimed movements; any movement planned at a given moment could become outdated within a few hundred milliseconds. This allowed us to examine the properties of adapted versus *de novo* learned controllers while limiting the confounding effects of re-aiming strategies.

The sinusoidal nature of the task also enabled us to analyze participants' behavior using a frequency-domain system identification approach. This approach characterizes the control capabilities of a linear (or close to linear) system in terms of "transfer functions", complex-valued functions which describe a system's input-output relationship at different frequencies. Although this specific approach has been previously used to investigate well-learned motor behaviors such as insect flight (Fuller et al., 2014; Sponberg et al., 2015; Roth et al., 2016), electric fish refuge tracking (Cowan and Fortune, 2007; Madhav et al., 2013), human posture (Oie et al., 2002; Kiemel et al., 2006), and human manual tracking (Yamagami et al., 2019; Yamagami et al., 2020; Zimmet et al., 2020), to our knowledge, it has not been used to characterize the properties of controllers during learning. The studies presented in Chapters 3 and 5 showcase how system identification can be used to understand people's behavior in continuous movement tasks.

Although we used mirror reversal to examine the properties of *de novo* controllers in Chapter 3, participants could learn this task within one day of practice. In contrast, many of the real-world skills that people learn *de novo* require months or years of practice. To push our studies towards tasks requiring longer timescales of learning, in Chapter 4, we introduced a *de novo* learning task which, similar to mirror reversal, challenges action selection but requires multiple days of practice to learn. In this study, participants controlled a cursor using a novel bimanual mapping where vertical movements of the left hand controlled the cursor's horizontal movements while horizontal movements of the right hand controlled the cursor's vertical movements. We used this task to investigate whether limitations in people's ability to select appropriate actions may explain why *de novo* learning a new skill is often so slow.

Finally in Chapter 5, I will present a study where we investigated how people form habits while learning to use this bimanual mapping. Whether one is playing basketball, typing on a keyboard, or driving a car, the effect that habits (and particularly bad habits) have on motor behavior is clear to everyone, and as such, habits have been widely discussed in the neuroscience and psychology literature. However, our empirical understanding of how habits form when people learn real-world motor skills is quite limited: studies of habits in animal models (e.g., reward devaluation) have shown little relation to the kinds of habits that humans demonstrate, and studies of habits in humans have typically used very simple tasks (e.g., arbitrary visuomotor associations) with questionable generalizability to more complex tasks. Instead, the bimanual mapping offered us an opportunity to examine habit formation in a task more similar to the complex skills that people learn in the real world. In this study, separate groups of participants learned to control the bimanual mapping over two, five, or ten days of practice. Following this practice period, we flipped the left hand's mapping to cursor movement and tested whether participants would habitually continue to control the cursor under the original bimanual mapping or would successfully use the new flipped mapping.

Briefly, I would like to acknowledge that much of the content of this chapter as well as Chapter 3 was adapted from Yang et al., 2021 and Chapter 4 was adapted from Haith et al., 2021. Chapter 5 is adapted from a manuscript that is currently under preparation. The present chapter was also adapted from the three papers listed here. I would also like to acknowledge that in Haith et al., 2021, while I was not the paper's primary author, my main contributions were to collect data/perform analysis for that study's final experiment, aid in the interpretation of data which I did not collect, and edit/finalize the manuscript.

Chapter 2

General Methods

Below, I will describe methods that were applicable to more than one study in this dissertation.

2.1 Participants

Participants between the ages of 18-40 with no prior history of neurological disorders were recruited. Informed consent was obtained all participants. All methods were approved by the Johns Hopkins School of Medicine Institutional Review Board and were carried out in accordance with relevant guidelines and regulations.

2.2 Experimental Setup

Participants were seated in front of a table with both of their hands supported on the table by frictionless air sleds (Figure 2.1A). The position of their hands were monitored at 130 Hz using a Flock of Birds magnetic tracker (Ascension Technology, VT, USA) placed near each hand's index finger. Participants

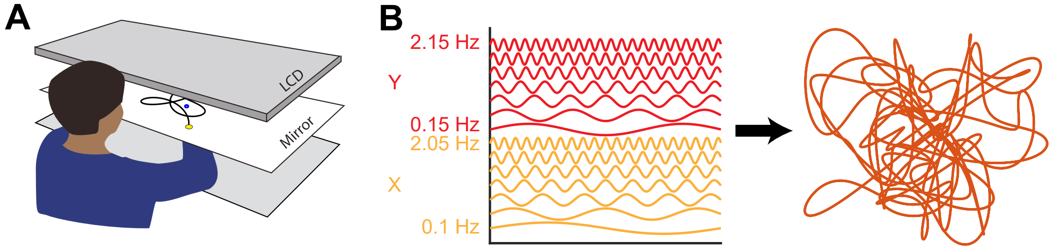

Figure 2.1: **A.** Participants performed planar movements with one or both hands while a target and cursor (blue) were presented to them on an LCD display. Participants were asked to either move the cursor to a static target (point-to-point task) or track a moving target with the cursor (tracking task). **B.** The target in the tracking task followed a sum-of-sinusoids trajectory, which was generated by combining single sinusoids of different frequencies (left) across two dimensions to generate the final trajectory (right). The target moved at different frequencies in the x- and y-axes.

viewed stimuli on a horizontal mirror which reflected an LCD monitor (60 Hz), and the mirror obscured vision of both hands.

2.3 Tasks

Participants in all studies performed a point-to-point reaching task where they moved a cursor (circle of 2.5 mm radius) towards stationary targets (circle of 10 mm radius). Participants initiated each block holding their cursor stationary in a target placed in the center of the screen. Each subsequent target would then appear 12 cm away from the location of the previous target in a random direction, subject to the constraint that the target lie within a 20 × 20 cm workspace. Participants were instructed to move as quickly and accurately as possible and to hold their cursor within the target to proceed to the next trial. We encouraged participants to move quickly to each target by providing feedback of their cursor's peak velocity in each trial. If participants reached too slowly (<0.3 m/s in Chapter 4 or <0.4 m/s in Chapters 3 and 5), then visual feedback was provided instructing them to move faster. We also encouraged participants to not move too quickly for the study in Chapter 4 (>0.4 m/s), providing them visual feedback to move slower if they exceeded this threshold. Positive feedback (a pleasant tone and the target turning yellow) was provided if participants moved with the appropriate peak velocity.

In the studies described in Chapters 3 and 5, participants also performed a tracking task. Here, participants were instructed to use their cursor to track a target moving in a two-dimensional, sum-of-sinusoids trajectory (Figure 2.1B). Specifically, the target's position along a single axis, r, was computed as:

$$r = \sum_{i=1}^{7} a_i \cos(2\pi t \omega_i + \phi_i). \tag{2.1}$$

where $\vec{a}$, $\vec{\omega}$, and $\vec{\phi}$ are vectors containing the amplitudes, frequencies, and phases of the sinusoids. For Chapter 3, in the x-axis, $\vec{a} = \{2.31, 2.31, 2.31, 1.76, 1.30, 0.97, 0.73\}$ (cm) and $\vec{\omega} = \{0.1, 0.25, 0.55, 0.85, 1.15, 1.55, 2.05\}$ (Hz). In the y-axis, $\vec{a} = \{2.31, 2.31, 2.31, 1.58, 1.03, 0.81, 0.70\}$ (cm) and $\vec{\omega} = \{0.15, 0.35, 0.65, 0.95, 1.45, 1.85, 2.15\}$ (Hz). For Chapter 5, we only used the first six values of each vector to design the target's trajectory. The phases of the sinusoids were randomized for each study.

2.4 Software

Data analyses were performed in MATLAB R2018b (The Mathworks, Natick, MA, USA) and R version 4.0.2 (R Core Team, 2020; RStudio, Inc., Boston, MA, USA) using the nlme (Pinheiro et al., 2016), lsmeans (Lenth, 2016), Matrix

(Bates and Maechler, 2019), lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), and emmeans (Lenth, 2020) packages. Figures were created using Adobe Illustrator (Adobe Inc., San Jose, CA, USA).

Chapter 3

De novo learning versus adaptation of continuous control

The following chapter is adapted from Yang et al., 2021, an article distributed under the terms of a Creative Commons Attribution License that permits unrestricted use and redistribution provided that the original author and source are credited.

3.1 Introduction

In many real-world motor tasks, skilled performance requires us to continuously control our actions in response to ongoing external events. For example, remaining stable on a bicycle depends on being able to rapidly respond to the tilt of the bicycle as well as obstacles in our path. The demand for continuous control in such tasks can make it challenging to initially learn them. In particular, new skills often require us to learn arbitrary relationships between our actions and their outcomes (like moving our arms to steer or flexing our fingers to brake). Learning such mappings is thought to depend on the use of time-consuming cognitive strategies (McDougle et al., 2016), but continuous control tasks require us to produce responses rapidly, leaving little time for deliberation about our actions. Exactly how we are able to learn new, continuous motor skills therefore remains unclear.

Previous studies have revealed that a variety of different learning processes are involved when people acquire new motor skills (Krakauer et al., 2019), two such processes being adaptation (recalibrating existing controllers) and *de novo* learning (generating new controllers from scratch). Can either of these processes explain how we learn continuous skills? Although adaptation may certainly contribute to learning, as discussed in Chapter 1, the scope of tasks which can be learned via adaptation is rather limited (Taylor et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011; Bond and Taylor, 2015). In contrast, *de novo* learning is more flexible, allowing one to learn any arbitrary mapping between sensory input to motor output. Thus, *de novo* learning likely plays a more major role in learning continuous skills.

However, people may also utilize a third learning process when learning to compensate for perturbations in sensory feedback: re-aiming strategies (Mazzoni and Krakauer, 2006; Taylor et al., 2014; Morehead et al., 2015; Schween et al., 2020; Rugy et al., 2012). This involves aiming oneâĂŹs movements towards a surrogate target rather than the true target of the movement. In contrast to adaptation—where an existing controller is itself altered to meet changing task demands—re-aiming entails feeding an existing controller a fictitious movement goal in order to successfully counter the perturbation without needing to alter the controller itself. Previous studies have shown that people use re-aiming strategies to compensate for many types of perturbations including visuomotor rotations (Mazzoni and Krakauer, 2006; Taylor et al., 2014; Morehead et al., 2015), imposed force fields (Schween et al., 2020), and perturbations to muscular function (Rugy et al., 2012). Even perturbations like mirror reversals—which have been suggested to be learned *de novo* (Telgen et al., 2014)—have also been suggested to be learned using a re-aiming strategy (Wilterson and Taylor, 2021). Given the omnipresence of re-aiming strategies (and more general cognitive strategies) during learning, it remains unclear whether people ever compensate for visuomotor perturbations by building a *de novo* controller

How might one dissociate re-aiming from building a new controller? A key property of re-aiming is that it is cognitively demanding and time-consuming to implement (Fernández-Ruiz et al., 2011; Haith et al., 2015; Leow et al., 2017). This leads to increased reaction times (Fernández-Ruiz et al., 2011), and performance worsens if reaction times are forced to be shorter (Fernández-Ruiz et al., 2011; Haith et al., 2015; Huberdeau et al., 2019; McDougle and Taylor, 2019). While this may not significantly hamper performance in tasks where movement goals are stationary (e.g., point-to-point reaching), in continuous control tasks where one's movement goal is constantly and unpredictably changing, movements to the goal cannot be completely planned in advance. Thus, continuous control tasks may severely limit one's ability to use re-aiming strategies and may not be solvable by the same means as point-to-point tasks. Although several studies have examined learning in continuous control tasks (Schugens et al., 1998; Bock and Schneider, 2001; Bock et al., 2001), these

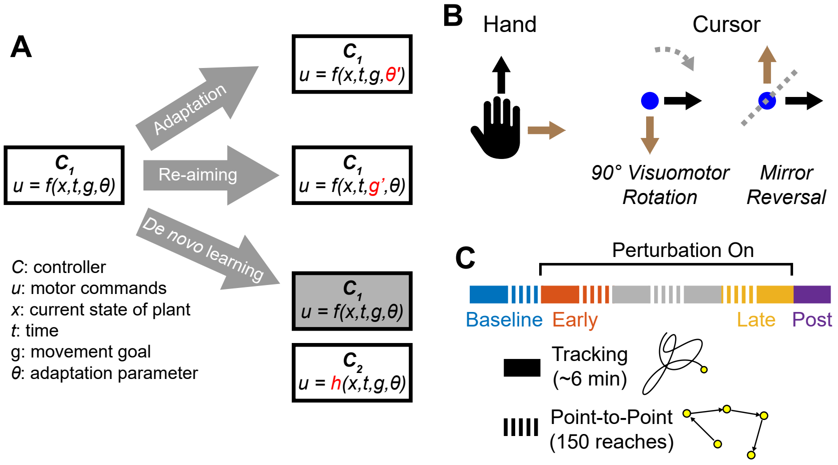

Figure 3.1: Conceptual overview and experimental design. **A.** We conceptualize adaptation as a parametric change to an existing controller (changing θ to θ'), re-aiming as feeding surrogate movement goals to an existing controller (changing g to g', and *de novo* learning as building a new controller (h) to replace the baseline controller (f). **B.** Twenty participants learned to control the cursor under one of two visuomotor perturbations: a 90° clockwise visuomotor rotation ($n = 10$), or a mirror reversal ($n = 10$. **C.** Participants alternated between point-to-point reaching (1 block = 150 reaches) and tracking (1 block = 8 trials lasting 46 seconds each) in a single testing session in one day. We first measured baseline performance in both tasks under veridical visual feedback (blue), followed by interleaved tracking and point-to-point blocks with perturbed visual feedback from early learning (orange) to late learning (yellow). Blocks between early and late learning are indicated in grey. At the end of the experiment, we assessed aftereffects in the tracking task by removing the perturbation (purple).

studies used relatively slow-moving targets (<0.35 Hz movement) which could potentially be tracked using intermittent "catch-up" movements that are strategically planned similar to explicit re-aiming of point-to-point movements (Craik, 1947; Miall et al., 1993a; Russell and Sternad, 2001; Susilaradeya et al., 2019). To more strictly limit peoples' ability to rely on re-aiming, it is necessary to consider tasks in which movement goals change more quickly than the time it takes for slow cognitive strategies to be applied.

In the present study, participants learned to counter a mirror-reversal of visual feedback in both a point-to-point movement task and a continuous tracking task in which a target moved in a pseudorandom sum-of-sinusoids trajectory (Figure 3.1B). In the tracking task, the target moved at frequencies up to 2 Hz, much faster than in previous tracking experiments, resulting in a target trajectory that was quick, unpredictable, and unlikely to be trackable while using a re-aiming strategy. In order to achieve good tracking performance, participants instead had to continuously generate movements to track the target. Critically, the sum-of-sines structure of the target motion allowed us to employ a frequency-based system identification approach (Miall et al., 1993b; Kiemel et al., 2006; Roth et al., 2011; Madhav et al., 2013; Sponberg et al., 2015; Yamagami et al., 2019) to characterize changes in participants' motor controllers during mirror-reversal learning. We compared learning in this group to that of a second group of participants that learned to counter a visuomotor rotation, where—presumably unlike mirror reversal—adaptation would contribute to learning.

We hypothesized that if participants learned to counter the mirror reversal via *de novo* learning, then they would be able to successfully track the target despite its rapid and unpredictable nature. If, however, the mirror reversal can only be learned through a re-aiming strategy, then we predicted that participants would have difficulty tracking the target and may have to generate intermittent catch-up movements to pursue the target. We further hypothesized that, under the rotation, participants would parametrically alter their baseline controller and would therefore be able to smoothly track the target.

3.2 Results

3.2.1 Participants learned to compensate for the rotation and mirror reversal but using different learning mechanisms

Twenty participants used their right hand to manipulate an on-screen cursor under either a 90° clockwise visuomotor rotation ($n = 10$) or a mirror reversal ($n = 10$) about an oblique 45° axis (Figure 3.1B). These perturbations were chosen such that, in both cases, motion of the hand in the x-axis was mapped to motion of the cursor in the y-axis and vice versa. Each group practiced using their respective perturbations by performing a *point-to-point task*, reaching towards stationary targets that appeared at random locations on the screen in blocks of 150 trials (Figure 3.1C). Each participant completed the experiment in a single session in one day. We assessed both groups' performance in this task by measuring the error between the initial direction of cursor movement and the direction of the target. For the rotation group, this error decreased as a function of training time and plateaued near 0° demonstrating that participants successfully learned to compensate for the rotation (Figure 3.2A, upper panel). For the mirror-reversal group, the directional error did not show any clear learning curve (Figure 3.2A, lower panel), but performance was better than would be expected if participants had not attempted to compensate at all (which would manifest as reach errors uniformly distributed between $\pm$ 180°). Thus, both groups of participants at least partially compensated for their perturbations in the point-to-point task, consistent with previous findings.

To test whether participants could compensate for these perturbations in a

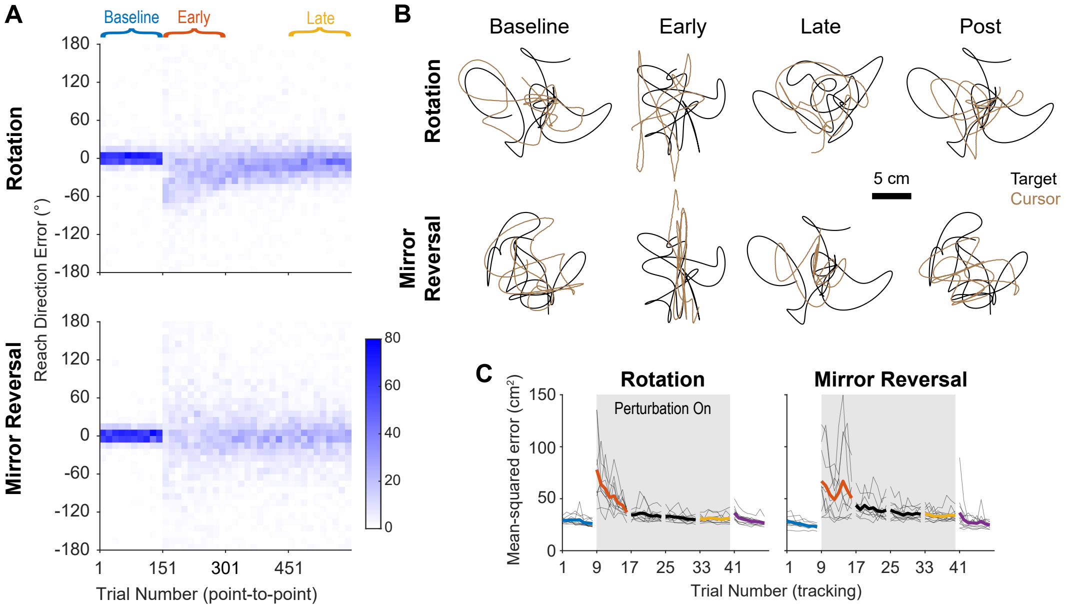

Figure 3.2: Task performance improves in the point-to-point and tracking tasks. **A.** Performance in the point-to-point task, as quantified by initial reach direction error, is plotted as heat maps for the rotation group (top) and mirror-reversal groups (bottom). Each column shows the distribution of initial reach direction errors, pooled across all participants, over a (horizontal) bin of 15 trials. The intensity of color represents the number of trials in each 10°vertical bin where the maximum possible value of each bin is 150 (15 trials for 10 participants for each group). **B.** Example tracking trajectories from a representative participant in each group. Target trajectories are shown in black while cursor trajectories are shown in brown. Each trajectory displays approximately 5 seconds of movement. **C.** Performance in the tracking task as quantified by average mean-squared positional error between the cursor and target during each 40-second trial. Individual participants are shown in thin lines and group mean is shown in thick lines.

continuous control task after having practiced them in the point-to-point task, we had them perform a manual tracking task. In each 46-second tracking trial (1 block = 8 trials), participants tracked a target that moved in a continuous sum-of-sinusoids trajectory at frequencies ranging between 0.1–2.15 Hz, with distinct frequencies used for x- and y-axis target movement. The resulting target motion was unpredictable and appeared random. Furthermore, the target's trajectory was altered every block by randomizing the phases of the component sinusoids, preventing participants from being able to learn a specific target trajectory. Example trajectories from single participants are presented in Figure 3.2B.

As an initial assessment of how well participants learned to track the target, we measured the average mean-squared error (tracking error) between the target and cursor positions during every trial (each tracking trial lasted 46 seconds, 40 seconds of which was used for analysis; see "Tracking task" in the Methods and Materials for more details). Tracking error improved with practice in both groups of participants, approaching similar levels of error by late learning (Figure 3.2C). Therefore, in both the point-to-point and tracking tasks, participants' performance improved with practice. However, much of this improvement can be attributed to the fact that participants learned to keep their cursor within the bounds of target movement; during early learning, participants' cursors often deviated far outside the area of target movement, thus inflating the tracking error.

To better quantify improvements in participants' ability to track the target,

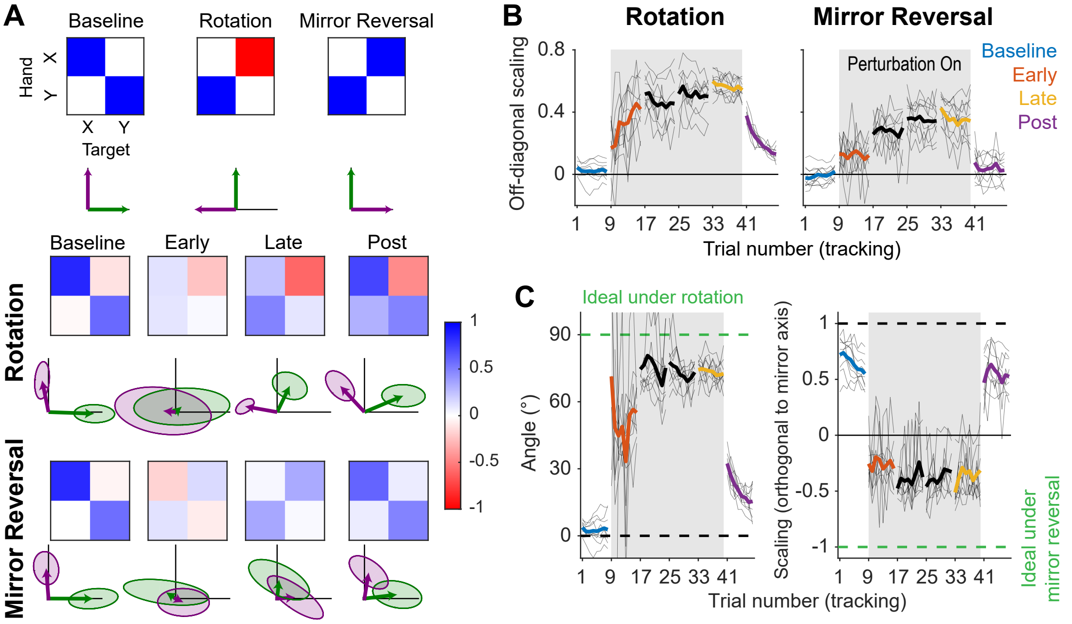

Figure 3.3: The rotation group exhibited reach-direction aftereffects while the mirror-reversal group did not. **A.** Alignment matrices relating target and hand movement established by trajectory alignment. The top row illustrates the ideal alignment matrices at baseline or to successfully compensate for each perturbation (blue represents positive values, red represents negative values). Alignment matrices (calculated from one trial averaged across participants) from the rotation (middle row) and mirror-reversal (bottom row) groups are depicted at different points during learning. Below each matrix, we visualized how the unit x and y vectors (black lines) would be transformed by the columns of the matrices (transformed x = green, transformed y = purple). Shaded areas are 95% confidence ellipses across participants. **B.** The average of the two off-diagonal elements of the estimated alignment matrices across all blocks of the experiment in the tracking task (for the rotation group, the negative of the element in row 1, column 2 was used for averaging). Grey boxes indicate when the rotation or mirror reversal were applied. Thin black lines indicate individual participants and thick lines indicate the mean across participants. **C.** (Left: rotation group) Angular compensation for the rotation, computed by approximating each alignment matrix with a pure rotation matrix. (Right: mirror-reversal group) Scaling factor orthogonal to the mirror axis. In each plot, dashed lines depict ideal performance when the perturbation is (green) or is not (black) applied. Thin black lines indicate individual participants and thick lines indicate the mean across participants.

we examined the geometric relationship between hand and target trajectories—an approach that would be more sensitive to the small changes in movement direction associated with rotation/mirror reversal learning, not just large deviations outside the target's movement area. We aligned the hand and target tracking trajectories with a linear transformation matrix (alignment matrix) that, when applied to the target trajectory, minimized the discrepancy between the hand and target trajectories (see Methods and Materials for details). This matrix compactly summarizes the relationship between target movements and hand movements and can be thought of as a more general version of reach direction for point-to-point movements. We visualized these matrices by plotting their column vectors (green and purple arrows in Figure 3.3A) which depicts how they would transform the unit x and y vectors.

In Figure 3.3A, we illustrate how ideal performance under different visual feedback conditions would manifest in the alignment matrices and vectors. These matrices should approximate the identity matrix when performing under veridical feedback and similarly approximate the inverse of the applied perturbation matrix under perturbed feedback. Incomplete compensation would manifest as, for example, a 45° counter-clockwise rotation matrix in response to the 90° clockwise rotation. For both the groups of participants, the estimated alignment matrices were close to the identity matrix at baseline and approached the inverses of the respective perturbations by late learning (Figure 3.3A), demonstrating that participants performed the task successfully at baseline and mostly learned to compensate for the imposed perturbations.

To test whether these changes were statistically significant, we focused on the off-diagonal elements of the matrices. These elements critically distinguish the different transformations from one another and from baseline. In the last trial of the late learning block, both the rotation (linear mixed effects model [see "Statistics" in Methods and Materials for details about the model structure]: interaction between group and block, $F(2,36) = 7.56$, $p = 0.0018$; Tukey's range test: $p < 0.0001$) and mirror-reversal groups (Tukey's range test: $p < 0.0001$) exhibited off-diagonal values that were significantly different from the first trial of the baseline block (Figure 3.3B), and in the appropriate direction to compensate for their respective perturbations.

From these matrices, we derived additional metrics associated with each perturbation to further characterize learning. For the rotation group, we computed a compensation angle, θ, using a singular value decomposition approach (Figure 3.3C; see "Trajectory-alignment analysis" in Methods and Materials for details). At baseline, we found that $\theta = 3.8 \pm 1.0°$ (mean ± SEM), and this increased to $\theta = 72.5 \pm 1.9°$ by late learning. For the mirror-reversal group, to assess whether participants learned to flip the direction of their movements across the mirroring axis, we computed the scaling of the target trajectory along the direction orthogonal to the mirror axis (Figure 3.3C). This value was positive at baseline and negative by late learning, indicating that participants successfully inverted their hand trajectories relative to that of the target.

Lastly, we sought to confirm that the rotation and mirror reversal were learned using different mechanisms, as has been suggested by previous studies (Gutierrez-Garralda et al., 2013; Telgen et al., 2014). We did so by assessing whether participants in each group expressed reach-direction aftereffects—the canonical hallmark of adaptation—at the end of the experiment, following removal of each perturbation in the tracking task (and with participants made explicitly aware of this). Again estimating alignment matrices (Figure 3.3B), we found that the magnitude of aftereffects (as measured by the off-diagonal elements of the alignment matrices) was different between the two groups in the first trial post-learning (Tukey's range test: $p < 0.0001$). Within groups, the off-diagonal elements for the rotation group were significantly different between the first trial of baseline and the first trial of post-learning (Tukey's range test: $p < 0.0001$), indicating clear aftereffects. These aftereffects corresponded to a compensation angle of $\theta = 32.4 \pm 1.4°$, similar to the magnitude of aftereffects reported for visuomotor rotation in point-to-point tasks (Bond and Taylor, 2015; Morehead et al., 2017). For the mirror-reversal group, by contrast, the off-diagonal elements from the first trial of post-learning were not significantly different from the first trial of baseline (Tukey's range test: $p = 0.2057$; baseline range: -0.11–0.11; post-learning range: -0.07–0.28), suggesting negligible aftereffects. The lack of aftereffects under mirror reversal implies that participants did not counter this perturbation via adaptation of an existing controller and instead used an alternative learning mechanism.

In summary, these data suggest that participants were able to compensate for both perturbations in the more challenging tracking task. Consistent with previous studies focusing on point-to-point movements, these data support the idea that the rotation was learned via adaptation while the mirror reversal was learned via a different mechanism—putatively, *de novo* learning.

3.2.2 Participants used continuous movements to perform manual tracking

Although participants could learn to successfully perform the tracking task under the mirror reversal, it is not necessarily clear that they achieved this by building a new, continuous controller; the largest amplitudes and velocities of target movement occurred primarily at low frequencies (0.1–0.65 Hz) which could potentially have allowed participants to track the target through a series of discretely planned "catch-up" movements (Craik, 1947; Miall et al., 1993a; Russell and Sternad, 2001; Susilaradeya et al., 2019) that might have involved re-aiming. If participants were employing such a re-aiming strategy, we would expect this to compromise their ability to track the target continuously. To examine the possibility that participants may have tracked the target intermittently rather than continuously, we turned to linear systems analysis to analyse participants behavior at a finer-grained level than was possible through the trajectory-alignment analysis.

According to linear systems theory, a linear system will always translate sinusoidal inputs into sinusoidal outputs at the same frequency, albeit potentially scaled in amplitude and shifted in phase. Additionally, linearity implies that the result of summing two input signals is to simply sum the respective outputs. Therefore, a linear system can be fully described in terms of how it maps sinusoidal inputs to outputs across all relevant frequencies. If participants' behavior can be well approximated by a linear model—as is often the case for planar arm movements (McRuer and Jex, 1967; Yamagami et al., 2019; Zimmet et al., 2020)—then we can fully understand their tracking

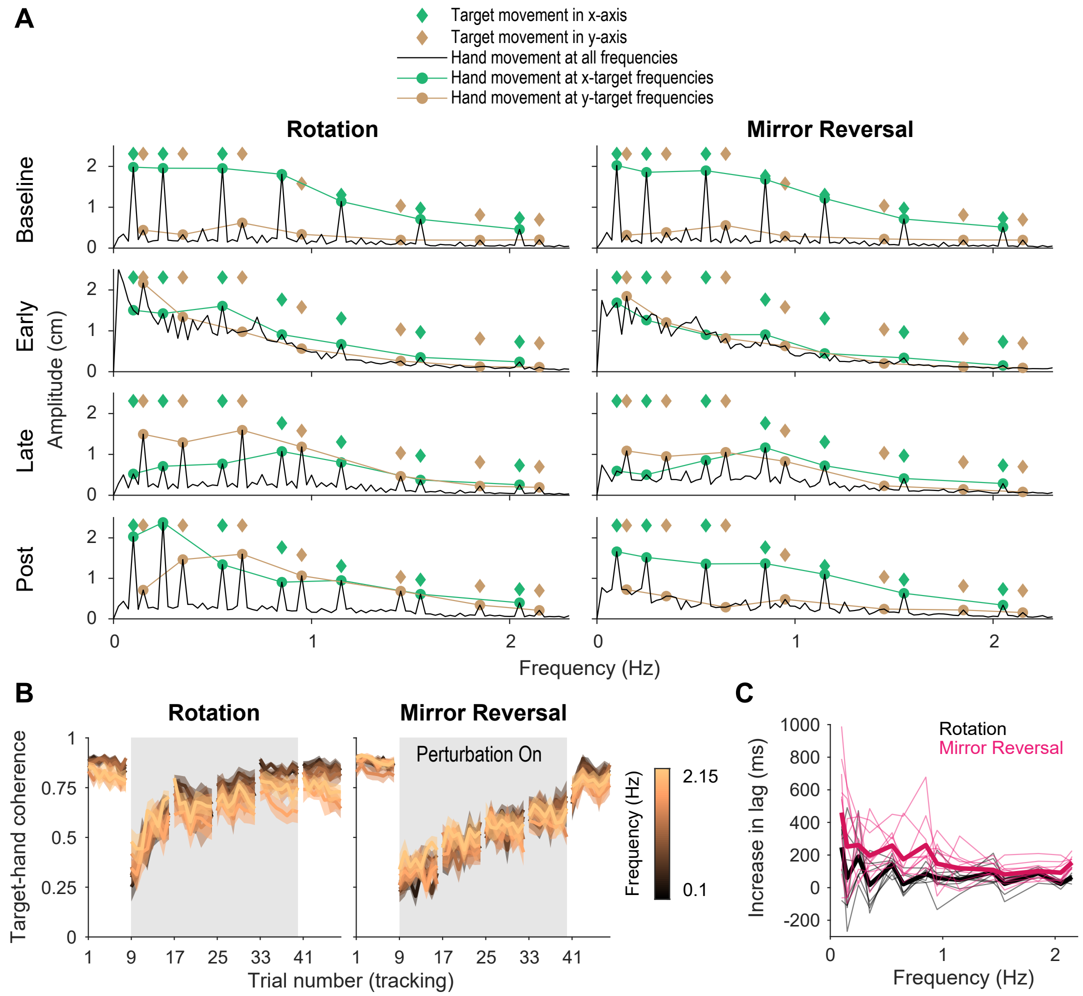

Figure 3.4: Tracking behavior was approximately linear, indicating that the hand tracked the target continuously. **A.** Amplitude spectra of x-axis hand trajectories (black line) averaged across participants from one trial in each listed block. In each plot, the amplitudes and frequencies of target motion are indicated by diamonds (green: x-axis target frequencies; brown: y-axis target frequencies). Hand responses at x- and y-axis target frequencies are highlighted as green and brown circles, respectively, and are connected by lines for ease of visualization. **B.** Spectral coherence between target movement in the x-axis and hand movement in both axes. This measure is proportional to the linear component of the hand's response to the target. Darker colors represent lower frequencies and lighter colors represent higher frequencies. Error bars are SEM across participants. **C.** Difference in phase lag between movements at late learning and baseline. Data from individual participants are shown as thin lines and averages for the rotation (black) and mirror-reversal (pink) groups are shown as thick lines.

behavior in terms of their response to different frequencies of target movement. The design of the tracking task enabled us to examine the extent to which participants' behavior was linear; if participants were indeed behaving linearly (which would suggest they were tracking the target continuously), then we should find that their hand also moved according to a sum-of-sines trajectory, selectively moving at the same frequencies as the target.

We assessed whether participants selectively moved at the same frequencies as target movement by first converting their trajectories to a frequency-domain representation via the discrete Fourier transform. This transformation decomposes the full hand trajectory into a sum of sinusoids of different amplitudes, phases, and frequencies. Figure 3.4A shows the amplitude spectra (i.e. amplitude of movement as a function of frequency) of hand movements in the x-axis at different points during the experiment, averaged across participants (analogous data for y-axis movements not shown because it appeared qualitatively similar). The amplitudes and frequencies of target movement are shown as diamonds (x- and y-axis sinusoids in green and brown, respectively) and the amplitude of participants' movements at those same frequencies are marked by circles.

At baseline, late learning, and post-learning, participants moved primarily at the frequencies of x- or y-axis target movement (Figure 3.4A). At frequencies that the target did *not* move in, the amplitude of hand movement was low. This behavior resulted in clearly discernible peaks in the amplitude spectra, which is consistent with the expected response of a linear system. In contrast, participants' behavior at early learning was qualitatively different, exhibiting high amplitude at movement frequencies below 1 Hz, regardless of whether the target also moved at that frequency. This suggests that a much greater proportion of participants' behavior was nonlinear/noisy, as would be expected during early learning when neither group of participants had adequately learned to counter the perturbations.

As a further test of the linearity of participants' behavior, we computed the spectral coherence between target and hand movement, which is simply the correlation between two signals in the frequency domain. As demonstrated by Roddey et al., 2000, for an arbitrary system responding to an arbitrary input, the fraction of the system's response that can be explained by a linear model is proportional to the coherence between the input and the system's output (a perfectly linear system would exhibit a coherence of 1 across all frequencies). At baseline, for both groups, we found that the coherence between target movement and participants' hand movement was roughly 0.75 in both the x- and y-axes (Figure 3.4B), meaning that 75% of participants' behavior could be accounted for by a linear model. Although dramatically lower during early learning, the coherence approached that of baseline by late learning, indicating that the proportion of participants' behavior that could be accounted for by a linear model increased with more practice time.

As with any correlation, the residual variance in behavior not explained by a linear model was attributable to either nonlinearities or noise. Because catch-up movements could manifest as nonlinear behavior, we estimated the additional variance that could be explained by a nonlinear, but *not* a linear, model by measuring the square root of the coherence between multiple responses to the same input (Roddey et al., 2000), i.e., hand movements from different trials within a block. We found that across all blocks, only an additional 5-10% of tracking behavior could be explained by nonlinear model (data not shown), suggesting that most of the residual variance was attributable to noise and that a linear model was almost as good as a nonlinear model at explaining behavior on a trial-by-trial basis. In summary, these analyses suggest that participants' behavior at baseline, late learning, and post-learning could be well described as a linear system, thereby suggesting that their movements were continuous.

Although behavior was approximately linear across all frequencies, it is possible that performing a sequence of discretely planned catch-up movements—which might have depended on the use of a re-aiming strategy—could approximate linear behavior, particularly at low frequencies of movement. As a result, we analyzed the lag between hand and target movements to examine the plausibility of participants repeatedly re-aiming in the tracking task. Previous work suggests that in tasks with many possible target locations, planning point-to-point movements under large rotations of visual feedback incurs an additional $\sim$300 ms of planning time on top of that required under baseline conditions (Fernández-Ruiz et al., 2011; McDougle and Taylor, 2019). In the context of the tracking task, this suggests that, compared to baseline, people would require an additional 300 ms of reaction time for each catch-up movement under the rotation or mirror reversal, which would increase the lag between hand movements relative to the target.

We computed this lag at late learning and baseline at every frequency of target movement. We then examined how much this lag increased from baseline to late learning (Figure 3.4C). For all but the lowest frequency of movement for the mirror-reversal group, the average increase in lag was below 300 ms. In fact, averaging across all frequencies, the increase in lag for the rotation and mirror-reversal groups were 83 ± 31 and 191 ± 62 ms (mean ± standard deviation across participants), respectively. This analysis suggests that participants responded to target movement quickly—more quickly than would be expected if participants tracked the target by repeatedly re-aiming towards an alternative target location.

In summary, the above analyses show that participants were able to track the target smoothly and continuously after learning to compensate for either the rotation or the mirror reversal. Participants did not appear to be making intermittent catch-up movements nor relying on a re-aiming strategy. Rather, their performance suggests that they were able to continuously track the target by building a *de novo* controller.

3.2.3 Adaptation and *de novo* learning exhibit distinct signatures in the frequency domain

The fact that tracking behavior could be well approximated as a linear dynamical system, particularly late in learning, facilitates a deeper analysis into how learning altered participants' control capabilities. Following this approach, we treated each 40-second tracking trial as a snapshot of participants' control capabilities at a particular time point during learning, assuming that the behavior could be regarded as being generated by a linear, time-invariant system. Although participants' behavior changed over the course of the experiment

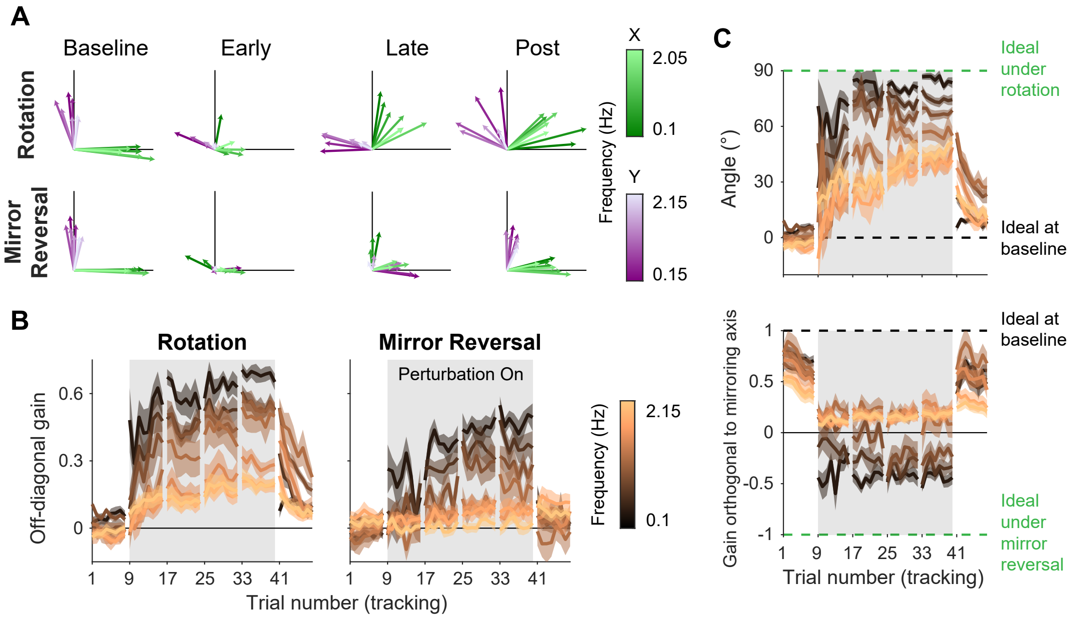

Figure 3.5: Adaptation and *de novo* learning exhibit distinct frequency-dependent signatures. We estimated how participants transformed target motion into hand movement across different frequencies (i.e., gain matrix analysis). **A.** Visualizations of the gain matrices relating target motion to hand motion across frequencies. These visualizations were generated by plotting the column vectors of the gain matrices from one trial of each listed block, averaged across participants. Green and purple arrows depict hand responses to *x*- and *y*-axis target frequencies, respectively. Darker and lighter colors represent lower and higher frequencies, respectively. **B.** Average of the two off-diagonal values of the gain matrices at different points during learning. Grey boxes indicate when the rotation or mirror reversal were applied. **C.** (Top) Compensation angle as a function of frequency for the rotation group. (Bottom) Gain of movement orthogonal to the mirror axis for the mirror-reversal group. Green and black dashed lines show ideal compensation when the perturbation is or is not applied, respectively. All error bars in this figure are SEM across participants.

due to the engagement of (likely nonlinear) learning processes, within the span of individual trials, our data suggest that their behavior was both approximately linear (Figure 3.4A–B) and changed only minimally from trial-to-trial (Figure 3.3B–C), suggesting the use of linear systems analysis on single-trial data was valid.

We first examined learning in the amplitude spectra analysis. To perfectly compensate for either the rotation or the mirror reversal, participants' responses to movement of the target in the x-axis needed to be remapped from the x-axis to the y-axis, and vice versa for movement of the target in the y-axis. Since the target moved at different frequencies in each axis, this remapping could be easily observed in the amplitude spectra as peaks at different frequencies. During early learning, both groups' movements were nonlinear and were not restricted to x- or y-axis target frequencies (Figure 3.4A). However, by late learning, both groups learned to produce x-axis hand movements in response to y-axis target frequencies, indicating some degree of compensation for the perturbation. However, they also inappropriately continued to produce x-axis hand movements at x-axis target frequencies, suggesting that the compensation was incomplete.

After the perturbation was removed, the rotation group exhibited x-axis hand movements at both x- and y-axis target frequencies, unlike baseline where movements were restricted to x-axis target frequencies (Figure 3.4A). The continued movement in response to y-axis target frequencies indicated aftereffects of having learned to counter the rotation, consistent with our earlier trajectory-alignment analysis. In contrast, the amplitude spectra of the mirror-reversal group's x-axis hand movements post-learning was similar to baseline, suggesting negligible aftereffects and again recapitulating the findings of our earlier analysis (analgous data for y-axis movements not shown because it appeared qualitatively similar).

Although the amplitude spectra illustrate important features of learning, they do not carry information about the directionality of movements and thus do not distinguish learning of the two different perturbations; perfect compensation would lead to identical amplitude spectra for each perturbation. In order to distinguish these responses, we needed to determine not just the amplitude, but the direction of the response along each axis, i.e. whether it was positive or negative. We used *phase* information to disambiguate the direction of the response (the sign of the gain) by assuming that the phase of the response at each frequency would remain similar to baseline throughout learning. We then used this information to compute signed gain matrices which describe the linear transformations relating target and hand motion. These matrices relay similar information as the alignment matrices in Figure 3.3 except that here, different transformations were computed for different frequencies of movement. To construct these gain matrices, the hand responses from neighboring pairs of x- and y-axis target frequencies were grouped together. This grouping was performed because target movement at any given frequency was one dimensional, but target movement across two neighboring frequencies was two dimensional; examining hand/target movements in this way thus provided two-dimensional insight into how the rotation/mirroring of hand responses varied across the frequency spectrum (see "Frequency-domain analysis" in Methods and Materials for details).

Similar to the trajectory-alignment analysis, these gain matrices should be close to the identity matrix at baseline but equal the inverse of the matrix describing the perturbation if participants are able to perfectly compensate for the perturbation. We again visualized these frequency-dependent gain matrices by plotting their column vectors, which illustrates the effect of the matrix on the unit x and y vectors, only now we include a set of vectors for each pair of neighboring frequencies (Figure 3.5A).

At baseline, participants in both groups responded to x- and y-axis target motion by moving their hands in the x- and y-axes, respectively, with similar performance across all target frequencies. Late in learning for the rotation group, participants successfully compensated for the perturbation—apparent through the fact that all vectors rotated clockwise during learning. The extent of compensation, however, was not uniform across frequencies; compensation at low frequencies (darker arrows) was more complete than at high frequencies (lighter arrows). For the mirror-reversal group, compensation during late learning occurred most successfully at low frequencies, apparent as the darker vectors flipping across the mirror axis (at 45° relative to the x-axis) from their baseline direction. At high frequencies, however, responses failed to flip across the mirror axis and remained similar to baseline.

To quantify these observations statistically, we focused again on the off-diagonal elements of the gain matrices from individual trials. The rotation group's gain matrices were altered in the appropriate direction to counter the perturbation, showing a significant difference between the first trial of baseline and the last trial of late learning at all frequencies (Figure 3.5B; linear mixed effects model [see "Statistics" in methods for details about the model structure]: interaction between group, block, and frequency, $F(12, 360) = 3.39$, $p = 0.0001$; data split by frequency for post hoc Tukey's range test: Bonferroni-adjusted $p < 0.05$ for all frequencies). Comparing the first trial of baseline and last trial of late learning for the mirror-reversal group revealed that the low-frequency gain matrices were also altered in the appropriate direction to counter the perturbation (Tukey's range test: Bonferroni-adjusted $p < 0.001$ for lowest three frequencies), but the high-frequency gain matrices were not significantly different from each other (Tukey's range test: $p > 0.6$ (not Bonferroni-adjusted) for highest three frequencies; baseline gain range: -0.18–0.18; late-learning gain range: -0.25–0.66).

Calculating a rotation matrix that best described the rotation group's gain matrix at each frequency (using the same singular value decomposition approach applied to the alignment matrices) revealed that participants' baseline compensation angle was close to 0° at all frequencies (Figure 3.5C). By late learning, compensation was nearly perfect at the lowest frequency but was only partial at higher frequencies. For the mirror-reversal group, the gains of participants' low-frequency movements orthogonal to the mirror axis were positive at baseline and became negative during learning, appropriate to counter the perturbation. At high frequencies, by contrast, the gain reduced slightly during learning but never became negative. Thus, both groups of participants were successful at compensating at low frequencies but, at high frequencies, the rotation group was only partially successful and the mirror-reversal group was largely unsuccessful.

The gain matrices also recapitulated the post-learning trends from the trajectory-alignment analysis in Figure 3.3. In the first post-learning trial, the rotation group's off-diagonal gains were significantly different from the first trial of baseline for all frequencies except the lowest (Figure 3.5B; Tukey's range test: Bonferroni-adjusted $p < 0.003$ for highest six frequencies). By contrast, there was no strong evidence that the mirror-reversal group's post-learning matrices were significantly different from baseline (Tukey's range test: $p > 0.04$ (not Bonferroni-adjusted) for all frequencies; baseline gain range: -0.18–0.18; post-learning gain range: -0.49–0.37). Additionally, the post-learning gains differed significantly between the rotation and mirror-reversal groups, albeit only for three of the intermediate frequencies (Tukey's range test: Bonferroni-adjusted $p < 0.001$). Similar trends were evident in the compensation angles for the rotation group and orthogonal gains for the mirror-reversal group (Figure 3.5C). These data again suggest that the rotation group expressed aftereffects while the mirror-reversal group did not.

To summarize, compensation for the visuomotor rotation was expressed at both low and high frequencies of movement, and this compensation resulted in reach-direction aftereffects of similar magnitude to that reported in previous studies using point-to-point movements (Taylor et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011; Bond and Taylor, 2015). This suggests that participants learned to compensate for the rotation through adaptation, i.e., by adapting their existing baseline controller. In contrast, the mirror-reversal group only expressed compensation at low frequencies of movement, exhibiting little to no compensation at high frequencies, and did not exhibit aftereffects, suggesting that they did not learn through adaptation of an existing controller. Combined with the results from Figure 3.4Figure 4 suggesting that participants did not utilize a re-aiming strategy while tracking, these data suggest that participants learned to counter the mirror reversal by building a new controller from scratch, i.e., through *de novo* learning.

Learning in the rotation group also appeared to be, to some extent, achieved through *de novo* learning. The magnitude of aftereffects in this group (∼25°) was only a fraction of the overall compensation achieved (∼70°) during late learning, suggesting that implicit adaptation cannot entirely account for the rotation group's behavior. The results from Figure 3.4 also suggest that the rotation group's behavior could not be explained by a strategy of tracking the target through a series of re-aimed catch-up movements. Examining the time course of learning for both groups in Figure 3.5B, while the rotation group's gains were overall higher than the mirror-reversal group's, there was a striking similarity in the frequency-dependent pattern of learning between the two groups. We therefore conclude that the residual learning not accounted for by adaptation was attributable to the same *de novo* learning process that drove learning under the mirror reversal.

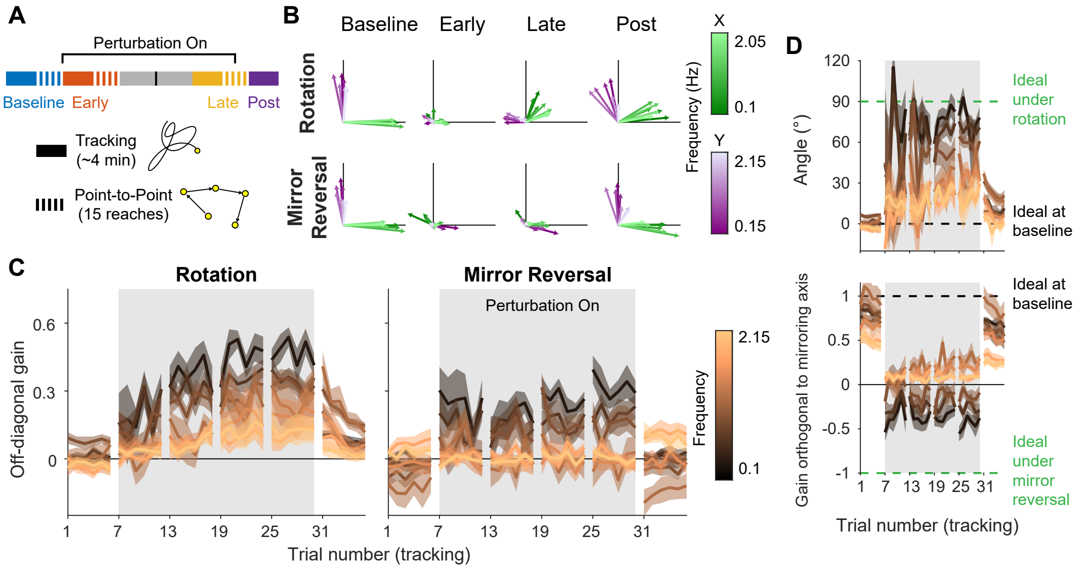

Figure 3.6: Making point-to-point reaches improves tracking performance, especially under mirror reversal. **A.** Participants learned to counter either a visuomotor rotation ($n = 10$) or mirror-reversal ($n = 10$). The experimental design was similar to the main experiment except point-to-point reaching practice was almost entirely eliminated; between the early- and late-learning tracking blocks, participants only performed 15 point-to-point reaches. The purpose of these reaches was not for training but simply to assess learning in the point-to-point task. **B–D.** Gain matrix analysis, identical to that in Figure 3.5, performed on data from the follow-up experiment. **B.** Visualization of the gain matrix from one trial of each listed block, averaged across participants. **C.** Off-diagonal elements of the gain matrices, averaged across participants. **D.** Computed rotation angle for the rotation group's gain matrices (upper) and gain orthogonal to mirroring axis for the mirror-reversal group (lower), averaged across participants. All error bars in this figure are SEM across participants.

3.2.4 Examining the effect of re-aiming strategies on learning

Although the data suggest that participants did not primarily rely on a re-aiming strategy while tracking, participants likely did use such a strategy to learn to counter the rotation/mirror reversal while performing point-to-point reaches. How important might such cognitive strategies be for ultimately learning the tracking task? To better understand this, we performed a follow-up experiment with twenty additional participants. This experiment was similar to the main experiment except for the fact that participants experienced the rotation/mirror reversal almost exclusively in the tracking task, performing only 15 point-to-point reaches between the early and late learning tracking blocks compared to the 450 reaches in the main experiment (Figure 3.6A).

We applied the gain matrix analysis from Figure 3.5 to data from this experiment and found that our previous results were largely reproduced despite the very limited point-to-point training (Figure 3.6B–D). The rotation group exhibited aftereffects in the gain matrices (linear mixed effects model [see “Statistics” in methods for details about the model structure]: interaction between block, frequency, and group, $F(12, 360) = 3.26$, $p = 0.0002$; data split by frequency for post hoc Tukey’s range test: Bonferroni-adjusted $p < 0.01$ for four out of seven frequencies) which were significantly greater than that of the mirror-reversal group (Tukey’s range test: Bonferroni-adjusted $p < 0.0005$ for two out of seven frequencies). In contrast, the mirror-reversal group did not express aftereffects (Tukey’s range test: $p > 0.4$ (not Bonferroni-adjusted) for all seven frequencies; Figure 3.6C). Furthermore, the rotation group exhibited compensation at high frequencies (Tukey's range test: Bonferroni-adjusted $p = 0.0073$ at third highest frequency) whereas the mirror-reversal group did not (Tukey's range test: $p > 0.5$ (not Bonferroni-adjusted) for highest four frequencies). Thus, the follow-up experiment provided evidence that the effects we observed in the main experiment were replicable.

Directly comparing the results between the two experiments (comparing Figure 3.6C and 3.5B), we found that participants in the follow-up experiment exhibited significantly less compensation in the last trial of late learning compared to participants in the main experiment, as quantified by the off-diagonal gain (two-way ANOVA [see "Statistics" in methods for details about the ANOVA]: main effect of experiment, $F(1, 252) = 37.69$, $p < 0.0001$, with no significant interactions between any predictors). It is unclear, however, whether this reduced learning was attributable to participants being unable to develop a re-aiming strategy without point-to-point training, or whether it could be explained by the fact that participants simply spent less total time being exposed to the perturbations.

Therefore, while virtually eliminating point-to-point training may have diminished participants' ability to learn the task, participants were still able to counter the perturbation to some extent, reproducing the most salient findings from the main experiment.

3.3 Discussion

In the present study, we tested whether participants could learn to successfully control a cursor to track a continuously moving target under either rotated or mirror-reversed visual feedback. Although previous work has established that participants can learn to compensate for these perturbations during point-to-point movements, this compensation often seems to depend upon the use of re-aiming strategies—a solution that is time-consuming and therefore does not seem feasible in a task in which goals are constantly changing.

We found that both groups' tracking behavior was inconsistent with that of a re-aiming strategy, suggesting other mechanisms were used to compensate for these perturbations. The rotation group exhibited strong aftereffects once the perturbation was removed, amounting to an approximately 25° rotation of hand motion relative to target motion—consistent with previous findings in point-to-point tasks (Taylor et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011; Bond and Taylor, 2015). This suggests that these participants learned to counter the rotation, at least in part, via adaptation. In contrast, participants who learned to compensate for the mirror-reversal showed no aftereffects, suggesting that they did not adapt their existing controller, but instead learned to compensate by establishing a *de novo* controller.

3.3.1 The role of re-aiming strategies in *executing* tracking behavior

In principle, a target can be tracked by executing a series of intermittent catch-up movements. However, our results suggest that this possibility was unlikely for three reasons. First, under both perturbations, a majority of participants' tracking behavior could be accounted for by a linear model, and the additional variance in behavior that could be accounted for by a *nonlinear* model was comparatively small. This implies that participants tracked the target continuously, rather than intermittently, which would likely have introduced greater nonlinearities. Although it might be possible for very frequent catch-up movements to appear approximately linear, the frequency of such catch-up movements would have to be at least double the frequency of target motion being tracked (i.e., the Nyquist rate). The highest frequency at which participants were able to successfully compensate for the mirror reversal was around 1 Hz. This means participants would have had to generate at least two re-aimed movements per second to track the target smoothly at this frequency, a process which would have been fairly rapid and cognitively demanding over the course of a trial.

The second reason we reject the idea of repeated re-aiming is based on the delay between hand and target movement. Compensation for either of the perturbations introduced some additional tracking delay relative to baseline. However, this delay was less than 200 ms, which is smaller than would be expected if the participants had compensated by repeated strategic re-aiming. It has been demonstrated in some circumstances that re-aiming can occur in as little as 200ms by caching the movement required for a given target location (Huberdeau et al., 2019; McDougle and Taylor, 2019). However, caching associations in this way appears to be limited to just 2-7 elements (McDougle and Taylor, 2019; Collins and Frank, 2012) and it seems doubtful that this mechanism could support a controller that must generate output when the state of the target (its location and velocity), as well as that of the hand, may vary in a continuous space.

Finally, participants' anecdotal reports also suggest they did not utilize a re-aiming strategy. After the experiment was complete, we asked participants to describe how they performed the tracking task under the perturbations. The vast majority of participants reported that when they tried to think about how to move their hand to counter the perturbations, they felt that their tracking performance deteriorated. Instead, they felt their performance was best when they let themselves respond naturally to the target without explicitly thinking about how to move their hands. Participants' disinclination to explicitly coordinate their hand movements provides further evidence against their use of a re-aiming strategy.

We believe, therefore, that it is unlikely that participants solved the tracking task under a mirror-reversal by using a deliberative re-aiming strategy that is qualitatively similar to that which has been described in the context of point-to-point reaching tasks. Instead, we believe that these participants constructed a new controller that instantiated a new, continuous mapping from current states and goals to actions.

However, it is possible that, given our experimental design, participants countered the perturbation in a way that is similar in some respects to traditional re-aiming and potentially indistinguishable from continuous control. Traditional accounts of re-aiming suggest that participants identify a fixed surrogate target location to aim their movements towards—effectively manipulating one of the inputs to the controller to achieve a particular desired output. Our results suggest that participants could not have performed the tracking task in this way. However, it is still possible for tracking to be performed by manipulating the input to a controller in a more general manner.

For instance, the output of the tracking controller could depend on the instantaneous position *and* velocity of the target, and participants may have been able to counter the perturbation by manipulating these inputs to a fixed underlying controller in order to achieve output that would successfully track the target under the mirror reversal. Although this solution bears similarities to re-aiming, it differs significantly in that it entails modifying potentially many different inputs and doing so in a continuously changing manner. Such a solution would be unlikely to be amenable to the deliberative processes responsible for static re-aiming and, in composite, could be considered a *de novo* controller.

3.3.2 The role of re-aiming strategies in *acquiring* a *de novo* controller

Although our analyses revealed that participants did not primarily rely on an aiming strategy to *execute* continuous tracking movements, they could have initially depended on such a strategy to *acquire* the controller necessary to perform these movements. In a follow-up experiment, we tested whether limited practice in the point-to-point task would impair how well participants could learn to counter the rotation/mirror reversal. Although we found that both groups expressed less compensation for the perturbations compared to the main experiment, both groups still expressed some compensation, reproducing the qualitative features of learning from the main experiment. The fact that there are multiple explanations for this reduction in compensation (failure to develop a re-aiming strategy versus less time on task) makes it difficult to draw any strong conclusions from these results about what role re-aiming strategies play in acquiring a new controller.

However, previous evidence clearly demonstrates that people can learn to counter a mirror reversal using a re-aiming strategy when performing point-to-point reaches (Wilterson and Taylor, 2021). It is possible, therefore, that re-aiming strategies could contribute to acquiring a *de novo* controller. How exactly might such strategies contribute to learning? One possibility is that the deliberative computations performed when planning upcoming movements are used to help build a *de novo* controller. Alternatively, it may be easier for people to evaluate the quality of straight-line reaches (e.g., reach direction, movement time, task error) compared to tracking a pseudo-random trajectory, allowing them to update the parameters of a nascent controller more readily. Ultimately, the question of how a *de novo* controller is constructed is a major open question for future research.

3.3.3 Frequency-domain signatures of adaptation and *de novo* learning

The pattern of compensation under the rotation and mirror-reversal was frequency specific (Figure 3.5B), with the nature of compensation at high frequencies revealing distinct signatures of adaptation and *de novo* learning between the two groups. At low frequencies, both groups of participants successfully compensated for their perturbations. But at high frequencies, only the rotation group was able to compensate; behavior for the mirror-reversal group at high frequencies was similar to baseline behavior. There were similarities, however, in the time course and frequency-dependence of learning under each perturbation (Figure 3.5B), with both groups exhibiting a steady increase in compensation over time, particularly at lower frequencies. Additionally, both groups' compensation exhibited a similar diminution as a function of frequency.

We believe these results show that distinct learning processes drove two separate components of learning. One component, present only in the rotation group, was expressed uniformly at all frequencies and exhibited aftereffects, likely reflecting a parametric adjustment of an existing baseline controller, i.e., adaptation. A second component of learning contributed to compensation in both groups of participants. This component was expressed primarily at low frequencies, exhibited a gradation as a function of frequency, and was not associated with aftereffects. We suggest this component corresponds to formation of a *de novo* controller for the task.

Although compensation for the rotation bore many hallmarks of adaptation, it also exhibited features of *de novo* learning seen in the mirror-reversal group, suggesting that participants in the rotation group employed a combination of the two learning processes. This is consistent with previous suggestions that residual learning under a visuomotor rotation that cannot be attributed to implicit adaptation may rely on the same mechanisms as those used for *de novo* learning (Krakauer et al., 2019). In summary, our data suggest that adaptation and *de novo* learning can be deployed in parallel to learn novel motor tasks.

3.3.4 Potential control architectures supporting multiple components of learning

The properties of adaptation and *de novo* learning we have identified here can potentially be explained by the existence of two distinct control pathways, each capable of different forms of plasticity but with differing sensorimotor delays. An inability to compensate at high frequencies (when tracking an unpredictable stimulus; see Roth et al., 2011) suggests higher phase lags, potentially due to greater sensorimotor delays or slower system dynamics; as phase lags approach the period of oscillation, it becomes impossible to exert precise control at that frequency. Therefore, we suggest that one control pathway may be slow but reconfigurable to implement arbitrary new controllers, while the other is fast but can only be recalibrated to a limited extent through adaptation. The existence of distinct control pathways is supported by studies which suggest that adaptation is dependent on the cerebellum (Maschke et al., 2004; Morton and Bastian, 2006) while *de novo* learning is dependent on the basal ganglia (Schugens et al., 1998; Gutierrez-Garralda et al., 2013; Choi et al., 2020).

It is possible that the two different control pathways that appear to learn differently might correspond to feedforward control (generating motor output based purely on target motion) and feedback control (generating motor output based on the cursor location and/or distance between cursor and target). Feedback control is slower than feedforward control due to the additional delays associated with observing the effects of one's earlier motor commands on the current cursor position. The observed pattern of behavior may thus be due to a fast but inflexible feedforward controller that responds rapidly to target motion, but always expresses baseline behavior (potentially recalibrated via implicit adaptation) interacting with a slow but reconfigurable feedback controller that responds to both target motion and the current cursor position. At low frequencies, the target may move slowly enough that any inappropriate feedforward control to track the target is masked by corrective feedback responses. But at high frequencies, the target may move too fast for feedback control to be exerted, leaving only inappropriate feedforward responses. It is not possible to dissociate the contributions of feedforward and feedback control on the basis of our current dataset, but in principle our approach can be extended to do so by including perturbations to the cursor position in addition to target movement (Yamagami et al., 2019; Yamagami et al., 2020).

An alternative possibility is that there may be multiple feedforward controllers (and/or feedback controllers) that incur different delays. A fast but inflexible baseline controller, amenable to recalibration through adaptation, might interact with a slower but more flexible controller. This organization parallels dual-process theories of learning and action selection (Day and Lyon, 2000; Huberdeau et al., 2015; Hardwick et al., 2019) and raises the possibility that the *de novo* learning exhibited by our participants might be, in some sense, cognitive in nature. Although we have rejected the possibility that participants countered the perturbation by repeated strategic re-aiming, recent theories have framed the prefrontal cortex as a general-purpose network capable of learning to perform arbitrary computations on its inputs (Wang et al., 2018). From this perspective, it does not seem infeasible that such a network could learn to implement an arbitrary continuous feedback controller that could compensate for the imposed perturbation or continuously modulate the input to an existing controller), albeit likely at the cost of incurring an additional delay over controllers that support task performance in baseline conditions.

3.4 Methods

3.4.1 Tasks

40 right-handed, healthy participants were recruited for this study (24.28 ± 5.06 years old; 19 male, 21 female), 20 for the main experiment and 20 for the follow-up experiment. In each experiment, half of the participants learned to counter a 90° clockwise visuomotor rotation while the other half learned to counter a mirror reversal of visual feedback. Participants performed interleaved blocks of point-to-point reaching (1 block = 150 trials) and tracking (1 block = 8 trials; 1 trial = 46 seconds of target movement).

In the main experiment, we first assessed the baseline control of the rotation and mirror-reversal groups by having them perform one block of the tracking task followed by one block of the point-to-point task under veridical cursor feedback. We then applied either the visuomotor rotation or mirror reversal to the cursor, and used the tracking task to measure their control capabilities during early learning. Afterwards, we alternated three times between blocks of point-to-point training and blocks of tracking. In total, each participant practiced their respective perturbation with 450 point-to-point reaches in between the early and late learning tracking blocks. Finally, we measured aftereffects in the tracking task by removing the rotation/mirror reversal.

The follow-up experiment followed a similar block structure as the main experiment, but there were two differences of note. Firstly, the number of point-to-point reaches was dramatically reduced per block to 15 reaches. Secondly, the number of point-to-point blocks was also reduced to 3 (one point-to-point block after the baseline, early, and late learning tracking blocks), providing participants only 15 point-to-point reaches between the early and late learning tracking blocks.

3.4.2 Trajectory-Alignment Analysis

In the point-to-point task, we assessed performance by calculating the angular error between the cursor's initial movement direction and the target direction relative to the start position. To determine the cursor's initial movement direction, we computed the direction of the cursor's instantaneous velocity vector $\sim$150 ms after the time of movement initiation. Movement initiation was defined as the time when the cursor left the start circle on a given trial.

In the tracking task, we assessed performance by measuring the average mean-squared error between the hand and target positions for every trial. For the alignment matrix analysis, we fit a matrix, $\hat{M} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$, that minimized the mean-squared error between the hand and target trajectories for every trial. In the latter analysis, the mean-squared error was additionally minimized in time by delaying the target trajectory relative to the hand. (While the time-delay allowed for the fairest possible comparison between the hand and target trajectories in subsequent analysis, changing or eliminating the alignment *did* *not* qualitatively change our results.) We estimated $\hat{M}$ as

$$\hat{M} = \underset{M}{\operatorname{argmin}} \left\{ \begin{bmatrix} H_x \\ H_y \end{bmatrix} - M \begin{bmatrix} T_x \\ T_y \end{bmatrix} \right\} \tag{3.1}$$

where H and T represent hand and target trajectories. These estimated $\hat{M}$'s were averaged element-wise across participants to generate the alignment matrices shown in Figure 3.3A. These matrices were visualized by plotting their column vectors, also shown in Figure 3.3A.

The off-diagonal elements of each participant's alignment matrix were used to calculate the off-diagonal scaling, S, in Figure 3.3B:

$$S_{\text{rotation}} = \frac{-b+c}{2}, \qquad S_{\text{mirror}} = \frac{b+c}{2}. \tag{3.2}$$

Compensation angles, θ, for the rotation group's alignment matrices were found using the singular value decomposition, $\text{SVD}(\cdot)$. This is a standard approach which, as described in Umeyama, 1991, identifies a 2D rotation matrix, R, that best describes $\hat{M}$ irrespective of other transformations (e.g., dilation, shear) (Figure 3.3C, left). Briefly,

$$U \Sigma V^T = \text{SVD}(\hat{M}^T), \tag{3.3}$$

$$R = VU^T \tag{3.4}$$

where U and V contain the left and right singular vectors and Σ contains the singular values. Note that R is a rotation matrix only if $\det(\hat{M}^T) \geq 0$, but R is a reflection matrix when $\det(\hat{M}^T) < 0$. Although Umeyama, 1991 described a method whereby all R can be forced to be a rotation matrix, we did not want to impose nonexistent structure onto R and, thus, did not analyze trials which yielded reflection matrices. However, this was not a major issue for the analysis as nearly all trials yielded rotation matrices (3205 out of 3360 data points for experiment 1; 2230 out of 2520 data points for experiment 2). Subsequently, θ was calculated as

$$\theta = \mathrm{atan2}(R_{2,1}, R_{1,1}) \tag{3.5}$$

where $\mathrm{atan2}(\cdot)$ is the 2-argument arctangent and the inputs to the arctangent are elements of R subscripted by the row and column numbers of the matrix.

Finally, for the mirror-reversal group, the scaling orthogonal to the mirror axis was found by computing how the matrix transformed the unit vector along the orthogonal axis (Figure 3.3C, right):

$$S_{\text{orthogonal}} = \frac{1}{2}\left(\begin{bmatrix}1 & -1\end{bmatrix}\begin{bmatrix}a & b\\ c & d\end{bmatrix}\begin{bmatrix}1\\ -1\end{bmatrix}\right) = \frac{1}{2}(a-b-c+d). \tag{3.6}$$

3.4.3 Frequency-Domain Analysis

To analyze trajectories in the frequency domain, we applied the discrete Fourier transform to the target and hand trajectories in every tracking trial. This produced a set of complex numbers representing the amplitude and phase of the signal at every frequency. We only analyzed the first 40 seconds of the trajectory that followed the 5-second ramp period so that our analysis period was equivalent to an integer multiple of the base period (20 s). This ensured that we would obtain clean estimates of the sinusoids at each target frequency. Amplitude spectra were generated by taking double the modulus of the Fourier-transformed hand trajectories at positive frequencies.

The spectral coherence between signals was computed using Welch's periodogram technique, implemented using the MATLAB function `mscohere`. Windowing was performed using a 1040-sample Blackman-Harris window with 50% overlap between windows. To evaluate the proportion of participants' behavior that could be explained by a linear model, for every trial, we evaluated the single-input multi-output coherence at every frequency of target motion ("linear coherence"), determining how target motion in one axis elicited hand movement in both axes. This best captured the linearity of participants' behavior as using hand movement in only one axis for the analysis would only partially capture participants' responses to target movement at a given frequency. To evaluate the additional proportion of participants' behavior that could be explained by a nonlinear model but not a linear model, we computed the square root of the single-input single-output coherence (i.e., movements from the same axis) between hand movements from every pairwise combination of trials within each block ("nonlinear coherence"). Because this nonlinear coherence is calculated from data across trials, it cannot be computed on a trial-by-trial basis so we averaged this coherence within blocks to obtain one coherence measure per block. We then averaged the linear coherence within blocks and subtracted the linear coherence from the nonlinear coherence.

During each 40 s stimulus period, we assumed the relationship between target position and hand position behavior was well approximated by linear, time-invariant dynamics; this assumption was tested using the coherence analysis described above. Under this assumption, pure sinusoidal target motion at each frequency should be translated into pure sinusoidal hand motion at the same frequency but with different magnitude and phase. The relationship between hand and target can therefore be described in terms of a 2×2 matrix of transfer functions describing the behavior of the system at each possible frequency:

$$\begin{bmatrix} H_x(\omega) \\ H_y(\omega) \end{bmatrix} = P(\omega) \begin{bmatrix} T_x(\omega) \\ T_y(\omega) \end{bmatrix}, \quad P(\omega) = \begin{bmatrix} p_{xx}(\omega) & p_{xy}(\omega) \\ p_{yx}(\omega) & p_{yy}(\omega) \end{bmatrix}. \tag{3.7}$$

Here, $H(\omega)$ and $T(\omega)$ are the Fourier transforms of the time-domain hand and target trajectories, respectively, and ω is the frequency of movement. Each element of $P(\omega)$ represents a transfer function relating a particular axis of target motion to a particular axis of hand motion; the first and second subscripts represent the hand- and target-movement axes, respectively. Each such transfer function is a complex-valued function of frequency, which can further be decomposed into gain and phase components, e.g.:

$$p_{xy}(\omega) = g_{xy}(\omega) e^{j\phi_{xy}(\omega)}, \tag{3.8}$$

where j is the imaginary number, $g_{xy}(\omega)$ describes the gain (ratio of amplitudes) between y-axis target and x-axis hand motion as a function of frequency, and $\phi_{xy}(\omega)$ describes the corresponding difference in the phase of oscillation.

We used this phase (in radians) to obtain the frequency-dependent lag between hand and target movement, $\delta(\omega)$, (in seconds) follows:

$$\delta(\omega) = \frac{\phi(\omega)}{2\pi\omega}. \tag{3.9}$$

The difference in $\delta(\omega)$ between baseline and late learning was used to generate

Figure 3.4C.

We estimated the elements of $P(\omega)$ for frequencies at which the target moved by first noting that, for x-axis frequencies ω, $T_y(\omega) = 0$. Consequently,

$$\begin{bmatrix} H_x(\omega) \\ H_y(\omega) \end{bmatrix} = \begin{bmatrix} p_{xx}(\omega) T_x(\omega) \\ p_{yx}(\omega) T_x(\omega) \end{bmatrix}, \tag{3.10}$$

and we can therefore estimate $p_{xx}(\omega)$ and $p_{yx}(\omega)$ as:

$$p_{xx}(\omega) = \frac{H_x(\omega)}{T_x(\omega)}, \qquad p_{yx}(\omega) = \frac{H_y(\omega)}{T_x(\omega)}. \tag{3.11}$$

We estimated $p_{yx}(\omega)$ and $p_{yy}(\omega)$ analogously at y-frequencies of target motion.

These estimates yielded two elements of the overall transformation matrix $P(\omega)$ at each frequency of target movement. In order to construct a full 2×2 matrix, we paired the gains from neighboring x- and y-frequencies, assuming that participants' behavior would be approximately the same at neighboring frequencies. The resulting 7 frequency pairings were (x then y frequencies reported in each parentheses in Hz): (0.1, 0.15), (0.25, 0.35), (0.55, 0.65), (0.85, 0.95), (1.15, 1.45), (1.55, 1.85), (2.05, 2.15).

The spatial transformation of target motion into hand motion at each frequency is described by the gain of each element of $P(\omega)$. However, gain and phase data can lead to certain ambiguities; for example, a positive gain with a phase of π radians is indistinguishable from a negative gain with a phase of 0. Conventionally, this is resolved by assuming that gain is positive. In our task, however, the sign of the gain was crucial to disambiguate the directionality of the hand responses (e.g., whether the hand moved left or right in response to upward target motion). We used phase information to disambiguate positive from negative gains. Specifically, we assumed that the phase lag of the hand response at a given frequency would be the same across both axes of hand movement and throughout the experiment, but the gain would vary:

$$p_{xx}(\omega) \approx g_{xx}(\omega) e^{j\widetilde{\phi}(\omega)}, \qquad p_{yx}(\omega) \approx g_{yx}(\omega) e^{j\widetilde{\phi}(\omega)}. \tag{3.12}$$

For a given movement frequency, $\widetilde{\phi}(\omega)$ was set to be the same as the mean phase lag during the baseline block, where the gain was unambiguously positive. This assumption enabled us to compute a signed gain for each transfer function by taking the dot product between the transfer function and $e^{j\widetilde{\phi}(\omega)}$. This method thus yielded gains for each axis of hand motion, at each target frequency, and at each point during learning.

As we did for the transfer-function matrix $P(\omega)$, we paired the gains from neighboring frequencies to obtain a series of seven gain matrices which geometrically described how target motion was translated into hand motion from low to high frequencies. Similar to the alignment matrix analysis, visualizations of these gain matrices were constructed by plotting the column vectors of the matrices. Off-diagonal gain, rotation angle, and gain orthogonal to the mirroring axis were calculated in the same way as in Equations 3.2–3.6.

3.4.4 Statistics

The primary statistical tests for the main and follow-up experiments were performed using linear mixed-effects models. These models were fit using data from three parts of the study: 1) alignment matrix analysis in the main experiment, 2) gain matrix analysis in the main experiment, and 3) gain matrix analysis in the follow-up experiment. The data used in these models were the off-diagonal values of the transformation and gain matrices. In all models, data from the first trial of baseline, the last trial of late learning, and the first trial of post-learning were analyzed. No outlier rejection was performed for these analyses. Using Wilkinson notation, the structure of the model for the alignment matrix analysis was [off-diagonal scaling] $\sim$ [block of learning] * [perturbation group] while the structure for both gain matrix analyses was [off-diagonal gain] $\sim$ [block of learning] * [perturbation group] * [frequency of movement]. Data were grouped within subjects (subjects were considered a random effect of the model).

We subsequently performed post hoc statistical comparisons as needed for each of the linear mixed-effects models. For the alignment matrix analysis, we performed pairwise comparisons using Tukey's range test. For the gain matrix analysis in the main and follow-up experiments, there was a 3-way interaction between frequency and the other regressors, so we fit seven different mixed-effects models for each frequency of movement post hoc. We performed pairwise comparisons on these frequency-specific models using Tukey's range test. Although this test corrects for multiple comparisons, it only corrected the p-values for comparisons within each of the seven frequency-specific models. Because we ran Tukey's range test seven times in total, we applied an additional Bonferroni correction by multiplying the p-values by seven.

We used a two-way ANOVA to compare the late-learning gain matrices between the main and follow-up experiments. Similar to the linear mixed effects analyses, we compared the off-diagonal elements of the matrices. No outlier rejection was performed for this analysis. Using Wilkinson notation, the structure of the ANOVA was [off-diagonal gain] $\sim$ [experiment] * [perturbation group] * [frequency of movement].

Chapter 4

De novo learning of a bimanual control task

The following chapter is adapted from Haith et al., 2021.

4.1 Introduction

One of the most defining features of *de novo* learning tasks is that they require relatively long periods of practice to master. In the case of many complex, real-world tasks such as piano or tennis, mastery may only be achieved after years or decades of practice. The reason why *de novo* learning requires such extensive practice has eluded explanation.

One potential explanation for why *de novo* learning is slow is that for certain tasks, it may be a significant challenge to discover what actions are needed to bring about a desired outcome. For instance, many putative, laboratory-based *de novo* learning tasks require people to learn an arbitrary mapping from body position (Casadio et al., 2012; Mosier et al., 2005; Ranganathan et al., 2014), muscle activity (Berger et al., 2013; Radhakrishnan et al., 2008; Rugy et al., 2012), or neural activity (Ganguly and Carmena, 2009; Sadtler et al., 2014; Orsborn and Carmena, 2013; Oby et al., 2019) to the location of an on-screen cursor. When learning such arbitrary and non-intuitive mappings, people may need to systematically search the space of possible actions available to them in order to identify a suitable solution, and this search process could account for why learning is so slow—particularly in high dimensional action spaces. Another possible explanation is that a task may require participants to generate unfamiliar actions, moving fingers or activating novel combinations of muscles or neurons (Koralek et al., 2012; Rugy et al., 2012; Sadtler et al., 2014). Learning to consistently generate these novel actions might require practice and could itself account for why overall performance improves slowly (Costa, 2011; Diedrichsen and Kornysheva, 2015; Oby et al., 2019).

A third possibility, however, is that even if we have explicitly identified what actions are needed to succeed at a task and can execute those actions reliably, substantial practice might still be needed to build a *de novo* controller that can rapidly select an appropriate action given the current states and goals. The benefit of practice for accelerating action selection is clear in discrete choice, arbitrary visuomotor association tasks (Hardwick et al., 2019) and assembling a controller that can select actions rapidly enough for smooth continuous control might similarly require extensive practice.

To better understand why *de novo* learning may be slow, we developed a task which isolated the learning problem to building a novel controller (Figure 4.1A). The task involved maneuvering an on-screen cursor using a mapping that could easily be understood by participants, thereby eliminating the problem of searching action spaces. Moreover, controlling the cursor required only planar arm movements, eliminating the problem of executing unfamiliar actions. Unlike the mirror reversal perturbation we used to study *de novo* learning in Yang et al., 2021—which participants could learn to counter in roughly an hour of practice—this mapping required multiple days of practice to achieve proficient control over the cursor and to generate appropriate rapid responses to online perturbations. Crucially, the simplicity of the task also allowed us to directly compare performance to a baseline condition, providing a ceiling on the performance level that could be expected under the bimanual mapping, and revealing clear limitations on the capability of controllers learned *de novo*.

4.2 Results

4.2.1 Performance improves gradually over multiple days of practice

Participants learned to maneuver an on-screen cursor using a non-intuitive bimanual control interface (Figure 4.1B). Forward-backward movement of the left hand controlled right-left movement of the cursor, and right-left movement of the right hand controlled forward-backward movement of the cursor (the "bimanual" mapping). This relationship between movement of the hands and movement of the cursor was explicitly described to participants. Nevertheless, they found it extremely challenging to control the cursor under this mapping. During the first block of point-to-point movements using the novel bimanual mapping, participants took, on average, over 7 seconds to complete each

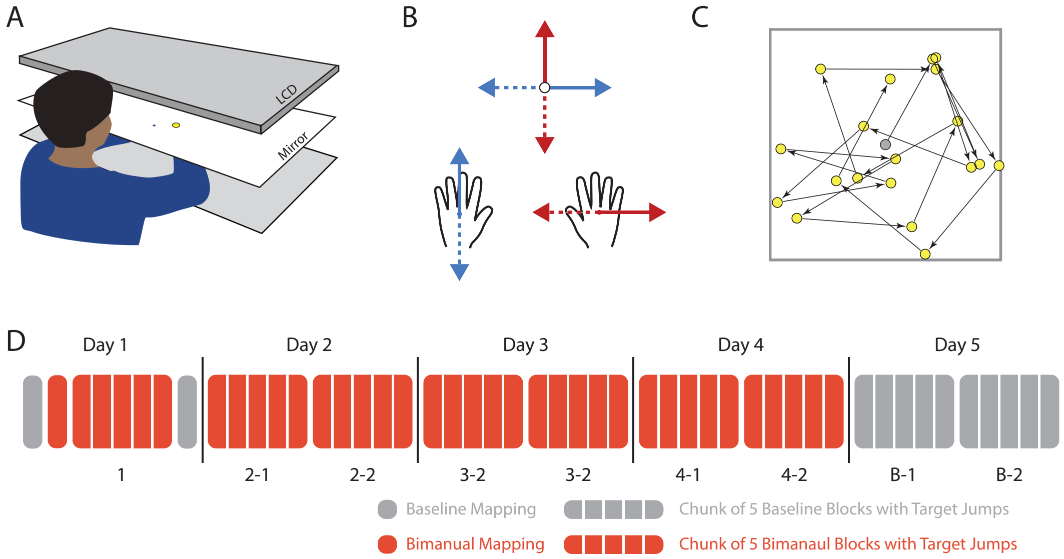

Figure 4.1: **A.** Participants moved both of their arms on a horizontal surface to maneuver an on-screen cursor which they viewed in the plane of their arm movements via a mirrored display. **B.** Participants learned to maneuver a cursor via a bimanual mapping by which forward-backward movement of the left hand led to right-left movement of an onscreen cursor, while right-left movement of the right hand led to forward-backward movement of the cursor. **C.** In each block, participants performed a series of 60 point-to-point movements within a 20 × 20 cm workspace, with each new target appearing after the previous target was successfully acquired. **D.** Participants completed testing over 5 consecutive days, performing either baseline blocks in which the cursor appeared at the location of the right hand (grey) or bimanual blocks (using the bimanual mapping in B) (red), arranged either as an isolated block with no target jumps (only on Day 1) or as a chunk of 5 blocks that included target jumps.

12 cm movement of the cursor (Figure 4.2D; 7.39 s ± 1.79 s, std. dev. in mean task duration across participants), compared to less than 1 second when performing the same task using only their right hand with veridical cursor feedback ("baseline" mapping; 0.94 s ± 0.13 s, std. dev. across participants). The trajectory of the cursor was erratic (Figure 4.2A), which we quantified in terms of the normalized path length (i.e., the total path length divided by distance from start to target; the lowest possible value is 1). Early trials

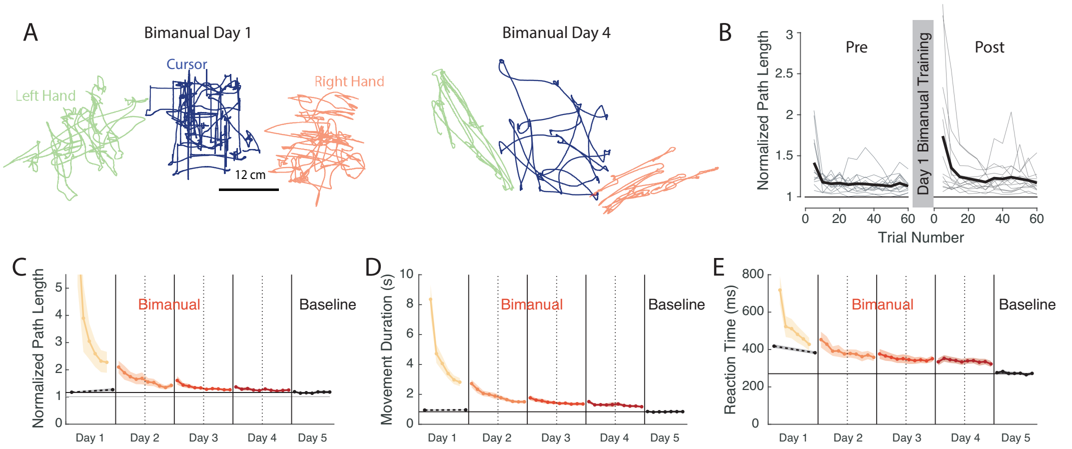

Figure 4.2: A. Example trajectories for a representative participant in Experiment 1, showing the first 20 movements of a block during Day 1 (left) and Day 4 (right). Green and red lines show trajectories of the left and right hands, respectively (which the participant could not see), while the dark blue lines show trajectories of the cursor. **B.** Normalized path length for each trial under the baseline mapping before (left) and after (right) training under the bimanual mapping on Day 1. Thick black line indicates average across participants. Thin gray lines indicate individual participants. **C.** Average normalized path length across each block for the duration of the experiment. Black points indicate performance under the baseline mapping. Colored lines indicate performance under the bimanual mapping. Solid vertical lines indicate breaks between days. Vertical dashed lines indicate brief breaks between chunks of blocks. Shaded regions indicate +/âĹŠ standard error in the mean across participants. **D–E.** Similar to C but for movement duration and reaction time, respectively.

under the bimanual mapping had an average normalized path length of 5.99 ± 3.41 (Figure 4.2C; 71.8 ± 40.79 cm path length to reach a target 12 cm away), in comparison to a normalized path length of 1.20 ± 0.24 in the baseline mapping with a veridical cursor (14.4 cm ± 2.9 cm un-normalized). Over five subsequent blocks of practice on Day 1, participants improved their performance considerably (Figure 4.2); by their sixth block of practice (360 trials), their average movement duration had reduced to 2.82 s ± 0.99 s, and the normalized path length reduced to near-baseline levels. Reaction times also decreased substantially.

To determine whether participants had learned this task through adaptation of their existing, baseline controller or by forming a brand new control policy (i.e., *de novo* learning), we removed the bimanual mapping at the end of Day 1 and reverted back to the baseline mapping to assess whether participants exhibited any aftereffects. A minority of participants initially made erroneous movements, despite having been clearly informed of the change back to a veridical cursor. However, these errors were transient rather than persistent; all participants had reverted to baseline performance levels within around 10 trials (Figure 4.2B). When averaged over the entire block of 60 trials, differences in path length and movement duration between the baseline blocks immediately preceding or immediately following the 6 bimanual practice blocks on Day 1 were small and non-significant (normalized path length, average difference $= 0.01$, $p = 0.093$, $t = 1.84$; duration, average difference $= 14.8$ ms, $p = 0.73$, $t = 0.35$), while reaction times decreased for the block after training with the bimanual mapping than for the block before ($p < .001$, $t = 5.1$; Figure 4.2E). Together, these results show that there were no systematic and persistent aftereffects from learning to use the bimanual mapping, indicating that they did not learn to do so through adaptation, but rather by constructing a new controller *de novo* (Yang et al., 2021).

Participants returned to practice the bimanual mapping for three more sessions on consecutive days, during which time their performance continued to improve steadily (Figure 4.2B–E). The cursor moved more directly towards the target (normalized path length, Day 2 first 5 blocks versus Day 4 last 5 blocks; paired t-test: $p < .01$, $t = 2.94$) and movement duration (paired t-test:

$p < .001$, $t = 4.60$) and reaction time (paired t-test: $p < .01$, $t = 2.73$) both decreased, while movement speed (assessed based on the peak velocity over the first second of each trial) increased significantly over the same period (paired t-test: $p < .01$, $t = 3.10$; not shown).

By the end of Day 4, participants' performance appeared to have reached a plateau. To test how their performance compared to baseline, we conducted a separated test session on Day 5 consisting of 10 blocks where participants controlled a veridical cursor. This test session allowed us to assess responses to target jumps under the baseline mapping (see next section) and controlled for the possibility that participants' performance may have improved in ways that were not directly related to learning a *de novo* controller. Performance under the bimanual mapping at the end of Day 4 was close to performance under the baseline mapping tested on Day 5 (Figure 4.2C–E). Performance did differ, however, in terms of movement duration (paired t-test, $p < .001$, $t = 4.6$), reaction time (paired t-test: $p < .001$, $t = 4.70$) and peak velocity (paired t-test: $p < .01$, $t = 3.61$), but not path length (paired t-test, $p = 0.19$, $t = 1.94$). Therefore, performance under the bimanual mapping came close to that under the baseline mapping but remained slightly poorer.

4.2.2 Rapid feedback responses emerged gradually with practice

In addition to quantifying the quality of participants' point-to-point movements, we also examined participants' ability to generate rapid corrections when the target jumped to a new location during movement. In $\frac{1}{3}$ of trials, the target was displaced orthogonal to the required movement direction by either

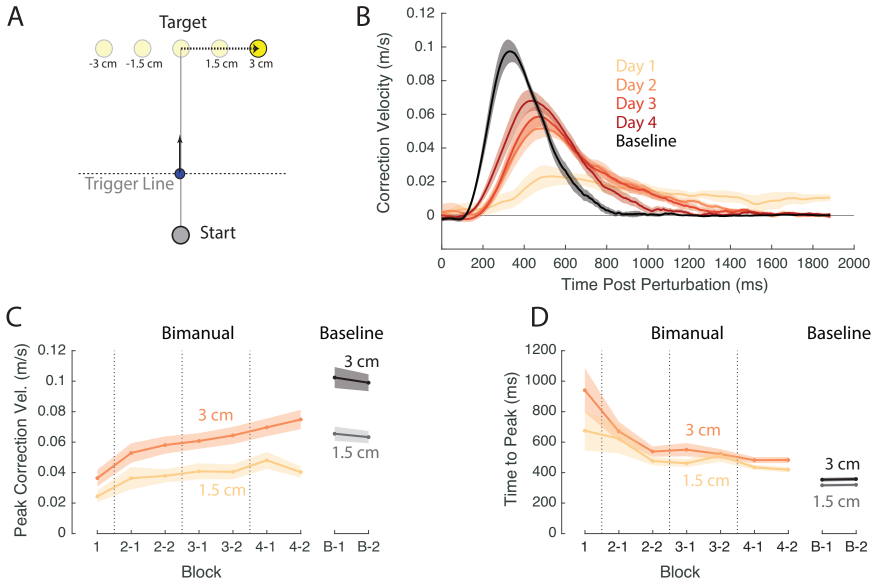

Figure 4.3: **A.** Within certain blocks, a subset (1/3) of targets could jump orthogonal to the primary direction of movement by 1.5 cm or 3 cm during movement, prompting a corrective response. Jumping of the target was triggered when the cursor crossed an invisible line 1/3 of the way to the original target location from the start position. **B.** Velocity profile of corrective responses in the direction parallel to the target jump for 3 cm jumps, averaged across jump directions (flipped accordingly). Colored lines indicate corrective response under the bimanual Mapping at different stages of learning. Black line indicates corrective response under the baseline Mapping. **C.** Peak correction velocity as a function of practice under the bimanual mapping (colored lines) and under the baseline mapping (black/gray lines). Error bars show +/âĹŠ standard error in the mean across participants. **D.** As C) but showing the latency to peak correction velocity.

± 1.5 cm or ± 3 cm, after the cursor crossed a line $\frac{1}{3}$ of the distance between the start position and the target (Figure 3A). On the first day of practice, participants generated weak and erratic responses to target jumps. Starting on the second day, however, a clear response emerged which became more rapid over subsequent days of practice (Figure 3B).

We quantified the strength of the feedback response in terms of the peak correction speed (parallel to the target displacement) and the latency to this peak speed. The peak speed of correction increased from the first to the fourth practice session for both large and small target jumps (Figure 4.3C; 1.5 cm jump: $p < .005$, $t = 4.15$; 3cm jump: $p < .0001$, $t = 6.39$) and the latency to this peak also decreased (Figure 4.3D; 1.5 cm jump: $p < .0001$, $t = 6.39$; 3 cm jump: $p = 0.014$, $t = 4.15$). However, the velocity of corrective movements remained slower than those under the baseline mapping (1.5 cm jump: $p < .005$, $t = 3.94$; 3cm jump: $p < .0001$, $t = 6.39$), and the peak velocity occurred later (1.5 cm jump: $p < .0001$, $t = 6.39$; 3 cm jump: $p = 0.002$, $t = 3.93$) suggesting that, even though the *de novo* skill had been well learned, performance was still substantially worse than their baseline performance. We also examined whether the latency of response onset differed across mappings or with extent of practice. We estimated response onset by fitting a piecewise linear-quadratic function to the early part of the response velocity profile (see Methods for details). We found that, under the baseline mapping, online corrective responses began at 186 ms and 196 ms after the target jump for small and large target jumps, respectively (average of both blocks on Day 5). Under the bimanual mapping, by contrast, responses began at 223 ms and 233 ms for small and large target jumps, significantly slower than under the baseline mapping (1.5 cm jump: $p = 0.032$, $t = 2.417$; 3 cm jump: $p = 0.043$, $t = 2.253$).

4.2.3 Slower feedback corrections under the bimanual mapping were not attributable to slower primary movements

A limitation of Experiment 1 is that participants typically moved more slowly under the bimanual mapping than under the baseline mapping (t-test on peak velocity of primary movement; $p = 0.0034$, $t = 3.64$). This difference in the speed of primary movements might have accounted for the slower feedback corrections under the bimanual mapping. We conducted a second experiment in which, starting on Day 2, we gave participants feedback about the peak velocity of the cursor at the end of each movement (Figure 4.4A), enabling them to achieve more consistent movement speeds across the baseline and bimanual mappings (Figure 4.4B; peak velocity on last day of bimanual practice vs baseline, $p = 0.821$, $t = 0.235$). Despite the speed of the primary movement being matched across mappings, the speed of feedback corrections remained significantly slower under the bimanual mapping than under the baseline mapping, even after 3 days of practice (Figure 4.4E; 1.5 cm jump: $p < 10^{-5}$, $t = 11.49$; 3 cm jump: $p < .01$, $t = 4.35$). The latency of peak responses was also greater for the bimanual mapping compared to under the baseline mapping (Figure 4.4F; 1.5 cm jump: $p < 10^{-7}$, $t = 25.4$; 3 cm jump: $p < 10^{-7}$, $t = 23.7$), as was the latency of response onset (1.5 cm jump: $p = 0.009$, $t = 3.58$; 3 cm jump: $p = 0.0014$, $t = 5.12$; not shown). Therefore, even when the vigor of primary movements was well matched across conditions, participants could not correct errors as rapidly under the *de novo* controller learned for the bimanual mapping.

4.2.4 Slow feedback corrections under the bimanual mapping were not due to controlling two hands rather than one

One possible explanation for why participants were able to respond more rapidly under the baseline mapping than under the bimanual mapping is that the bimanual mapping required them to use both hands, whereas the baseline

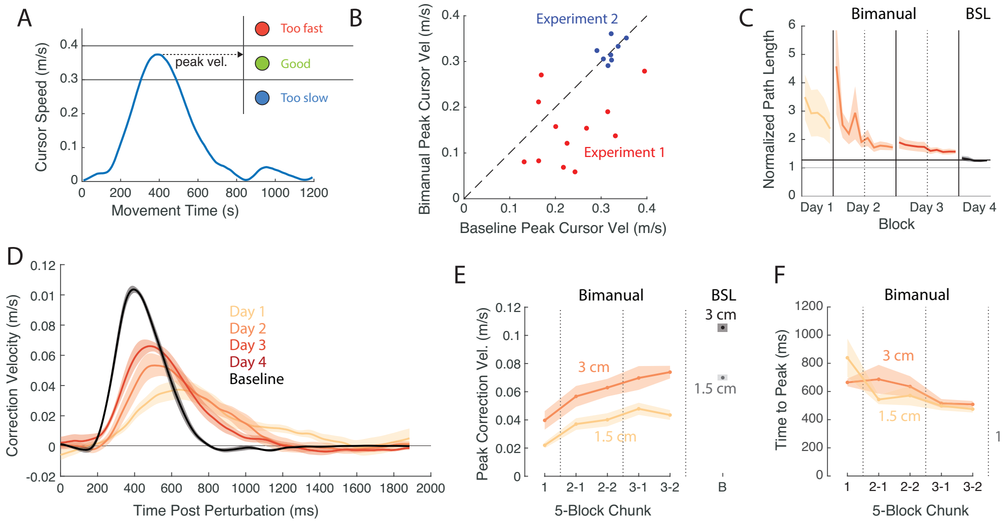

Figure 4.4: **A.** In Experiment 2, we controlled movement speed by providing participants with feedback about the peak cursor velocity. Upon reaching the target, it changed color to indicate whether the peak cursor velocity was within the required range (green) or above or below it (red/blue). **B.** Comparison of peak velocity under the baseline mapping and in the final block of practice under the bimanual mapping for Experiment 1 (red dots) and Experiment 2 (blue dots). Each represents an individual participant. **C.** Normalized path length while practicing the bimanual mapping in Experiment 2 (as Figure 4.2C). Shaded regions indicate +/âĹŠ standard error in the mean across participants. **D.** Averaged velocity profiles of corrective movements following target jumps in Experiment 2 (as Figure 4.3B). **E.** Peak correction velocity (as Figure 4.3C). **F.** Latency to peak correction velocity (as Figure 4.3D).

mapping only required them to use their dominant right hand. The slower response under the bimanual mapping could conceivably be attributable to having to coordinate the use of both effectors, or might reflect slower responses of the nondominant hand. To test whether the use of both hands versus a single hand could account for the discrepancy in behavior, we performed an additional experiment (Experiment 3) in which participants controlled the cursor either with their dominant (right) hand, non-dominant (left) hand, or both hands together with the cursor appearing at the average position of the two hands.

Participants' corrections to target jumps did appear slightly faster when using their right hand alone in comparison to using both hands to control the cursor (Figure 4.5A). The peak velocity did not differ significantly according to how the cursor was controlled (ANOVA, $p = 0.07$, $F(2, 54) = 2.77$), but the latency to peak correction did (ANOVA, $p = 0.016$, $F(2, 54) = 4.47$). Critically, however, the differences in correction velocity when using the right hand versus using both hands in Experiment 2, where the mapping was veridical in both cases, was significantly less than the same difference for Experiment 2 (two-way ANOVA, main effect of experiment: $F(1, 32) = 28.94$, $p < .0001$), and the same was true for the latency to peak velocity (two-way ANOVA, main effect of experiment: $F(1, 32) = 16.76$, $p = 0.0003$). These data demonstrate that even if the use of both hands causes movements to slow down compared to movements with just the dominant hand, this difference cannot entirely account for the difference in performance between the baseline and bimanual mappings in Experiment 2. Instead, the slower feedback corrections under the bimanual mapping were a property of the learned controller.

4.3 Discussion

We have introduced a novel motor learning paradigm for studying *de novo* motor learning. Our paradigm is simple in that it involves only a linear mapping from planar arm movements to cursor movements that can be easily explained to participants. However, the mapping itself is very challenging to learn, requiring multiple sessions of practice to gain proficiency. The use of

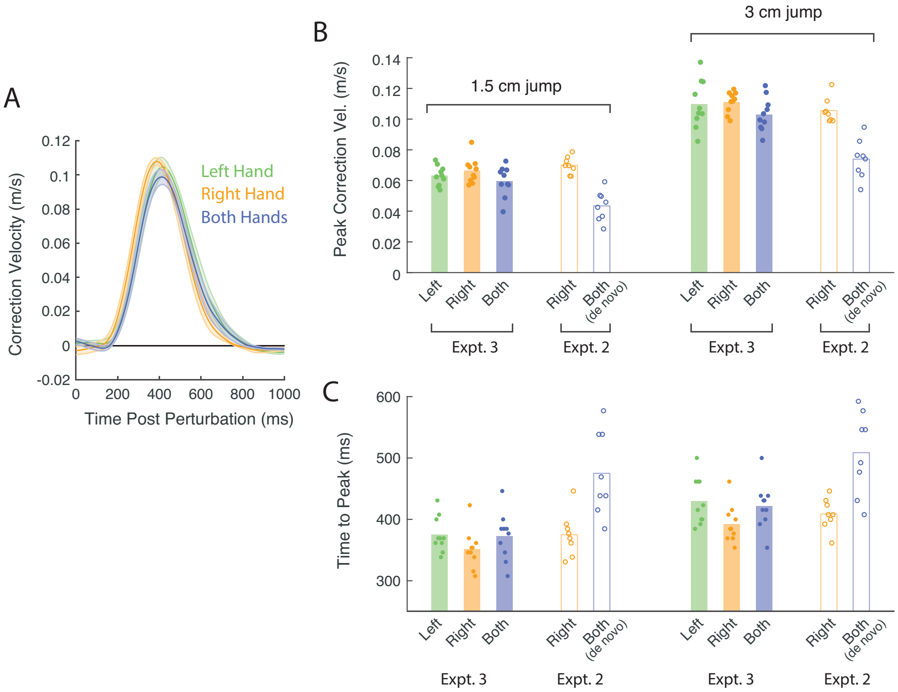

Figure 4.5: **A.** Velocity profile of corrective responses parallel to the direction of the target jump in the left-hand (green), right-hand (orange), and both-hands (blue) conditions, as in Figure 4.3B. **B–C.** Peak correction velocity and latency to peak correction velocity for different handedness conditions and jump sizes in Experiment 3 (filled markers and bars) and Experiment 2 (unfilled markers and bars). Dots represent behavior of individual participants. Colored bars indicate mean behavior across participants.

planar arm movements means that participants do need to learn to generate unfamiliar movements, as is often the case in many kinematic, myo-electric and body-machine interface learning tasks. Furthermore, by testing participants' behavior in the same tasks but with a veridical cursor (the baseline mapping), we are able to establish a ceiling on the performance level that could be expected of participants in this task. Our results clearly demonstrate gradual improvements in performance over multiple sessions of practice, and also show that, even after 4 days of training, participants' performance under the bimanual mapping still remained worse than under the baseline mapping.

In principle, learning to control a cursor under our bimanual mapping could be construed as countering a perturbation, rather than as acquiring a new skill. However, the absence of persistent aftereffects demonstrates that participants did not learn the task through adaptation mechanisms, but instead built a new policy, i.e. through "de novo" learning (Yang et al., 2021). In this respect, the learning we observed here might be similar to that seen in response to mirror reversals of visual feedback (Lillicrap et al., 2013; Telgen et al., 2014; Yang et al., 2021). However, an important difference between our bimanual mapping and a mirror reversal is that, under a mirror reversal, the required movement under the reversal is in direct conflict with the movement that would be required at baseline. By contrast, under the bimanual mapping, the hand movements required under the bimanual mapping are orthogonal to those required at baseline. Moreover, a mirror reversal can be solved via a simple re-aiming strategy (Wilterson and Taylor, 2021), whereas such a strategy is not readily available under the bimanual mapping.

A major question not resolved by our present experiments is whether, with additional practice, performance under the bimanual mapping could eventually match that under the baseline mapping, both in terms of the quality of point-to-point movements and of rapid corrective responses. Anecdotally, we found that two authors of this study who practiced the bimanual mapping extensively (about 3 weeks) did not appear to exhibit any performance gains beyond those seen in the results of Experiment 1. A larger cohort will be required to rigorously test whether this is the case in general. It is possible that extremely rapid responses using a veridical cursor is achieved by engaging rapid subcortical pathways (Perfiliev et al., 2010), whereas using the bimanual mapping requires engagement of slower cortical circuitry, accounting for the seeming limit on performance under the bimanual mapping. However, the extent of subcortical involvement in simple arm movements in humans remains unclear.

When thinking about what makes motor skill learning difficult, one often thinks first about the challenge of learning to execute unfamiliar movements. However, our results suggest that the challenge of learning to map familiar states to familiar actions is another potential bottleneck that can explain why many real-world skills take so long to learn. We believe that the bimanual mapping introduced here can serve as a useful paradigm for investigating the nature of this performance bottleneck and, more generally, *de novo* learning.

4.4 Methods

A total of 31 participants (9 male, 22 female; average age 24.7) were recruited for this study, of which 13 participated in Experiment 1 (3 male, 10 female; average age 24.2), 8 participated in Experiment 2 (3 male, 5 female; average age 23.8), and 10 participated in Experiment 3 (3 male, 7 female; average age 26.1).

4.4.1 Experiment 1

Participants controlled an on-screen cursor using either a baseline or bimanual hand-to-cursor mapping. Under the baseline mapping, the cursor appeared at the true position of their right hand. Under the bimanual mapping, the x-location of the cursor was determined by the y-location of their left hand and the y-location of the cursor was determined by the x-location of their right hand. Changes in the x-location of the left hand and the y-location of the right hand had no effect on the location of the cursor. This mapping was explicitly explained to participants prior to the start of their first time experiencing the bimanual mapping. Participants used both of these mappings to perform point-to-point reaches in blocks of 60 trials.

In some blocks, we probed online rapid responses with target jumps. In a given block, $\frac{1}{3}$ of targets (nonconsecutive) were selected as targets that could jump. During movements to these targets, the target would jump once the cursor crossed a perpendicular line $\frac{1}{3}$ of the distance to the target (Figure 4.3A) by ± 1.5 cm, ± 3 cm, or 0 cm. Participants completed blocks in chunks of 5 with the same target sequence each time, experiencing each jump amplitude once at each jump target, in a different pseudorandom order across trials for each target. Thus, within each chunk of 5 blocks, participants experienced 20 jump trials of each possible size.

Participants first completed an initial block of 60 movements without target jumps. They then completed a chunk of five 60-trial blocks with target jumps, structured as described above. For the final block on the first day, participants performed a single block of movements under the baseline mapping to assess any potential aftereffects from learning to control the cursor under the bimanual mapping. Participants returned to practice the bimanual mapping for three further sessions on consecutive days. In each of these sessions, they completed two chunks of five blocks (600 trials total) that included target jumps, which lasted approximately half an hour. On Day 5, participants returned to complete two more chunks of five blocks (600 trials total) under the baseline mapping.

4.4.2 Experiment 2

In Experiment 2, we sought to better control the speed of participants movements across the baseline and bimanual mappings. Participants were instructed to try to keep the speed of their movements consistent throughout the experiment. After each target was acquired, we provided participants feedback about the peak velocity of their movement. If the peak speed of the cursor was less than 0.3 m/s, the target they had just reached turned blue, indicating that the movement was too slow. If the peak speed of the cursor was greater than 0.4 m/s, the target turned red, indicating that the movement was too fast. If the peak speed was between 0.3 m/s and 0.4 m/s, the target turned green, indicating a good speed.

Experiment 2 followed a similar structure to Experiment 1, except that participants only practiced the bimanual mapping for 3 days instead of 4. Feedback about movement speed was not given on Day 1, since it was very difficult to comply with this requirement while initially learning the vimanual mapping. Feedback about movement speed was provided on Day 2 onwards.

4.4.3 Experiment 3

In order to determine whether the differences we observed in feedback corrections between the baseline and bimanual mappings was due to using one hand or two hands, we performed an additional control experiment to assess performance using different effectors. Participants completed 3 chunks of 5 blocks with target jumps and feedback about movement speed. For each chunk, the cursor was aligned either to: i) the veridical location of the participant's left hand, ii) the veridical location of the participant's right hand, or iii) the location halfway between their left hand and right hand.

4.4.4 Data analysis

Position data of both hands and the cursor were smoothed using a Savitzky-Golay filter and numerically differentiated to obtain movement velocity. The movement onset time was determined based on the first timepoint when the cursor's movement velocity exceeded 0.025 m/s after the target was presented and this was also used to determine the reaction time. The movement end time was determined based on the earliest time at which participants successfully held the center of the cursor stationary (tangential velocity < 0.025 m/s) within the target. Movement duration was determined based on the difference between movement onset and movement end time. The path length was computed as the total length of the smoothed trajectory between the movement onset time and the movement end time. The normalized path length was this distance divided by the distance between the center of the start position and the target position (12 cm). Only movements in which the target did not jump were included in the path length analysis. Differences in performance between mappings and between different points during learning were assessed using paired t-tests.

To analyze corrective movements in response to target jumps, we extracted the velocity of the cursor parallel to the direction of the target jump (perpendicular to the straight line between the start position and initial target position for each movement) and aligned these trajectories to the time at which the target jumped. We averaged velocity profiles for leftward and rightward jumps of the same magnitude by flipping the sign of the data for responses to leftward target jumps. To quantify corrections, we computed the peak correction velocity for each trial and averaged these across jumps of similar size within each chunk of 5 blocks. We also computed the average time at which this peak correction velocity was attained.

We estimated the time at which the response to the target jump was first initiated by fitting the averaged velocity profiles using a simple model of the corrective velocity profile consisting of a linear portion before the onset of the response, and a quadratic portion after the response was initiated:

$$v(t) = \begin{cases} at + b, & t < t_{\text{init}} \\ at + b + c(t - t_{\text{init}})^2, & t \geq t_{\text{init}} \end{cases} \tag{4.1}$$

Here, t_{init} represents the time of response initiation. This function was fit to the region of the velocity profile spanning 100 ms before the target jump up to the point at which the velocity reached half of its peak value. To avoid spurious estimates of t_{init} under the bimanual mapping, particularly during early blocks in which corrections were often weak, we constrained the parameter c to be greater than 10, to match the lowest estimates identified for the baseline mapping. We fitted this model to averaged velocity profiles for each participant for a given target jump size and chunk of blocks after excluding extreme trials in which the cursor position at the time of the target jump deviated from the straight line to the target by more than 5 cm, or in which the absolute velocity of the cursor parallel to the target jump at the time of the target jump exceeded 0.2 m/s.

For the control experiment, we assessed whether movement corrections depended on the control interface (left hand, right hand or both hands) using a one-way repeated measures ANOVA. To assess whether possible differences between one-hand and both-hands could account for the observed differences in correction speed between the baseline and bimanual mappings in Experiments 1 and 2, we compared the difference in behavior (the peak correction velocity and latency to peak correction velocity) between one-hand and both-hands condition in the control experiment and the baseline and bimanual mappings in Experiment 2 using a two-way ANOVA with experiment (Experiment 2 vs Experiment 3) and target-jump size (1.5 cm vs 3 cm) as factors.

Chapter 5

Emergence of habitual control in a bimanual control task

The following chapter is adapted from a manuscript that is currently under preparation.

5.1 Introduction

Everyone has experienced the frustration of having to overcome old habits when we need to alter the way we perform a task. In a recent striking example of this, YouTuber Destin Sandlin created a “backwards bicycle”, a bicycle where rotation of the handlebar in one direction causes the front tire to rotate in the opposite direction (i.e., opposite of a normal bicycle; Sandlin, 2015). Although it is easy to understand how the handlebar moves the tire and it is trivial to rotate the handlebar, people find it very difficult to ride the backwards bicycle, seemingly because they habitually try to balance themselves using the same movements they would perform on a normal bicycle.

In neuroscience and psychology, habits are generally defined as behaviors which, through extensive repetition, have become inflexible to changes in the goals or structure of a task (Wood and Neal, 2007; Seger and Spiering, 2011; Hélie and Cousineau, 2014). Habit formation has almost exclusively been studied in the context of *discrete* choices (Adams and Dickinson, 1981; Balleine and O'Doherty, 2010; Wit et al., 2018; Luque et al., 2020; Ceceli et al., 2020; Popp et al., 2020), like which button to press on a keypad, or whether or not engage in a particular behavior. In such cases, habits are conceptualized as stimulus-response associations that have become obligatory through repetition (McDonald et al., 2001; Faure et al., 2005; Yin and Knowlton, 2006; Robbins and Costa, 2017).

Perhaps surprisingly, habit formation has hardly been studied in the context of *continuous* motor skills like riding a bicycle. In this case, the analog of a stimulus–response association guiding behavior is a *controller*, a mapping from the instantaneous states of the environment and one's body to outgoing motor commands. Under this framework, behavior can be considered to be habitual if one's controller for a task becomes habitual. That is, if the mapping between states and motor commands becomes inflexible to change and one persists in using this controller even if it no longer successfully achieves control objectives. Although it is conceptually straightforward to extend the concept of a habit from discrete tasks to continuous movement control, it is by no means clear that habits form in the same way in both cases. A key tenet of the stimulus-response framework is that a particular stimulus and resulting response must be paired repeatedly for a habit to form, but in continuous control tasks there are a continuum (i.e., infinity) of possible states and actions and it is unclear whether one will ever repeat the same action in the same state enough times for a habit to form.

Nevertheless, habits have been hypothesized to be a key aspect of motor skill acquisition, enabling more rapid behavioral responses and freeing up valuable cognitive resources (Salmon and Butters, 1995; Bernacer and Murillo, 2014; Graybiel and Grafton, 2015; Haith and Krakauer, 2018; Marien et al., 2018). However, the exact relationship between habits and skills remains unclear (Du et al., 2021), and progress in our understanding of this relationship is hampered by a dearth of empirical evidence examining how quickly behavior becomes habitual when learning a new motor skill. To a limited extent, behavior which could be interpreted as habits has been studied in continuous skills like javelin throwing (Collins et al., 1999), swimming (Hanin et al., 2004), and weightlifting (Carson et al., 2014). However, such work has examined the process of replacing old movement patterns (i.e., unwanted habits) with new ones in already highly skilled individuals, rather than how habits form when *initially* learning a skill.

We performed an experiment to directly examine the process of habit formation in the context of *de novo* learning a continuous motor skill. Participants learned to control an on-screen cursor using a non-intuitive bimanual mapping (introduced in Chapter 4) where vertical movements of the left hand were mapped to horizontal movements of the cursor while horizontal movements of the right hand were mapped to vertical movements of the cursor. Three separate groups of participants learned to use the bimanual mapping over two, five, or ten days of practice. At the end of the final day of practice, we flipped the direction of the mapping between movement of the left hand and movement of the cursor (i.e., a mirror reversal) and assessed whether participants would habitually continue to control the cursor according to the originally practiced mapping, or whether they would be able to flexibly adjust their control to accommodate the new flipped mapping.

Previous studies of habit formation have suggested that the expression of habits may be masked by goal-directed processes that might override habitual responses during the reaction time prior to movement, particularly if participants are allowed ample time to prepare their movements (Hardwick et al., 2019). To account for habitual control potentially being masked in this way, we assessed habitual behavior using two different approaches with differing reaction time constraints. In the first task, participants made point-to-point reaches towards targets in random locations, and they were allowed unlimited time to deliberate about each reach. In the second task, participants tracked a target moving in an unpredictable, sum-of-sinusoids trajectory. Here, the amount of time participants had to prepare their movements varied with the frequency of the target's movement, with movements at high frequencies requiring particularly rapid responses and therefore minimal scope for deliberation.

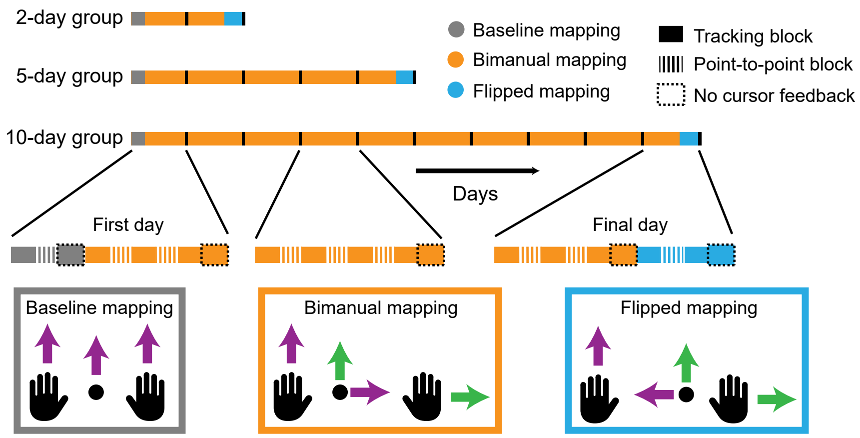

Figure 5.1: Participants learned to control an on-screen cursor using a bimanual hand-to-cursor mapping (orange) over two ($n = 13$), five ($n = 14$), or ten ($n = 5$) days of practice. Half of the participants in each group practiced the depicted bimanual mapping while the other half practiced an alternate version where cursor movements were rotated 180° relative to the depicted mapping (this was done to counterbalance any effects of biomechanics). On each day, participants performed blocks of point-to-point reaching (hashed rectangle; 1 block = 100 trials) and continuous tracking (1 block = 5 minutes) both with (solid rectangle) and without (solid rectangle with dashed outline) visual feedback of the cursor. Learning was compared relative to a baseline mapping where the cursor was placed at the average position of the two hands (gray). At the end of each group's final training day, we flipped the left hand's mapping to cursor movements (blue) and assessed whether participants would habitually continue to use the bimanual mapping they originally learned.

5.2 Results

5.2.1 Participants use of the bimanual mapping became more skilled with up to five days of practice

Three different groups of participants learned to control an on-screen cursor using a novel bimanual hand-to-cursor mapping over two ($n = 13$), five ($n = 14$), or ten ($n = 5$) days of practice (two different versions of the bimanual mapping were used for different subsets of participants to control for potential biasing effects of biomechanics; see "Tasks" section of Methods). Participants practiced this mapping by performing a series of 12 cm point-to-point reaches towards targets, following a random walk within a 20×20 cm workspace. They alternated this point-to-point task with a tracking task in a block-wise manner (Figure 5.1).

Figure 5.2A shows representative raw cursor trajectories at baseline, early learning, and at late learning for each group in the point-to-point task. As we have found previously (Haith et al., 2021), participants initially experienced great difficulty in coordinating their two hands together to move the cursor straight towards each target. But they gradually improved their performance with practice, eventually moving between targets in a straight line, similar to their performance when using an easy mapping in which the cursor appeared exactly halfway between the left and right hand ("baseline"; Figure 5.1).

We assessed each groups' skill level by quantifying how precisely they aimed the cursor's initial movement towards the target (Figure 5.2B-C). Precision improved with practice, reaching a plateau after roughly 5 days that was close to baseline levels. Although there were small improvements in performance from day 5 to day 10 in the 10-day group, these improvements were not statistically significant (linear mixed effects model with post-hoc Tukey test [see Methods for details about statistical analyses]: $t = -0.79$, $p = 0.9665$). Thus, participants became more skilled in performing point-to-point reaches under the bimanual mapping, mostly over the first five days of practice.

Participants also used the bimanual mapping to perform a second task where they tracked a target moving in a sum-of-sines trajectory (Figure 5.3A). Unlike the point-to-point task where participants had an unlimited amount

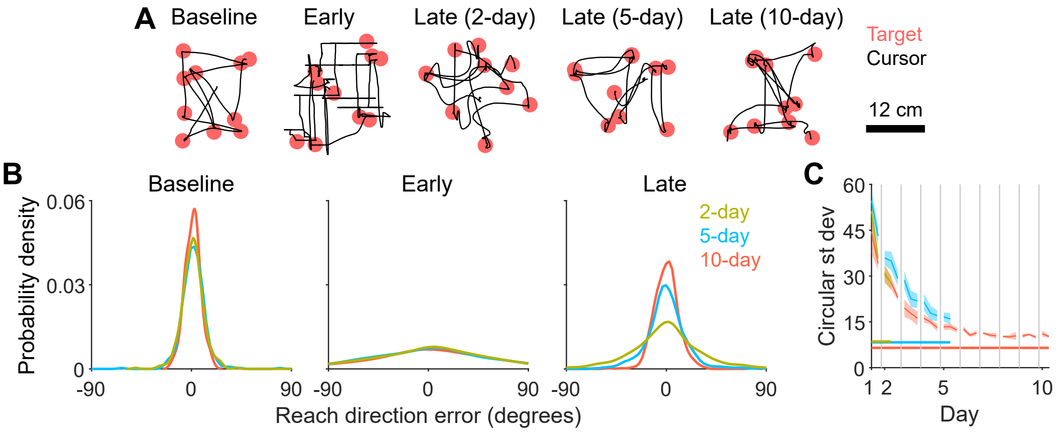

Figure 5.2: **A.** Examples of raw cursor trajectories (black line) from baseline, early learning, and late learning (last block before flip block). Targets are displayed as red circles. Data from ten trials are shown for each block. **B.** Kernel-smoothed probability density of reach direction errors pooled over all subjects and trials for a given block. All blocks were the same as those shown in Figure 5.2A. **C.** Circular standard deviation of reach direction errors, computed by fitting a mixture model to the data in Figure 5.2B (see "Analysis of point-to-point task" section of Methods for more details). Each point corresponds to data from a single block and error bars indicate SEM across participants. Baseline standard deviations for each group are shown as horizontal lines. Days are demarcated by gray vertical lines.

of time to plan their movements at the start of each trial, in the tracking task, the target moved quickly and pseudorandomly, limiting the amount of time participants had to plan their movements; any movements planned at one moment would become outdated within hundreds of milliseconds as the target would move to a new, unpredictable location. Moreover, the amount of planning time afforded to participants depended on the frequency at which the target moved. At low frequencies, the target oscillated slowly, providing people ample time to respond to the target. However, at high frequencies, the target oscillated quickly, forcing people to respond quickly.

With practice, participants learned to reduce the positional error between the target and cursor (Figure 5.3B). We examined participants' tracking performance at different frequencies of movement using a system identification approach (Roth et al., 2011; Madhav et al., 2013; Sponberg et al., 2015; Zimmet et al., 2020; Yang et al., 2021), which allowed us to separately examine the behavioral responses to target movements at different frequencies. Specifically, we computed the gain and direction of cursor movements relative to the target at each frequency of movement, which can be interpreted analogously to the reach direction analysis for the point-to-point task in Figure 5.2B (see Methods for more details). Each arrow in Figure 5.3C shows the gain and direction of cursor movements in response to target movement at a particular frequency. Ideally, participants would track the target by moving their cursor in the same direction as the target. Thus, cursor responses to positive x-axis target movement (green) should be pointed rightwards while responses to positive y-axis target movement (purple) should be pointed upwards, which indeed was the case at baseline. By late learning, all groups exhibited movement amplitudes and directions that approached that of baseline performance.

To statistically compare each group's performance, we computed the gain of horizontal cursor movements at the frequencies of x-axis target movement (x-component of green arrows in Figure 5.3C) as this gain would be directly affected by our subsequent manipulation to assess habits (Figure 5.7). Movement amplitudes improved from day 1 to day 2 in the 2-day group (Figure 5.3D; linear mixed effects model with post-hoc Tukey test; Bonferroni-corrected $p < 0.05$ for 4 out of 6 frequencies) and from day 2 to day 5 in the

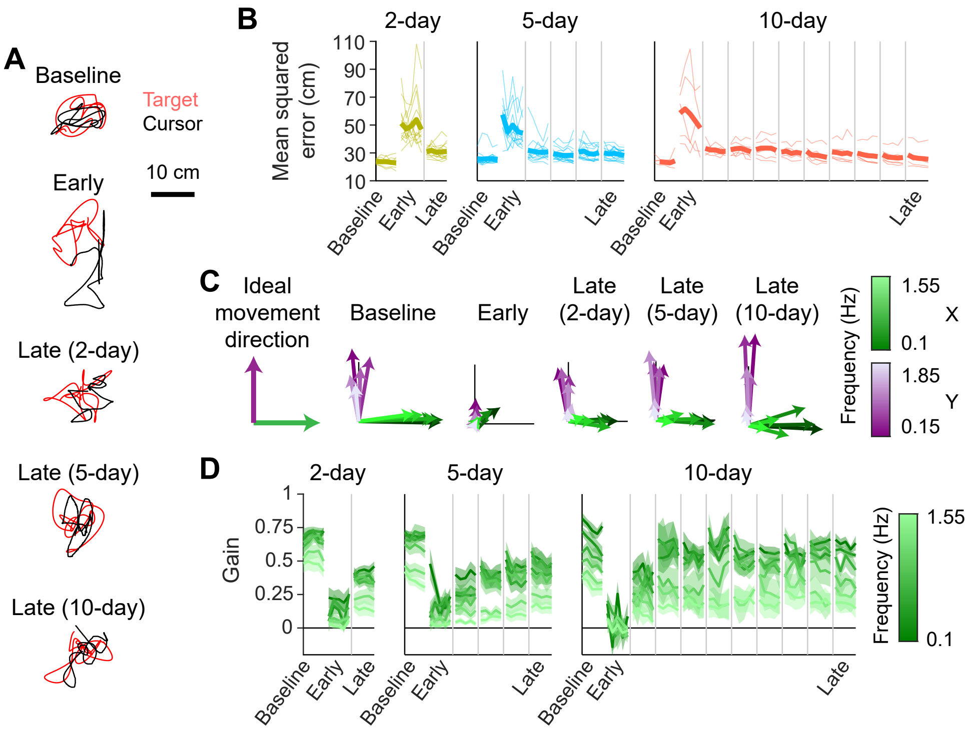

Figure 5.3: **A.** Example cursor (black) and target (red) trajectories from single trials. **B.** Mean-squared error between cursor and target positions. Thin lines indicate individual participants while thick lines indicate group averages. Data collected from different days are separated by gray lines. Data from only one or two blocks are shown for each day for ease of visualization. **C.** Visualization of the cursor's movement direction and gain (relative to the target) at frequencies of x- (green) and y-axis (purple) target movement. Each arrow depicts the direction and gain averaged across participants at a single frequency. Lower and higher frequencies are depicted as darker and lighter colors, respectively. Black lines are scale bars indicating a movement gain of 0.5. Visualization of ideal movement direction is shown on the left. **D.** Gain of horizontal cursor movements at frequencies of x-axis target movement (horizontal component of green arrows in Figure 5.3B). Error bars indicate SEM across participants.

5-day group (Bonferroni-corrected $p < 0.05$ for 3 out of 6 frequencies). However, amplitudes did not improve past day 5 in the 10-day group ($p > 0.05$ for all frequencies). These data demonstrate that, within 5 days of practice, participants became able to successfully move their hands in the appropriate direction to track the target.

Lastly, at the end of each day, participants performed an additional tracking block without visual feedback of the cursor's position. We used this block to examine the extent to which participants' learning could be attributed to improvements in feedforward control. However, we found that for all groups, there was negligible improvements in mean-squared tracking error and movement gains throughout learning (Figure 5.4), indicating that participants were not capable of expressing their learned behavior without visual feedback of their cursor being available.

5.2.2 Behavior became habitual after only two days of practice

We found that participants became skilled in controlling the cursor using the bimanual mapping within about five days of practice, with only marginal further improvements in skilled beyond this time. We next turned to the questions whether and when their behavior became habitual. Might participants' behavior become habitual around the same time their skill plateaued (i.e. by Day 5), early in learning (i.e. by Day 2), or only after significant repetition of the stably learned skill (i.e. by Day 10)? Or, lastly, might participants behavior never have become habitual? To determine this, at the end of each groups' final day of practice, we had participants use a new flipped mapping

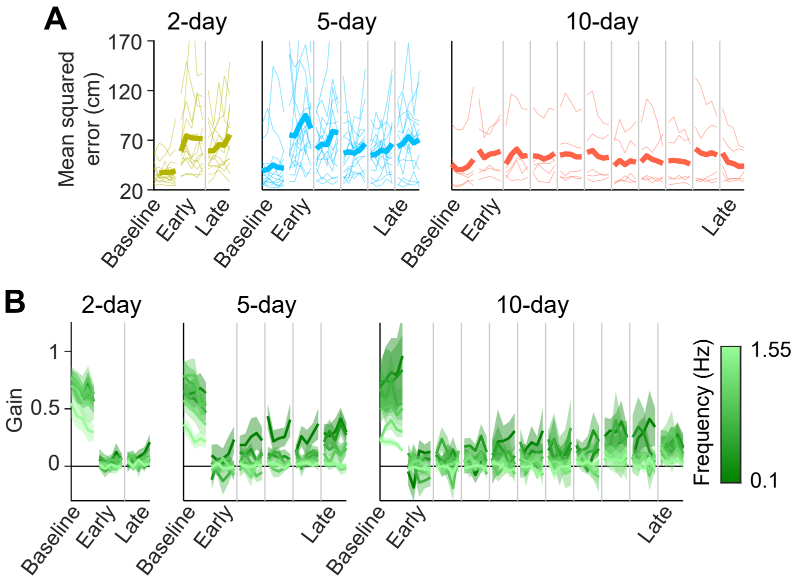

Figure 5.4: **A.** Mean-squared error between cursor and target positions. Thin lines indicate individual participants while thick lines indicate group averages. Data collected from different days are separated by gray lines. **B.** Gain between target and cursor movements at frequencies of x-axis target movement. Lower and higher frequencies are depicted as darker and lighter colors, respectively. Error bars indicate SEM across participants.

to control the cursor where the left hand's mapping to cursor movement was exactly the opposite of what they had originally practiced ("flip" block), effectively amounting to a mirror reversal applied on top of the originally practiced bimanual mapping. Participants were explicitly informed about the reversal of their left hand's mapping, and we tested whether participants would habitually continue to use the originally learned bimanual mapping to control the cursor or successfully use the flipped mapping.

First, we assessed whether participants exhibited habitual behavior in the point-to-point task. On a given trial, if participants could successfully control the cursor under the flipped mapping, then we would expect their cursor's initial movement to be aimed towards the true target (i.e., goal-directed). But if participants habitually controlled the cursor using the original bimanual mapping, then we would expect their cursor's initial movement to be consistent with the original mapping, which would correspond to the movement being aimed towards a virtual target reflected directly across a vertical mirroring axis. We found that participants in all three groups exhibited both goal-directed and habitual behavior during the flip block (Figure 5.5A). We visualized how often participants' movements were aimed towards the virtual mirrored target as a heat map plotting the cursor's initial movement directions as a function of the target's direction (Figure 5.5B). If participants reached towards the virtual mirrored target, their reach directions would lie along the $y = -x$ line. Although none of the groups exhibited initial reach directions along this line at late learning, all groups did exhibit such behavior during the flip block.

We estimated the proportion of trials where participants initially reached towards the mirrored target by fitting a mixture model to the reach direction data (see "Analysis of point-to-point task" section in Methods for more details), using this as a metric for how strongly participants exhibited habitual behavior. We found that the proportion of habitual movements was significantly higher in the flip block compared to late learning for all three groups (Figure 5.5C; linear mixed effects model with post-hoc Tukey test; 2-day: $t = -5.89$, $p < 0.0001$; 5-day: $t = -9.18$, $p < 0.0001$; 10-day: $t = -4.61$, $p = 0.0010$). These data demonstrate that all groups exhibited habitual behavior in the point-to-point task.

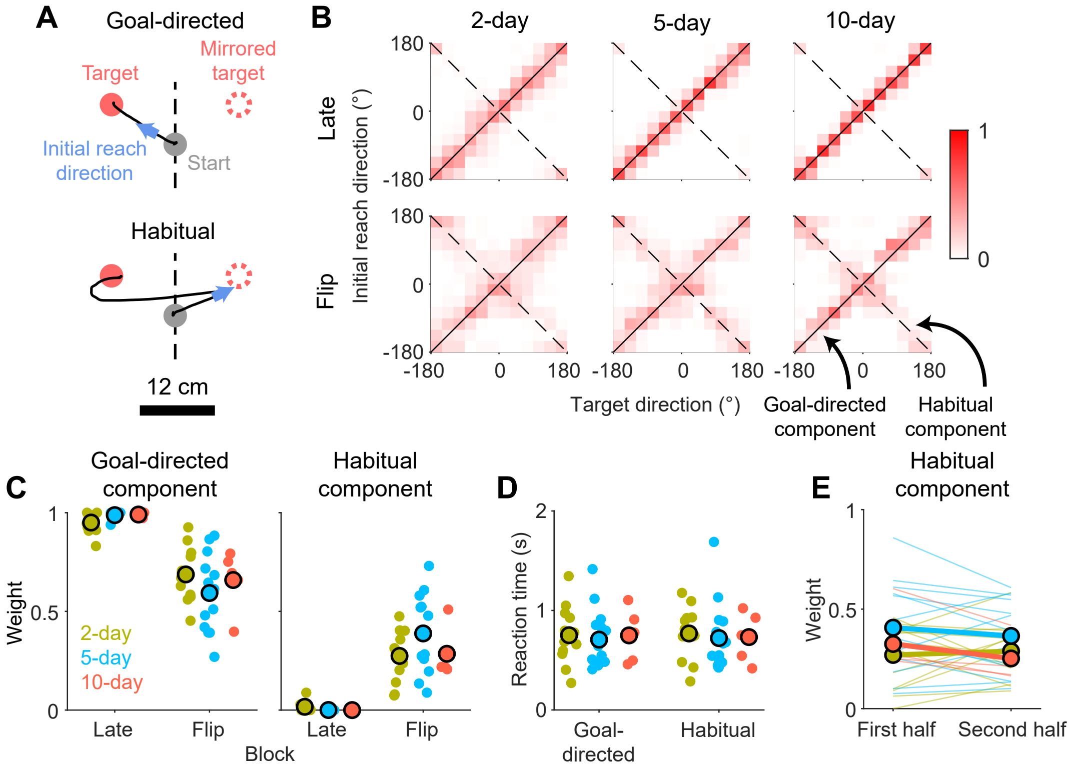

Figure 5.5: **A.** Cursor trajectories (black line) from single trials in the flip block. The trajectories show trials where the cursor's movement was initially aimed straight towards the target (upper) or aimed towards a virtual target (lower) mirrored across the vertical axis (dashed line). **B.** Heat map of cursor's initial movement direction as a function of target directions. Data were pooled from all subjects and grouped into bins of 30° on both axes. We defined 0° as the positive y-axis (i.e., the mirroring axis). Within each target direction bin, we computed the fraction of trials which fell in a particular reach direction bin, plotting this fraction as color intensity in the heat map. To measure the proportion of trials where participants exhibited habitual behavior, we fit a mixture model composed of two weighted von Mises distribution centered on either the $y = x$ (goal-directed) or $y = -x$ line (habitual behavior). **C.** Fitted weights for the goal-directed (left) and habitual (right) components of the mixture model depicted in Figure 5.5B. Fits for individual participants shown as small circles and group means shown as large circles. **D.** Reaction time for reaches towards the actual target (goal-directed) versus a virtual mirrored target (habitual). **E.** Weight of the habitual component of the mixture model when fit to data from either the first or second half of the flip block. Thin lines are individual participants and thick lines are group means.

Perhaps surprisingly, the proportion of reaches towards the mirrored target was not significantly different between groups (Figure 5.5C; linear mixed effects model with post-hoc Tukey test; 2-day vs. 5-day: $t = 2.08$, $p = 0.3098$; 2-day vs. 10-day: $t = -0.46$, $p = 0.9973$; 5-day vs. 10-day: $t = 1.08$, $p = 0.8887$). In other words, despite the fact that the 10-day group practiced using the original bimanual mapping for five times as long as the 2-day group, they did not exhibit more strongly habitual behavior in the point-to-point task. Moreover, the reaction times for goal-directed reaches were not significantly different from habitual reaches (Figure5.5D; linear mixed effects model; no main effect of group [$F(2, 29) = 0.09$, $p = 0.9168$], reach [$F(1, 29) = 0.03$, $p = 0.8705$], or interaction [$F(2, 29) = 0.09$, $p = 0.9167$]), suggesting that the lack of differences across groups in Figure 5.5C could not be explained by differences in the amount of time participants had to plan their movements.

In the flip block, we noted that participants occasionally adopted a strategy of initially moving the cursor vertically (the axis along which the mapping had not changed) before initiating the horizontal component of their movement. As an alternative assay for habitual behavior, we computed the proportion of trials where the cursor moved horizontally in the opposite direction of the target. We found more or less identical results, with no significant differences in the strength of habits across groups (Figure 5.6; linear mixed effects model with post-hoc Tukey test; 2-day vs. 5-day: $t = -0.79$, $p = 0.9685$; 2-day vs. 10-day: $t = 0.30$, $p = 0.9996$; 5-day vs. 10-day: $t = -0.28$, $p = 0.9998$). Collectively, these results suggest that in the point-to-point task, participants exhibited equally strong habitual behavior regardless of how long they had

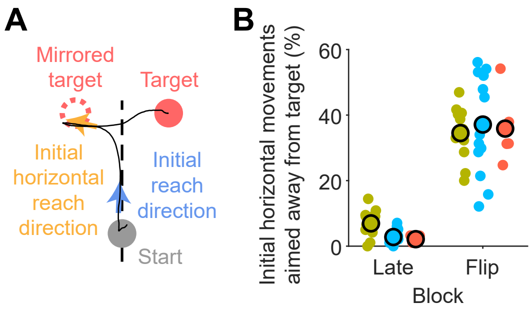

Figure 5.6: The analysis in Figure 5.5C quantified habitual behavior based on the cursor's *initial* reach direction, which may not have captured habitual behavior which occurred *later* in the trial. As a result, we performed an additional analysis quantifying the proportion of horizontal cursor movements initially aimed away from the target. **A.** Example cursor trajectory (black line) where habitual behavior occurred towards the end of a reach; although the cursor's movement was initially aimed along the mirroring axis (blue), the cursor was aimed away from the true target towards the end of the movement (orange). Mirroring axis shown as a dashed line. **B.** Percentage of trials where the cursor's initial horizontal movement was aimed away from the target.

practiced using the bimanual mapping.

We next examined participants' behavior in the tracking task to see whether they would exhibit a similar trend of habitual behavior under the flipped mapping, or whether habit effects might be exacerbated given the imperative to generate movements rapidly while tracking the target. We compared the direction of participants' responses (i.e. cursor movement) to movements of the target between late learning and the flip block (Figure 5.7A). If participants habitually continued to use the original bimanual mapping during the flip block, then when tracking the same sinusoidal stimulus, the cursor would move in the opposite (horizontal) direction relative to late learning. To quantify this, we normalized the cursor's horizontal movement gain from the flip block by the gain from late learning such that normalized gains of -1 would indicate habitual behavior. (In subsequent analyses, we removed data from one outlier participant in the 10-day group who exhibited erratic behavior in the flip block, with negative gains that were greater in amplitude than at late learning.) In the first flip block, all groups on average exhibited negative gains at two or more frequencies (Figure 5.7B; one-sample t-test with Holm-Bonferroni correction at $\alpha = 0.05$; 2-day: 2 of 6 frequencies; 5-day: 3 of 6 frequencies; 10-day: 2 of 6 frequencies), particularly at higher frequencies as we expected. However, we did not find any evidence that groups with more practice exhibited significantly more negative gains than groups with less practice (linear mixed effects model with post-hoc Tukey test: Bonferroni-corrected $p > 0.05$ for all comparisons of gains within frequencies).

The above analyses considers differences in behavior across groups. However, in previous work, we have found that habitual behavior can vary greatly across individuals (Hardwick et al., 2019). We therefore also examined whether or not behavior was habitual at an individual-participant level. We calculated the proportion of participants in each group who exhibited significantly negative gains during the flip block. In all three groups, we found a mixture of habitual and non-habitual participants (one-sample t-test with Holm-Bonferroni correction at $\alpha = 0.05$; 2-day: 5 of 13 participants; 5-day: 7 of 14 participants; 10-day: 3 of 4 participants). Although the proportion of participants who were habitual did appear to increase with practice, it is difficult to conclude whether or not this trend was meaningful, particularly given the small sample size of the 10-day group.

An alternative way in which behavior may become habitual is by becoming more persistent, i.e., resistant to extinction. In other words, as one's skill

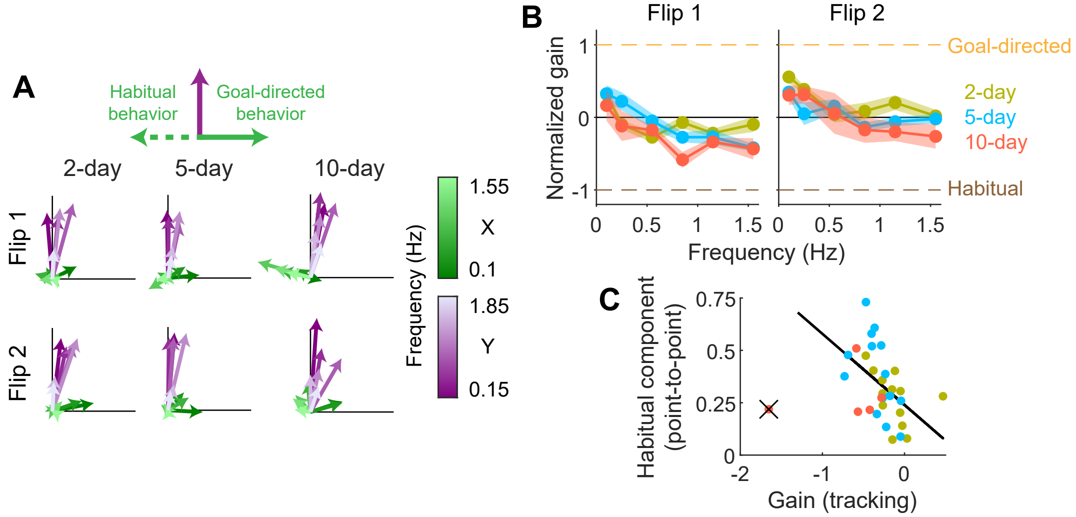

Figure 5.7: A. Visualization of the cursor's movement direction and gain (relative to the target) while using the flipped mapping, similar to Figure 5.3B. Each arrow depicts the average across participants at x- (green) and y-axis (purple) frequencies. Lower and higher frequencies are depicted as darker and lighter colors, respectively. Black lines are scale bars indicating a movement gain of 0.5. Flip 1 and Flip 2 are the first and second tracking blocks under the flipped mapping, respectively. At the top, we depict the direction the green arrows should point if participants exhibit goal-directed (right) or habitual (left) behavior. **B.** Gain of horizontal cursor movements under the flipped mapping normalized to the gain under the original bimanual mapping at late learning. If participants responded to target movement by moving their cursor in the same direction under both the original and flipped bimanual mappings, then the gain would be positive, approaching 1 if the movement gains were the same (goal-directed; yellow dashed line). But if they moved their cursor in opposite directions under the two mapping, then the gain would be negative, approaching -1 (habitual; brown dashed line). Error bars indicate SEM across participants. **C.** Linear regression between average gains of the highest 3 frequencies from the first flipped tracking block and the proportion of habitual reaches from the flipped point-to-point block in Figure 5.5C. Data from one outlier subject in the 10-day group (crossed out in black) was not used for fitting.

increases, the habits one forms may persist for longer. To assess whether habitual behavior would became more persistent with more training, we examined participants' performance in a second tracking block under the flipped mapping, after having practiced the flipped mapping in a point-to-point block Figure 5.1). At the group level, participants no longer exhibited significantly negative gains at any frequency (Figure 5.7B; one-sample t-test with Holm-Bonferroni correction at $\alpha = 0.05$), suggesting that the habits had been largely extinguished in all groups. However, at the level of individual participants, all 3 of participants in the 10-day group who exhibited negative gains in the first tracking block still did so in the second tracking block. Meanwhile, only 1 of 5 of participants in the 2-day group and 2 of 7 of participants in the 5-day group still exhibited significantly negative gains. While these data suggest that habitual behavior may have been more persistent in the 10-day group, again, they must be interpreted with caution given the small sample size of this group.

We attempted a similar analysis of the persistence of participants' habits by fitting the mixture model from Figure 5.5D to the first and last 50 reaches in the block instead of all 100 reaches. However, we found no evidence for any difference in the strength of habitual behavior between the first and last half of the block for all groups (Figure5.5E; linear mixed effects model with post-hoc Tukey test; 2-day: $t = -0.49$, $p = 0.9963$; 5-day: $t = 1.11$, $p = 0.8747$; 10-day: $t = 1.17$, $p = 0.8493$), suggesting that habitual behavior did not extinguish over this period.

Might there be any relationship between the habitual behavior we observed in the point-to-point and tracking tasks? To examine this, we compared how strongly participants exhibited habitual behavior between the two tasks. First, we averaged the gains of each participant's tracking behavior at the highest three frequencies, given that we expected habitual behavior to be strongest at these frequencies (Yang et al., 2021). We then correlated each subject's average gain with the proportion of habitual reaches they made in the point-to-point task, as in Figure 5.5C. Indeed, we found a correlation between tasks (Figure 5.7C, slope $= -0.34$, Pearson's $r = 0.49$, $p = 0.0052$), suggesting that the tasks may have indeed assessed the same underlying habit.

5.3 Discussion

In the present study, we examined the time course over which habitual behavior emerged as participants learned a new continuous motor skill—controlling a cursor under a bimanual hand-to-cursor mapping. Participants became more skilled in using this mapping by practicing with a combination of point-to-point reaches and continuous tracking, and their skill level plateaued after around five days of practice. After either two, five, or ten days, we flipped the left hand's control of the cursor and tested whether participants would habitually continue to control the cursor according to the original mapping they had learned. We found that habitual behavior emerged after only two days of practice, which we observed in both the point-to-point and tracking tasks. We did not find compelling evidence, however, that habitual behavior became stronger with more practice.

While we mainly focused on assessing how *strong* habitual behavior became during learning, to a limited extent, we also assessed how *persistent* habits became, examining whether habits were extinguished through exposure to the flipped mapping. While this short period of practice seemed to be sufficient to extinguish the habit in the tracking task, we did not observe extinction in the point-to-point task. It is unclear why we observed a difference between the two tasks; although we expected the strength of habitual behavior to be affected by the amount of preparation time participants were afforded in each task, we did not expect habit persistence to be affected. However, we would like to emphasize that we did not find strong evidence to suggest that the persistence of habitual behavior depended on how long participants practiced the bimanual mapping.

It is important to note that when we analyzed behavior at the level of single participants, we found that a greater proportion of participants exhibited habitual behavior with more practice. Therefore, taking a conservative interpretation, one could say that our results are inconclusive as to whether behavior became more habitual with more practice. However, the inferences we could draw from the individual participant analysis were limited because they critically relied on data from our most practiced group which had a small sample size ($n = 5$), and if one were to only use data from the other two groups with ample participants, there is little evidence to suggest more participants in the 5-day group exhibited habitual behavior than the 2-day group. Furthermore, our main result that the emergence of skill and habit dissociated during learning would not be impacted by the findings of the individual participant analysis.

Collectively, our results suggest a dissociation between the emergence of skill and habit during motor learning: behavior can become habitual early in learning before one's skill level has reached asymptote, and likewise, behaviors which have already become habitual can still become more skillful through practice. Our findings parallel that of Hardwick et al., 2019 who demonstrated that participants learning an arbitrary visuomotor association task exhibited improved speed-accuracy tradeoffs (i.e., improved skill) over twenty days of practice, even after behavior had become habitual after four days of practice. They further found that the habits could be explained as an all-or-none phenomenon (i.e., one either is or is not habitual), consistent with our observation that habitual behavior did not become stronger with more practice. The present study builds on Hardwick et al., 2019 by extending the dissociation between skill and habit from the domain of discrete tasks into the domain of continuous motor skills. Given the lack of empirical studies of habits in continuous tasks, it was unclear whether the findings of habits in discrete tasks would generalize to the continuous domain. However, the similarity of the results between the two studies suggest a potential commonality between the habits which form when people learn discrete versus continuous tasks.

A question which remains about habits is the following: what does it mean for a behavior to become more strongly habitual? Should we quantify this in terms of how likely a habit is to be expressed, how much the habitual behavior persists, or perhaps in some other way? And what metrics should we use to quantify these characteristics of habits? For instance, in our study, we quantified habit strength differently between the point-to-point (probability of expressing a habitual reach) and tracking tasks (gain of habitual movement), and habit strength could be quantified using other metrics as well (e.g., stereotypy of movements). Characterizing the ’strength’ of a habit is further complicated by the fact that multiple component processes/computations may be involved in generating movement behavior, and any one of these processes may become habitual. For instance, one’s ability to select what action to do (e.g., move the cursor to the right) may become habitual independently of one’s ability to execute that action (e.g., stereotyped kinematics of rightward movement; see Du et al., 2021 for a more in-depth discussion of this idea). Such a dissociation could explain why we observed different trends between habit strength and persistence in our two tasks.

More generally, the present study provides a new empirical foundation for theoretical accounts of habits. A wide variety of theories have been proposed to explain the cognitive basis of habits, including stimulus-response associations (McDonald et al., 2001; Faure et al., 2005; Yin and Knowlton, 2006; Robbins and Costa, 2017), model-free learning (Daw et al., 2005; Dolan and Dayan, 2013; Hogarth, 2018), and caching of computations (Haith and Krakauer, 2018; Maisto et al., 2019). Central to these theories is the idea that habitual behavior is inflexible to change. Though behavioral inflexibility is central to the definition of habits, our findings suggest that habitual behavior can nevertheless change over longer timescales through practice, as participants whose behavior had already become habitual could still improve their skill. In other words, just because a behavior has become habitual does not mean that it cannot be altered in the future. In this regard, theoretical accounts of habits which lack learning rules to update habitual behavior (e.g., stimulus-response associations, cached computation) may benefit from incorporating such rules, such as those seen in model-free frameworks (Daw et al., 2005; Dolan and Dayan, 2013; Hogarth, 2018). Currently, it is unclear how habits that have been created through repetition can be modified with further experience. For instance, might it have been possible for the controller to be adjusted while remaining habitual if the change to the mapping was less drastic than a mirror reversal?. Understanding the interplay between habits and learning should be a focus of future work.

What do our results ultimately suggest about the role that habits play when we learn new motor skills? During learning, one may encounter situations where they must alter their behavior to improve task performance, and often these behaviors will have already become habitual through practice. Overcoming habits will likely be frustrating when one must substantially alter their behavior (Toner et al., 2015). But if only slight alterations are needed, then one may be able to fine tune their habit without having to break it.

5.4 Methods

5.4.1 Tasks

A total of 32 right-handed participants were recruited for this study (23.0 ± 4.3 [mean ± standard deviation]; 13 male, 19 female), 13 for the 2-day group, 14 for the 5-day group, and 5 for the 10-day group (recruitment for the 10-day group was cut short due to the COVID-19 pandemic). Participants learned to maneuver an on-screen cursor (circle of radius 2.5 mm) using one of two versions of a bimanual hand-to-cursor mapping. Half of the participants learned one version where up-down movements of the left hand produced right-left movements of the cursor while right-left movements of the right hand produced up-down movements of the cursor. The other half of participants learned a different version where the mapping from hand to cursor movements were 180° rotated relative to the previous version. We counterbalanced these two versions of the mapping to ameliorate any effects biomechanics may have had on our results.

Three different groups practiced the bimanual mapping over either two, five, or ten days by performing a combination of point-to-point reaches (1 block consisted of 30 trials at baseline and 100 trials for every other block) and continuous tracking (1 block consisted of 5 66-second trials). Periodically, participants also performed a tracking block without visual feedback of their cursor. To assess the extent to which participants use of the bimanual mapping had become habitual, at the end of each groups' final day of training, we flipped the left hand's mapping to cursor movement (flip block): up-down movements of the left hand now resulted in left-right movements of the cursor instead of right-left (in the case of the 180° rotated bimanual mapping, right-left movements of the cursor became left-right). We required three different groups of participants for this experiment because we assessed habitual behavior at different time points during learning, and after a participant has used the flipped mapping once, any future learning of the original bimanual mapping would be contaminated. The order of all blocks during the experiment is depicted in Figure 5.1.

5.4.2 Data analysis

5.4.2.1 Analysis of point-to-point task

The cursor's position in each trial was smoothed using a third-order Savitzky-Golay filter. Path length was defined as the total distance that the cursor traveled in a single trial. Movement time was defined as the time between movement initiation (when the cursor left the start target) and termination (when the cursor was in the end target with speed < 0.065m/s). Reaction time was defined as the time between when the target appeared and the cursor's tangential velocity exceeded 0.1 m/s. Reaction time was not computed for a small minority of trials (1260 out of 41560) where the velocity did not exceed 0.1 m/s. Peak velocity was defined as the cursor's highest tangential velocity. We computed the tangential velocity by linearly resampling the cursor's position at the times recorded by the Flock of Birds and computing the distance traversed by the cursor between two consecutive samples divided by the time elapsed. Resampling was necessary because, occasionally, the recorded time at which a sample was collected by the Flock of Birds did not match the true time at which it was collected, causing the calculated velocity to be inaccurate. Velocity profiles were also smoothed using a third-order Savitzky-Golay filter.

Initial reach direction was defined as the direction of the instantaneous velocity vector 150 ms after movement initiation. Initial reach direction error was computed as the difference in angle between this instantaneous velocity vector and the vector pointing from the target on the previous trial to the target on the current trial. Probability density functions were estimated for reach direction errors using a kernel smoothing function, implemented as the `ksdensity` function in MATLAB. We measured the variability in participants' initial reach direction errors (i.e., how consistently straight participants reached towards the target) by fitting a mixture model to this data. In the model, we assumed that participants' reach direction errors, x, were generated by one of two causes: 1) an error from a goal-directed reach towards the target (modeled as a von Mises distribution) or 2) an error from a reach in a random direction (modeled as a uniform distribution). The probability density function of the mixture model, $\mathrm{mix}(\cdot)$, was defined as

$$\mathrm{mix}(x \mid \mu, \kappa, \alpha) = \alpha \cdot \mathrm{vm}(x \mid \mu, \kappa) + (1 - \alpha) \cdot \mathrm{unif}(x) \tag{5.1}$$

where α is a parameter valued between 0 and 1 weighting the probability density functions of the von Mises, $\mathrm{vm}(\cdot)$, and uniform distributions, $\mathrm{unif}(\cdot)$. The probability density functions of the individual distributions were defined as

$$\mathrm{vm}(x \mid \mu, \kappa) = \frac{e^{\kappa \cos(x-\mu)}}{2\pi I_0(\kappa)}, \qquad \mathrm{unif}(x) = \frac{1}{2\pi}. \tag{5.2}$$

Here, μ and κ are the mean and concentration of the von Mises distribution and $I_0(\cdot)$ is the modified Bessel function of the first kind with order 0.

The parameters μ, κ, and α were fit to the data from single participants in each block via maximum likelihood estimation. Specifically, we used the MATLAB function `fmincon` to determine the values of the parameters that would maximize the below likelihood function over the n trials within one block:

$$\hat{\mu}, \hat{\kappa}, \hat{\alpha} = \underset{\mu,\kappa,\alpha}{\operatorname{argmax}} \left\{ \sum_{i=1}^{n} \log \left[\operatorname{mix}(x_i \mid \mu, \kappa, \alpha) \right] \right\}. \tag{5.3}$$

Then, using the fitted concentration parameter of the von Mises distribution, $\hat{\kappa}$, we computed the circular standard deviation, σ, as

$$\sigma = \sqrt{-2\ln(R)}, \qquad R = I_1(\hat{\kappa})/I_0(\hat{\kappa}). \tag{5.4}$$

We used σ as our measure of the variability of participants' reach direction errors.

To assess the whether participants exhibited habitual behavior during the flip block, we quantified each participant's tendency to reach towards the true target versus a virtual target flipped across the mirroring axis. More specifically, we assumed that for each trial, participants' initial reach direction could be explained by at least one of three causes: 1) a goal-directed reach towards the target, 2) a habitual reach towards the mirrored target, and 3) a reach aimed towards neither target (i.e., random movement). We modeled the first two causes as von Mises distributions with different means—ϕ_a and ϕ_m, set by the direction of the actual and mirrored targets, respectively—but the same concentration parameter, κ. For each participant, we fixed the concentration parameter to be equal to the $\hat{\kappa}$'s estimated for late learning in Eq 5.3. We modeled the third component, random movements, as a uniform distribution.

Assuming that each participant's behavior within one block could be modeled as a weighted mixture of these three distributions, $\operatorname{mix}'(\cdot)$, we used the MATLAB function `fmincon` to determine the weights, α_a and α_m, that would maximize the following likelihood function over the n trials within one block:

$$\hat{\alpha}_{\mathrm{a}}, \hat{\alpha}_{\mathrm{m}} = \underset{\alpha_{\mathrm{a}}, \alpha_{\mathrm{m}}}{\operatorname{argmax}} \Big\{ \sum_{i=1}^{n} \log \left[\operatorname{mix}'(x \mid \phi_a, \phi_m, \kappa) \right] \Big\} \tag{5.5}$$

where

$$\begin{aligned} \operatorname{mix}'(x \mid \phi_a, \phi_m, \kappa) = & \alpha_{\mathrm{a}} \cdot \operatorname{vm}(x \mid \phi_a, \kappa) + \alpha_{\mathrm{m}} \cdot \operatorname{vm}(x \mid \phi_m, \kappa) + \\ & (1 - \alpha_{\mathrm{a}} - \alpha_{\mathrm{m}}) \cdot \operatorname{unif}(x) \,. \end{aligned} \tag{5.6}$$

Here, x represents participants' reach directions while α_{a} and α_{m} correspond to the probabilities that a participant reached towards the actual, and mirrored targets, respectively. Definitions for $\operatorname{vm}(\cdot)$ and $\operatorname{unif}(\cdot)$ can be found in Eq 5.2. We used $\hat{\alpha}_{\mathrm{m}}$ as our metric for the strength of habitual behavior. For Figure 5.5E, instead of fitting this model to all trials in the flip block, we fit the model to either the first or second half of trials in this block.

We used the fitted weights from this approach to classify each trial as either goal-directed, habitual, or random. For each trial, we computed the probability that the reach direction was generated from each of the three mixture components under the fitted mixture model's probability density function (in essence, computing $p(\text{reach direction} \mid \text{goal-directed})$, $p(\text{reach direction} \mid \text{habitual})$, and $p(\text{reach direction} \mid \text{random})$. Trials were classified as goal-directed, habitual, or random based on which of these three probabilities was the highest. We excluded trials where the direction of the target was within 30° of the mirroring axis (the y-axis) as the von Mises distributions for the goal-directed versus habitual reaches would have similar means and, therefore, would be too difficult to distinguish from each other (1153 out of 3200 data points excluded). We used this classification to compute the reaction times of goal-directed versus habitual reaches in Figure 5.5D.

Additionally, we compared the model in Eq 5.6 with an alternative model which was designed to capture behavior where participants would move their right hand (controls vertical cursor movement) in the correct direction but their left hand (controls horizontal cursor movement) would generate random movements. We modeled participants reach directions, x, given the target's direction, ϕ_a, as a mixture of two weighted uniform distributions:

$$\text{mix}^*(x \mid \phi_a) = \begin{cases} \alpha \cdot \text{unif}^*(x), & [\sin(x) \geq 0 \;\wedge\; \sin(\phi_a) \geq 0] \vee \\ & [\sin(x) < 0 \;\wedge\; \sin(\phi_a) < 0] \\ (1-\alpha) \cdot \text{unif}^*(x), & [\sin(x) < 0 \;\wedge\; \sin(\phi_a) \geq 0] \vee \\ & [\sin(x) \geq 0 \;\wedge\; \sin(\phi_a) < 0] \end{cases} \tag{5.7}$$

where

$$\text{unif}^*(x) = \frac{1}{\pi}. \tag{5.8}$$

Here, α is the probability that the cursor moved vertically in the correct direction. The fits for the models in Eq 5.6 and Eq 5.7 were compared using BIC. Model recovery analyses were performed by simulating data from both of these models, fitting both models to each simulated dataset, comparing fits using BIC, and generating a confusion matrix. To generate data from Eq 5.6, we used values for α_a and α_m that ranged between 0 and 1, and we fixed $\kappa = 3$. Lower κ's set higher variability for the von Mises distributions (i.e., harder to distinguish from the model in Eq 5.7), so we fixed κ to be the lowest average κ that we observed in the late learning data from any group, as estimated in Eq

5.3. Model recovery across different choices of parameters were compared by computing the accuracy of the confusion matrices.

As an alternative approach to assessing whether participants exhibited habitual behavior while using the flipped mapping, we assessed whether their horizontal cursor movements were aimed away from the target. Using only the cursor's x-axis position, for each trial, we determined whether the cursor's instantaneous velocity vector was aimed towards the right or left 150 ms after the cursor deviated 1 cm from the center of the starting target (i.e., the radius of the target). We classified cursor movements in each trial as moving away from the target if the velocity vector's direction was opposite of the direction of the target relative to the starting position (e.g., target located to the left but cursor moving towards the right). This method was unable to compute an initial horizontal reach direction on a small minority of trials (95 out of 3200 trials) where the target on the current trial was either directly above or below the target from the previous trial. This was because either: 1) the cursor did not deviate 1 cm horizontally away from the center of the starting target (i.e., the radius of the target), making it impossible to detect the time of movement initiation, or 2) the detected movement initiation time was less than 150 ms prior to the end of the trial, meaning that the trial ended before the time at which we assessed reach direction. These trials were excluded from the analysis.

5.4.2.2 Analysis of tracking task

Data from two tracking trials (each from different subjects) were excluded from the analysis because our experiment hardware failed to accurately record the positions of stimuli with known positions. Tracking error was computed as the mean-squared error between the cursor's and target's positions. Time-domain trajectories of the cursor's and target's position (the first 60 seconds of each trial following the initial 5 second ramp period) were converted to phasors (complex numbers representing sinusoids) in the frequency domain via the discrete Fourier transform. An input-output transfer function was computed at every frequency by dividing the cursor's phasor by the target's phasor. This transfer function described the relationship between the cursor and target sinusoids in terms of gain (relative amplitude) and phase (difference in time).

Using these transfer functions, we sought to describe the direction that participants moved their cursor to track the target. In this task, participants' cursor movements would conventionally be described as phase lagged relative to the target with a positive gain (i.e., moving in the same direction as the target with a time delay). However, when a mirror reversal has been applied (such as in the flipped mapping), participants' may habitually continue to use their original control policy, causing their movements to be flipped across the mirroring axis relative to before. Although the relationship between movements before and after the flip could be described as movements with positive gain but now in antiphase (i.e., moving in the same direction as the target but with more time delay), a better way to describe them would be to say that the movements have the same phase but a negative gain (i.e., moving with the same time delay but in the opposite direction of the target).

Given that conventional analysis methods always yield a positive gain to describe frequency-domain data, we used the method described in Yang et al., 2021 to compute a signed gain, g, relating cursor and target movements. This was computed as the dot product between transfer functions:

$$g = a \cdot \hat{b} \tag{5.9}$$

where a is the transfer function for a given block of interest and $\hat{b}$ is the transfer function at baseline with unit length. Computing the dot product implicitly fixes the phase of cursor movements to be the same as baseline across all blocks, allowing a signed gain to be computed. This assumption of fixed phase is valid for analyzing data in late learning as participants' phase lags under the bimanual mapping became more similar to baseline through practice. We computed this signed gain between each axis of target and cursor movement (x-axis target movement and x-axis cursor movement, x-axis target movement and y-axis cursor movement, etc.), building a series 2×2 matrices relating the transformation between the two trajectories where each matrix represented the transformation within a small bandwidth of frequencies. The green (purple) arrows in the Figure 5.3C and 5.7A were generated by plotting the first (second) column of each matrix. Figure 5.3D was generated by plotting the element in the first row and first column of each matrix.

To quantify the strength of habitual behavior in Figure 5.7B, we reanalyzed the gain between x-axis target and x-axis cursor movements from the flip blocks by fixing their phases to be the same as late learning. We did this because any habitual behavior would manifest as lingering usage of the originally learned bimanual mapping, and the habit should be measured with respect to behavior under this mapping. When analyzing these normalized gains at the group level, we excluded one outlier participant in the 10-day group who exhibited dramatically more negative gains than other participants within the group. To compare the habitual behavior we observed between the point-to-point and tracking tasks, we correlated each participant's α_m from Eq 5.5 with their normalized gains (averaged over the highest three frequencies) from Figure 5.7B via linear regression.

5.4.2.3 Statistics

Most primary statistical analysis were performed by fitting linear mixed effects models to the data. For all analyses in Figure5.2, the models used group (2-, 5-, or 10-day) and block (2-day: day 1 vs. day 2; 5-day: day 2 vs. day 5; 10-day: day 5 vs. day 10) as fixed effects and subject as a random effect. For Figure 5.5C and E, models used the same group and subject effects but with a different set of blocks being compared ([late learning vs. flip block] and [first half of flip block vs. second half of flip block], respectively). For Figure 5.5D, models used the same group and subject effects but with reach type as an additional fixed effect (goal-directed vs. habitual). Post-hoc pairwise comparisons were performed using the Tukey test.

For data from the tracking task, mixed effects models were fit using the same effects as Figure 5.2 but with an additional fixed effect of frequency. We also fit separate models to data from each frequency because behavior varied dramatically as a function of frequency. Post-hoc pairwise comparisons were performed using the Tukey test. An additional Bonferroni correction factor of 6 was applied to the p-values for pairwise comparisons to account for the separate models fits for each frequency. Additionally, to determine whether participants exhibited significantly negative gains in the tracking task, for each frequency, we performed a series of one-sample t-tests and corrected for multiple (6) comparisons using a Holm-Bonferroni correction with $\alpha = 0.05$.

Chapter 6

General Discussion

In this dissertation, I have detailed a collection of studies that I performed seeking to understand how humans learn new motor skills *de novo*. In Chapter 3, I examined how humans acquire continuous motor skills. By having participants track a continuously moving, pseudorandom target, I was able to observe how participants learn to compensate for a rotation or mirror reversal of visual feedback when they could not effectively use a cognitive re-aiming strategy (which may dominate learning when movement goals are static). I analyzed participants' tracking behavior using a novel system identification approach and found that participants learned to compensate for both perturbations by building and utilizing *de novo* controllers. This suggests that continuous motor skills are learned, at least in part, *de novo*.

In Chapter 4, I examined why people often learn new motor skills so slowly. In particular, I investigated whether a potential botttleneck could be the process of generating a *de novo* controller that generates well-practiced actions in response to familiar stimuli, as opposed to challenges associated with executing unfamiliar actions or exploring large action spaces. I designed a novel bimanual control task which isolated the challenge of learning to the building a *de novo* controller. Indeed, I found that participants' ability to respond to mid-movement perturbations remained limited after several days of training, suggesting that one's ability to select actions via a *de novo* controller may partially explain why motor skill learning is often slow.

Finally, in Chapter 5, I assessed how people's behavior becomes habitual as they learn new motor skills. I observed the time course over which particpants' behavior became habitual as they learned the same bimanual control task I introduced in Chapter 4 over up to ten days of practice. I found that participants' behavior became habitual early in learning and did not become more habitual with more practice. However, their behavior continued to become more skilled after having become habitual. This suggests that during motor learning, the emergence of skills and habits are dissociable.

6.1 System identification as a tool for characterizing motor learning

In this dissertation, I made use of a novel frequency-based system identification approach. Although system identification and other sinusoidal perturbation techniques have previously been applied to characterize the trial-by-trial dynamics of learning from errors in adaptation tasks (Baddeley et al., 2003; Ueyama, 2017; Miyamoto et al., 2020), my approach differs critically from these previous applications in that I used system identification to assess the state of learning and properties of the learned controller at a given time. In this latter sense, frequency-based system identification has not, to my knowledge, previously been applied to investigate motor learning. I have shown that this approach provides a powerful means to identify distinct forms of learning based on dissociable properties of the controllers they give rise to.

My system identification approach has several advantages over other methods for studying motor control. In terms of practicality, this approach is more time efficient for data collection compared to the standard point-to-point reaches used in motor learning studies. Compared to time-domain methods, the frequency domain is particularly amenable for system identifcation given the rich suite of tools that have been developed for it (Schoukens et al., 2004). Moreover, my approach is also general as it can be applied to assess learning of arbitrary linear visuomotor mappings (e.g., 15° rotation, body-machine interfaces; (Mussa-Ivaldi et al., 2011)). Under previous approaches, characterizing the quality of movements under different types of learned mappings (rotation, mirror-reversal) has necessitated different *ad hoc* analyses that cannot be directly compared (Telgen et al., 2014). In contrast, my frequency-based approach provides a general method to characterize behavior under rotations, mirror-reversals, or any linear mapping from effectors to a cursor, owing to my "multi-input multi-output" approach of identifying the 2×2 transformation matrix relating target movement and hand movement.

While the system identification approach used in the present study does capture learning, the results obtained using this approach do warrant careful interpretation. In particular, one must not interpret the empirical relationship that I measured between the target and hand as equivalent to the input-output relationship of the brain's motor controller. The former measures the response of the entire sensorimotor system to external input. The latter only measures how the controller sends motor commands to the body in response to input from the environment/internal feedback. Estimating the latter relationship requires a more nuanced approach that takes into account the closed-loop topology (Roth et al., 2014; Yamagami et al., 2019). Despite this, changes to the controller are still revealed using my approach; assuming that learning only drives changes in the input-output relationship of the controller—as opposed to, for example, the plant or the visual system—any changes in the overall target–hand relationship will reflect changes to the controller. Thus, my approach is a valid way to investigate learning.

Although the primary goal of my frequency-based analysis was to establish how participants mapped target motion into hand motion, system identification yields more detailed information than this; in principle, it provides complete knowledge of a linear system in that knowing how the system responds to sinusoidal input at different frequencies enables one to predict how the system will respond to arbitrary inputs. These data can be used to formally compare different possible control system architectures (Zimmet et al., 2020) supporting learning.

6.2 Potential neural mechanisms supporting *de novo* learning

Although I have characterized *de novo* learning on a behavioral level, I did not attempt to elucidate the neural mechanism(s) which underlie *de novo* learning. Whereas the canonical use of the term “adaptation” refers to a specific learning mechanism (sensory-prediction error based updates of a forward model in the cerebellum), there is currently no consensus on the mechanism which drives *de novo* learning. In this dissertation, I have taken an agnostic stance, using the term "*de novo* learning" to refer to any mechanism, aside from adaptation and re-aiming, that leads to the creation of a new controller.

What are some of the potential mechanisms underlying *de novo* learning? One idea is that brain generates novel movements by generating novel patterns of neural activity. To see this, we can describe the collective activity of many neurons in a "state space" where each dimension of the space describes the firing rate of a single neuron. At any given time, the activity of this set of neurons will be represented as a point in the state space, and changes in neural activity over time will cause the point to move around in the state space. Previous studies have found that the activity of neurons involved in generating movements does not fill the entire high-dimensional state space but rather lives on a low-dimensional subspace (sometimes referred to as an "intrinsic manifold"; Sadtler et al., 2014; Hwang et al., 2013). At any given time, the repertoire of movements that an agent is capable of skillfully generating is limited to the corresponding neural activity on the intrinsic manifold. Indeed, monkeys learning to control brain-machine interfaces exhibit difficulty generating patterns of neural activity existing off the intrinsic manifold (Sadtler et al., 2014; Golub et al., 2018). Thus, one could reframe the challenge of *de novo* learning as the challenge of generating off-manifold neural activity.

How exactly off-manifold neural activity is generated is an open question. Several studies suggest that basal ganglia circuits may play a critical role in generating novel patterns of activity. As touched on in Section 1.2, the basal ganglia appears to serve a critical role in skill learning as impairments in basal ganglia function produce deficits in learning arbitrary visuomotor associations (Wise and Murray, 2000), mirror reversal (Schugens et al., 1998; Gutierrez-Garralda et al., 2013), and birdsong (Ölveczky et al., 2005). While its exact function in skill learning is still unknown, it has been hypothesized that the basal ganglia may be involved in learning sequences of actions (Bapi et al., 2006; Doyon et al., 1997), modulating the vigor of movements (Dudman and Krakauer, 2016), and potentially selecting actions (Mink, 2018). Cortico-basal ganglia circuits exhibit spontaneous activity, the variability/asynchronicity of which can be upregulated or downregulated by increases or decreases in dopaminergic input, respectively (Costa et al., 2006; Brown et al., 2001). Moreover, the variability in this activity appears to decrease as animals learn motor tasks (Hahnloser et al., 2002; Costa et al., 2004). Costa, 2011 thus proposed that dopamine could serve as a potential mechanism for *de novo* action learning, where increases in dopamine early in skill learning allows for acquisition of novel patterns of neural activity and subsequent decreases in dopamine results in consolidation of these novel patterns.

While the basal ganglia has been widely implicated in motor skill learning, many other structures in the brain could potentially contribute to learning. One such area is the prefrontal cortex. Motor learning has often been conceptualized as an implicit process, i.e., not requiring explicit awareness to occur. However, as discussed in great depth in Krakauer et al., 2019, motor learning is likely highly cognitive and explicit, relying on our ability to think about where, when, and how to execute movements. Accordingly, the prefrontal cortex is thought to play a major role in cognitive control (Miller and Cohen, 2001) and has been implicated in humans' ability to store motor memories (Shadmehr and Holcomb, 1997) as well as learn arbitrary visuomotor associations (Wise and Murray, 2000) and sequences (Grafton et al., 1995).

Motor cortex has also been shown to contribute to skill learning. The motor cortex is comprised of three different regions: the primary motor cortex, premotor cortex, and supplementary motor area. Whereas primary motor cortex directly commands muscle contraction throughout the body, premotor cortex and supplementary motor area are thought to be involved in planning movements that are to be carried out by the primary motor cortex. Learning can alter both the movement planning and execution capabilities of motor cortex. On the planning side, it has been suggested that through learning, the premotor cortex and supplementary motor area may form hierarchical representations of a task's component features (e.g., short sequences of movements; Diedrichsen and Kornysheva, 2015), potentially allowing one to flexibly combine different representations to form novel movement plans. On the execution side, increases in the accuracy and precision of movements has been correlated with changes in primary motor and premotor cortex (Nudo et al., 1996; Shmuelof et al., 2014).

The discussion above outlines some of the potential neural bases for *de novo* learning. But what might the learning algorithm for *de novo* learning look like? Although there is no consensus on this matter as of yet, I can suggest a couple possibilities here. One possibility is that *de novo* learning occurs by simultaneously updating forward and inverse models by simple gradient descent, as described in Pierella et al., 2019.

Another possibility is that a new controller could be learned through reinforcement learning. In motor learning tasks, reinforcement has been demonstrated to engage a learning mechanism that is independent of implicit adaptation (Izawa and Shadmehr, 2011; Cashaback et al., 2017; Holland et al., 2018) potentially via basal ganglia-dependent mechanisms (Schultz et al., 1997; Hikosaka et al., 2002). Such reinforcement could provide a basis for forming a new controller. In line with this view, Wang et al., 2018 proposed that the prefrontal cortex (with inputs from thalamus and basal ganglia) may be able to learn arbitrary policies via reinforcement learning, and such policies could serve as the basis for *de novo* learning. Although prior work on motor learning has focused on simply learning the required direction for a point-to-point movement, theoretical frameworks for reinforcement learning have been extended to continuous time and space to learn continuous controllers for robotics (Doya, 2000; Theodorou et al., 2010; Smart and Kaelbling, 2000; Todorov, 2009), and such theories could be applicable to the studies contained in this thesis.

Does the present thesis help us to identify the neural bases or mechanisms underlying *de novo* learning? While the studies I conducted do not provide strong evidence for or against any particular theory, they do provide some guidelines for the kind of neural activity we should look for in the brain. Taking the perspective that novel actions are learned by increases and subsequent decreases in neural activity in the basal ganglia, one could potentially frame skills and habits in terms of a continuum parameterized by variability in activity. When variability is high, people's movements may be unskilled but flexible. As variability reduces with practice, their behavior becomes more skillful and habitual.

However, this simple framework is, to a certain extent, incompatible with the results we observed in Chapter 5. We found that participants' control of the bimanual mapping became more skillful with up to five days of practice but became maximally habitual after only two days of practice. Habitual behavior is characterized by its inflexibility to change, and one might assume that behavioral inflexibility might arise because the neural activity which generates the behavior is itself inflexible to change. If the degree to which a behavior is habitual only varies as a function of variability in activity, once a behavior has reduced its variability enough to become habitual, it should now be resistant to change and not continue to become more skillful. However, this is not what we observed, arguing against this simplistic model. One can easily extend the activity variability framework, though, to accommodate our findings. For instance, habit and skill could each arise from separate reductions in variability, therefore allowing for improvements in skill even after a behavior has become habitual.

In summary, there are many potential neural bases and mechanisms that can explain *de novo* learning. I would like to stress, however, that at the current time we should not attribute *de novo* learning to a single neural basis or mechanism. This is not just because we do not know the mechanism underlying *de novo* learning, but more importantly because our use of the term “*de novo* learning” may in fact refer to a collection of different mechanisms which co-occur as people learn motor skills. In other words, there is no reason to believe that any one mechanism is solely responsible for *de novo* learning. Although this makes *de novo* learning a somewhat nebulous concept, it also highlights the fact that this learning process is deserving of more dedicated investigation in future studies. One important aim of such studies will be to elucidate the exact mechanism(s) underlying *de novo* learning.

6.3 Future directions

In Chapters 3–5, I have already discussed several future directions related specifically to each project. Here, I would like to take a step back and discuss broader future directions related to motor skill learning as well as others I have not yet touched upon.

Thus far, I have discussed three main learning processes: adaptation, re-aiming, and *de novo* learning. While each of these processes can potentially be studied in isolation from one another, it is likely that all three are simultaneously engaged and interact with each other when people learn motor skills. Many such interactions can be imagined. For instance, after the brain has assembled a *de novo* controller, this new controller could be recalibrated via adaptation. Another possibility is that a re-aiming strategy (or more generally, a cognitive strategy) might accelerate the rate at which a *de novo* controller can be assembled (which we attempted to address in Chapter 3). And as mentioned above, *de novo* may in fact be a collection of motor learning mechanisms, each with different interactions amongst themselves as well as with adaptation and re-aiming. Because a mature theory of motor learning will likely require us to consider the interactions between different motor learning mechanisms, one aim of future studies should be to elucidate and understand the nature of these interactions.

In the present work, I focused on studying tasks which challenge people's ability to select actions. While this was an intentional choice, it also meant that I did not investigate another important aspect of motor learning: increasing the accuracy and precision of movement execution (i.e., motor acuity). As described in Chapter 1, people are often faced with learning tasks where they must perform totally novel patterns of movements, such as fingerings on a cello or flipping on a balance beam. Movement execution can be challenging even in scenarios where one already knows what actions they will select. An example of this is the "arc-pointing" task used in Shmuelof et al., 2012. Here, participants were instructed to guide a cursor throw a semicircular tube by making quick, curved movements of the wrist. The movements required were easily understood by participants and remained the same throughout the experiment. Thus, the main challenge that participants were faced with was learning to perform accurate and precise write movements. This task was challenging to learn, as people's success at moving the cursor through the tube continued to significantly improve with up to three days of practice.

As discussed in Chapter 4, there are many potential reasons why *de novo* learning may be slow or may hit performance plateaus with extended practice. In Haith et al., 2021, we found that the inability to generate rapid corrections to mid-movement perturbations using the bimanual mapping may be one of the bottlenecks causing performance plateaus. There are almost certainly analogous bottlenecks in one's ability to execute movements, but what are those bottlenecks? Addressing this question is likely much harder than it was in our study of the bimanual mapping. Tasks which challenge action selection (like the bimanual mapping) have a clear baseline (in the case of the bimanual mapping, a veridical cursor) to compare performance with, allowing one to quickly identify the aspects of performance which have failed to reach baseline levels. In contrast, there is no analogous baseline for tasks that challenge action execution (this is because if participants had an action execution baseline to compare against, then they would already be able to perform the desired behavior, eliminating any learning challenge).

Instead of comparing against a baseline, one could identify bottlenecks in learning action execution by training participants in an appropriate task until they reach a performance plateau. Then through trial and error, one can add careful manipulations to the experiment aimed at improving a specific aspect of performance. For example, how people accomplish a task depends strongly on how they cognitively conceptualize the task, and providing different types of visual feedback or verbal instruction can alter their conceptualization, allowing them to break through a potential plateau. Although this may be a time-consuming process, one can potentially understand where bottlenecks occur by identifying which manipulations produced improvements in performance. Such an experiment could be done in the aforementioned arc-pointing task, albeit likely for much longer than the three days used in Shmuelof et al., 2012 as participants had not yet reached a performance plateau. Ultimately, we should aim to understand not just how people learn action selection or execution in isolation but also how these aspects of learning interact with each other, as many real-world tasks often involve both challenges simultaneously.

In Chapter 5, I investigated habit formation in the context of learning continuous motor skills. More generally, habit formation and skill improvement are just two behavioral changes which occur during learning and are part of a wider collection of practice-induced behavioral changes known as “automaticity” (Moors and De Houwer, 2006; Haith and Krakauer, 2018). One major aspect of “automaticity” that my study did not examine is reduction in cognitive load. As people practice a task, the amount of attention/cognitive effort required to perform the task decreases with practice; whereas novice drivers must dedicate their full attention to operating their car, experts do not need to devote as much attention to driving, allowing them to simultaneously perform other tasks such as conversing with passengers. One potential future direction for this line of work is to consider whether there is any relationship between reductions in cognitive load and habits or skills. For example, might a task’s cognitive load be reduced because one’s behavior has become habitual, freeing them to expend cognitive resources elsewhere? Or might a task’s cognitive load have no dependence on one’s behavior becoming habitual? Currently, there are ongoing experiments in the lab designed to address these questions.

The system identification approach that I’ve used throughout this thesis can be extended to perform more detailed modeling of the sensorimotor system than I have performed here. In general, gaining experimental access to more physiological/behavioral variables will increase the complexity of the models one can fit, potentially increasing their informative power. If, for example, one records EMG activity from the arm during a reaching task, one can include this data in the closed-loop model as motor commands to the plant. One particularly interesting extension of the system identification approach was formulated in Yamagami et al., 2019. Here, the authors describe a method to separately identify feedforward and feedback contributions to movement by introducing sinusoidal disturbances to one's cursor position in a manual tracking task. Feedforward and feedback control have long been of interest to the motor control/learning communities, and the approach described by Yamagami et al., 2019 could easily be used to investigate these phenomena. As pertaining to *de novo* learning, one can use this method ask whether the performance improvements we observe during learning arise from improvements of feedforward control, feedback control, or both.

Finally, one of the main limitations facing the present work—and one which plagues many fields that study learning—is the complexity of tasks that are studied. In an ideal world, we would like to understand how people achieve expertise in tasks like playing the violin by studying these tasks in and of themselves, i.e., observing a violinist progress from novice to expert. However, such experiments are obviously infeasible as these tasks may require decades to master. Out of pragmatism, we often study motor learning in the lab using simpler tasks which can be learned much more quickly, hoping that our findings from these laboratory tasks will extrapolate to the real-world tasks we are interested in, but such extrapolations are not guaranteed. Thus, there is a tradeoff between task complexity and experimental feasibility. How can we design reductionist laboratory tasks which are qualitatively similar to the complex, real-world tasks we are interested in? And how long will it take people to learn them? These are important questions which must be kept in mind for future research in motor skill learning.

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Yang, C. S., Cowan, N. J., and Haith, A. M. (2021). De novo learning versus adaptation of continuous control in a manual tracking task. *eLife* 10:e62578. DOI: `10.7554/eLife.62578`.

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Education

Johns Hopkins University – *Baltimore, MD* Ph.D. Neuroscience Advisors: Dr. Adrian M. Haith, Dr. John W. Krakauer	8/2016–2022 (anticipated)
University of Virginia – *Charlottesville, VA* B.A. Neuroscience with Highest Distinction Thesis: The regulation of sympathetic drive to adipose tissue in response to diet Advisor: Dr. Christopher D. Deppmann	8/2012–5/2016

Awards and Honors

Link Foundation Modeling, Simulation & Training Fellowship	7/2019–6/2021
Fozdar Symposium: 1st place for best presentation	4/2016
Phi Beta Kappa	4/2016
Ingrassia Family Echols Scholar Research Grant	11/2015
College Council Fall Scholars Award	10/2015
Small Research and Travel Grant	6/2015
Harrison Undergraduate Research Award	2/2015
Small Research and Travel Grant	11/2014
University of Virginia Intermediate Honors	9/2014
University of Virginia Echols Scholar	2013–2016
College Science Scholar Spring Research Award	1/2013
Dean’s List	2012–2016
College Science Scholar Fall Research Award	9/2012
University of Virginia College Science Scholar	2012–2016
John W & Ardell T Brumit Educational Trust Scholarship	2012–2016

Other Professional Activities

Student, Santa Fe Institute Complexity Interactive	6/2021
Student, Computational Sensory-Motor Summer School	7/2018–8/2018
Teaching Assistant, Neuroscience and Cognition II	1/2018–6/2018
Attendee, Workshop on FLIM and FRET Microscopy	3/2016

Publications

1. **Yang, C.S.**, Cowan, N.J., Haith, A.M. *De novo* learning versus adaptation of continuous control in a manual tracking task. *eLife*. 10:e62578.

2. Sipe L.M., **Yang C.S.**, Ephrem J., Garren E., Hirsh J., Deppmann C.D. Differential sympathetic outflow to adipose depots is required for visceral fat loss in response to calorie restriction. *Nutr. Diabetes.* 7, e260, 2017.

Preprints

1. Haith, A.M., **Yang, C. S.**, Pakpoor, J., Kita, K. *De novo* motor learning of a bimanual control task over multiple days of practice. *bioRxiv*, 2021.

In preparation

1. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Emergence of habitual control in a novel motor skill over multiple days of practice.

Refereed abstracts

1. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Automatization of control under a complex visuomotor mapping. *ICRA Workshop on Learning of Manual Skills in Humans and Robots*. 2020.
2. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Contrasting *de novo* learning with adaptation by the expression of aftereffects. *Proc. Motor Learning and Motor Control*. 2018.

Invited Talks

1. Department of Neuroscience Annual Retreat, Johns Hopkins University, Baltimore MD (2021)
2. Cheese & Wine Seminar, Newcastle University, Newcastle upon Tyne, UK (2021)
3. Nu Rho Psi Seminar, Johns Hopkins University, Baltimore, MD (2021)
4. Burden Lab Meeting, University of Washington, Seattle, WA (2021)
5. ReNeu Robotics Lab Meeting, University of Texas at Austin, Austin, TX (2020)

Other Non-Refereed Oral Presentations

1. Sensorimotor Research Day, Johns Hopkins University, Baltimore, MD (2019)
2. Department of Neuroscience Lab Lunch, Johns Hopkins University, Baltimore, MD (2018)
3. Fozdar Symposium, University of Virginia, Charlottesville, VA (2016)

Posters

1. **Yang, C.S.**, Haith, A.M. Comparing the time course of skill versus habit development in a visuomotor control task. Cognitive Neuroscience Society Annual Meeting, March 2021.
2. Kita, K., **Yang, C.S.**, Du, Y., Haith, A.M. Comparing latencies of information processing supporting feedforward and feedback control of reaching. Society for Neuroscience Annual Meeting, October 2019.
3. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Characterizing *de novo* learning of continuous motor skill. Society for Neuroscience Annual Meeting, October 2019.
4. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Contrasting *de novo* learning with adaptation by the expression of aftereffects. Society for Neuroscience Annual Meeting, November 2018.

5. **Yang, C.S.**, Cowan, N.J., Haith, A.M. Contrasting *de novo* learning with adaptation using a system identification approach. Annual Meeting of the Society for the Neural Control of Movement, May 2018.
6. Ishida, M., **Yang, C.S.**, Akazome, Y., Oka, Y., Kanda, S. Characiform GnRH neuronal systems provides a good model for functional compensation by paralogous genes. Joint meeting of the 22nd International Congress of Zoology and the 87th Meeting of the Zoological Society, 2016.
7. Sipe, L.M., **Yang, C.S.**, Jansch, C., Ephrem, J., Garren, E., Neff, P., Hirsh, J., Deppmann, C.D. The Regulation of Sympathetic Drive to Adipose Tissue in Response to Diet. Center for Undergraduate Excellence Symposium, 2016.
8. **Yang, C.S.**, Sipe, L.M., Deppmann C.D. Imaging the Sympathetic Innervation of Adipose Tissue. Microscopy Imaging Symposium, 2015.
9. **Yang, C.S.**, Sipe, L.M., Hirsh, J., Deppmann, C.D. Treating Obesity and Related Metabolic Disorders through a Sympathetic Approach. Society for Neuroscience Annual Meeting, 2015.
10. **Yang, C.S.**, Sipe, L.M., Hirsh, J., Deppmann, C.D. Treating Obesity and Related Metabolic Disorders through a Sympathetic Approach. Central Virginia Chapter Society for Neuroscience Conference, 2015.