

EMPIRICAL STUDIES ON THE COMPUTATIONAL AND
COGNITIVE MECHANISMS OF HUMAN LEARNING AND
MOVEMENT

by
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Abstract

The topic of human movement, and the question of how humans learn new behaviors, has puzzled philosophers and scientists since classical times. A commonly held assumption is that there are two qualitatively distinct learning systems, one responsible for remembering knowledge of facts and events, and the other responsible for forming associations and learning new skills, including motor learning. The evidence in support of this dissociation has been independently reproduced through many different experiments and methods of analysis.

One line of evidence that has recently been investigated is the dual-component nature of adaptation learning. When humans and animals are challenged with a change in their environment or the physiology of their bodies, such as what might happen through growth and development or because of injury, the nervous system adjusts its control mechanisms to maintain accurate movements. Learning of this form is known as adaptation, and had originally been theorized to be achieved through an implicit learning mechanism. Furthermore, it was often thought that this same learning mechanism was responsible for more general forms of learning, such as learning the use of new tools.

This model has recently come under scrutiny as evidence has emerged demonstrating a role for memory of facts in adaptation. If there are at least two mechanisms responsible for adaptation learning, which one of them, if either, is actually responsible for more general skill learning? If one, but not the other, of

these mechanisms is responsible for skill learning, what is adaptation really a model of? And how might the conclusions of other studies that used adaptation as a general model for learning need to be reconsidered? For instance, the results from neurophysiological studies of adaptation may find neural correlates that are uniquely related to adaptation but not to other types of motor learning. Having a better behavioral- and computational-level understanding of the mechanisms involved in adaptation learning is necessary to address these and potentially many other questions.

Given the challenges present in the study of adaptation, there is a need for other models of learning and movement that give different perspectives and emphasize other aspects of learning that might be missing from adaptation. For instance, adaptation involves correction of movements around an existing ability, such as reaching. How is reaching itself learned? Acquiring or building new behavioral abilities might involve qualitatively different mechanisms compared to adaptation. Furthermore, new methods for analyzing the kinematics of movements are necessary, as adaptation paradigms typically limit their analysis to the choice of reaching direction only.

In this dissertation, I will present several original, empirical studies on the role of cognition and explicit knowledge in motor learning. I will investigate the computational mechanisms that underlie learning new behaviors. I will introduce a new model for human motor skills and skill learning, and show how this model fills

gaps that exist in the repertoire of models, methods, and concepts currently popular in the science of learning. I will show evidence that adaptation learning is made up of at least two qualitatively distinct learning components. One component appears to be deliberate, driven by explicit knowledge, and is computationally expensive. The other is implicit, driven by sensory-prediction errors, and is automatic and readily expressed. I will demonstrate that the deliberate component becomes automatic following practice, and will argue that this process is a plausible mechanism for how more general motor skills are learned. Implicit recalibration does not change with practice and therefore appears unlikely to be responsible for skill learning. I will show that learning a new continuous-movement behavior, like skiing or riding a bike, is done through the creation of a flexible feedback control policy. I will discuss the inconsistency of sequence learning and chunking hypotheses, and contrast them with the control policy theory.

The studies, results, and conclusions presented here demonstrate that motor learning intrinsically involves cognition and explicit representations of knowledge. The classical concept of motor learning being a subset of implicit memory is inconsistent with the present findings and other recent work. Instead, a view of motor learning as being a phenomenon emergent from the interaction of multiple forms of memory and algorithms of learning is emerging.

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Preface

Empirical investigation is a uniquely challenging endeavor within science. There may be unusual or difficult methods to master, advanced theories to learn, a mountain of prior work to become familiar with, and bureaucratic obstacles at every step. Success requires a set of skills rarely found concurrently in any individual. When universities are lucky, a set of people choose to congregate who possess a minimum threshold of abilities and motivations to undertake original, interesting, and valuable work. Even more rare are individual labs that attract people with those necessary qualities. The Brain, Learning, Animation, and Movement (BLAM) Lab comes as close as any I have seen to attaining that threshold.

The BLAM Lab has become an intellectual crucible. Each member may have had his or her own goals and theories when they joined, but subsequently evolved to adopt far greater understanding and purpose. My work, and that of my advisors and coauthors, emerged from the BLAM broth to be more interesting and subversive than any of us imagined it would be. I sought to better understand learning and movement, and discovered psychology, biology, and complexity along the way.

I would like to acknowledge that two of the Chapters contained herein, Chapters 3 & 4, have been previously published. Chapter 3 appeared in the Journal of Neurophysiology as

Huberdeau, Haith, Krakauer (2015). Formation of long term memory for adaptation following only a few trials of practice. J Neurophys.. 114(2): 969-77.

I wrote the manuscript, assisted in the conceptualization of the study, collected the data, and analyzed the data. I have adopted it for this dissertation with the permission of Adrian Haith, John Krakauer, and the Journal of Neurophysiology.

Chapter 4 appeared in the Journal of Neuroscience as

Haith; Huberdeau; Krakauer (2015). The influence of movement preparation time on the expression of adaptation and savings. J Neurosci. 35(13) 5109-17.

Adrian Haith wrote the Journal of Neuroscience manuscript. I edited the manuscript, assisted in the conceptualization of the study, collected some of the data, and assisted in the analysis of the data. I have adopted it for this dissertation with permission from Adrian Haith, John Krakauer, and the Journal of Neuroscience. For the remaining chapters, I wrote them, contributed to their conceptualization, collected the data, and analyzed the data.

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I must also acknowledge the critical contribution that Omar Ahmad, Promit Roy, and Kat McNally, who together make up Max and Haley, Inc. and the Kata Project. They were responsible for building the video game that I describe in Chapter 6, and provided critical technical support.

I would also like to recognize those individuals who so steadfastly encouraged and supported me throughout my graduate school endeavor. To my parents, Mark and Terri Huberdeau, for their support and limitless, holistic nourishment all of these years; my partner, Jennie Choi, and her family, to whom I owe a debt of gratitude for their encouragement and caring; my brother, William Huberdeau, for always pushing me (whether you knew it or not) to be a better person, and for being my friend; and to the rest of my family, for their endless love and encouragement, thank you Elsie Schaar, William (Bill) Huberdeau, Dave Schaar, Cindy and Troy Ray, Elaine and Tom Huberdeau, Anne and Joe Nadeau, Cathy Huberdeau, Linda Huberdeau, Steve Huberdeau, and Jeanne and Larry Gray; and to my friends and lab mates, for their entertainment, company, and love, especially Hansen Bow, Chris Douville, Graham Belton, Nathan Kim, Ben Williams, Alex Forance, Michelle Harran, Jing Xu, Alkis Hadjiosif, Rob Hardwick, Aaron Wong, Field Blauvelt, Omar Ahmad, Promit Roy, Kat McNally, Shaoyi Zhang, Mike Azzarello, Juan Camillo, Kevin Olds, Steve Zieler, David Zee, Justin McCarthur, Amy Bastian, Reza Shadmehr, and President Ron Daniels.

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1 Introduction

Humans have long lauded ourselves for our remarkable capabilities. Feats of the mind and feats of physical dexterity are commonly cited as characteristics that set humans apart from other animals^{1,2}; traits that make mankind king of the animal kingdom. Might these remarkable mental and physical abilities be related? Might the mental computational power that produced language and algebra also assist in learning the nuanced limb coordination required of painting, wielding a hammer, or swimming the breast stroke?

The history of this question – what the relationship is between cognitive faculties and dexterity of movement – is as old as recorded philosophy. In the treatise *De Anima*, Aristotle suggested that there is a distinction in human thought between theoretically reasoning and practically reasoning³. One interpretation of his stance is that practical reasoning includes the computations and processes for acquiring goals through action, while theoretical reasoning is responsible for representing objects or abstract ideas, much like the blueprints of a building represent the building itself³. The question and concept is clear, though, that there appears to be a distinction between abstract thought and the faculty to execute goal directed

behavior. The spirit of this philosophical position persists, reflected in contemporary theories related to the existence of dichotomy in memory, learning, and mental processing between two qualitatively distinct systems.

Much of the foundational evidence for contemporary theories of the existence of multiple memory systems comes from lesion studies, particularly selective memory deficits resulting from damage to the medial temporal lobe in humans⁴⁻⁸. Brenda Milner, for instance, found that a patient with severe amnesia could nevertheless learn a new motor skill, mirror drawing, despite this patient's severe memory deficit for facts and events⁵. The subject of that study, the now-famous patient H.M., suffered from severe retrograde and anterograde amnesia (he could neither remember new information nor recall information learned within several years of the existence of his lesion) as a result of a surgery to remove tissue from both of his medial temporal lobes⁹.

Many additional studies have expanded on the earlier findings from amnesic patients to discover additional dissociations or double dissociations that appear to demonstrate the existence of multiple distinct memory systems⁷. For instance, despite their memory deficits, amnesic patients can learn to handle a stylus while viewing it through a mirror⁵, improve in the rotary pursuit task⁶, and learn to read words that have been mirror-reversed⁴. Amnesic patients are also equally sensitive to priming effects as controls¹⁰⁻¹², and can form habits normally^{8,13}. These results support the idea that multiple memory systems exist and are differentially sensitive to specific types of neurological damage. Other forms of brain damage or

degeneration, such as Parkinson's Disease (PD), engender different behavioral and learning deficits that appear to confirm the concept of multiple memory systems. For instance, while amnesic patients can learn habits as normally as control subjects, PD patients are impaired in the opposite way – they have relatively normal memory for events and facts, but are impaired in learning new habits⁸. Thus, lesion studies demonstrate that manipulation of particular circuits within the brain can selectively repress one or the other of seemingly two memory systems.

There are other, behavioral ways to obtain or infer dissociation in memory and processing aside from selective brain lesions or circuit deactivation. Manipulations such as diverting attention through dual-tasking¹⁴, or limiting reaction time^{15,16}, also demonstrate memory system dissociation. For instance, manipulating attention during a serial reaction time task through a dual-task condition selectively impaired recall memory but not the ability to reduce reaction times under the repeating sequence¹⁴, which is thought to happen because of a procedural learning process¹⁷⁻²¹ or some other implicit mechanism²². This result implies that learning of one type – whatever was responsible for reducing reaction times under a repeating sequence – was independent of the memory responsible for learning the sequence explicitly.

One of the leading theories for the nature of the multiple systems of learning is that one is declarative and the other is non-declarative⁷. This model suggests that the declarative memory system is responsible for knowledge of facts and events, is impaired through lesions of the medial temporal lobe that causes amnesia, and is

sensitive to manipulations that divert attention¹⁴ or that eliminate the chance for intentional reflection or recall^{15,16,23,24}. The non-declarative system, on the other hand, is thought to be responsible for learning and retaining skills, habits, and associations, functions that can be impaired in patients with conditions such as PD. This system is also thought to be responsible for the effects of priming, where explicitly undetectable stimuli nevertheless affect behavior, e.g. by instilling emotions or biasing choices²⁵. Furthermore, the model suggests that declarative memory is explicit, i.e. accessible to conscious awareness, while non-declarative memory is implicit. This latter concept is so intrinsic to the model that the terms “declarative” and “explicit”, and likewise the terms “non-declarative” and “implicit”, are sometimes interchanged^{26,27}.

The dual-systems model of learning has been highly influential⁷. However, many questions remain about the validity of the explicit-vs-implicit dichotomy, and about the true nature of skill learning. For instance, recent work has suggested that knowledge of facts may be intrinsic to learning behaviors that otherwise would be considered as procedural²⁸. For example, would an amnesic patient be able to appropriately serve a tennis ball after having been taught the actions to do so? Serving in tennis is a learned motor behavior that would seem to fall within the category of procedural memory. However, without knowledge of what a tennis racquet is, how it is meant to be used, or what the goal of a serve is meant to be, would normal serving behavior be expected? An experiment in amnesic patients tested this very question²⁹. Patients were trained to use obscure, novel objects, and

then were tested for their ability to recall the use of those same objects later. Amnesic patients learned the correct use of the objects just as well as control participants when they were reminded of the intended use on each day of training. However, the amnesic patients were not able to recall details about the objects (e.g. color or function), or how to grasp the objects to initiate their use, while control participants were able to do these things. If a patient's hand was placed in the correct configuration for manipulating the tool, they could perform the correct actions normally. Thus, it appeared that declarative memory was necessary to recall the intended use and correct initial configuration for the use of the novel objects, but was not necessary for doing the appropriate actions themselves. This study also demonstrates the precariousness of categorizing behavior as being either declarative or procedural; using these tools required both types of memory and thus cannot accurately be called either.

If skills are neither wholly procedural nor wholly declarative in nature, what are they? One idea is that learning new skilled behaviors is supported in parts by both systems^{16,23,29-34}. Under this hypothesis, it should be possible to interrupt learning, or even manipulate the outcome of learning, by selectively modulating one of the component systems. Modulation of the systems allegedly involved in learning could, in theory, be achieved through any of the methods previously mentioned as selectively affecting one or the other of the separate memory systems. Several studies have attempted precisely this. One study of visuomotor adaptation learning instructed participants in what the appropriate action should be to cancel an

imposed rotation of their computer cursor. After being provided with this “cheat”, participants cancelled the perturbation, but with additional practice, their reach directions gradually drifted so that the absolute error of their reaches actually increased²³. This finding demonstrated the independence of a declarative-like component, that appeared to be deliberate, and an implicit and seemingly automatic component that reacted to sensory-prediction errors regardless of intention. Other studies have confirmed this conclusion, including one that limited the amount of preparation time prior to movement to eliminate the use of deliberate action¹⁶, and another that directly measured the deliberative component on each trial of adaptation by simply asking participants where they were aiming each reach³⁵. These studies demonstrated that, at least for visuomotor adaptation, learning is supported by at least two qualitatively distinct mechanisms, one that is deliberate, sharing characteristics with declarative memory, and one that is implicit and seemingly automatic or not under deliberate control.

One question that remained, however, was which of the two learning components was responsible for retention of the memory for adaptation. Adaptation is an unusual model for skill learning because it is subject to decay, where behavior reverts to baseline with the passage of time or when feedback is removed³⁶. One sign that anything is retained from prior experiences at all is savings, or faster re-learning under similar perturbations³⁷⁻⁴³. Understanding how motor skill are learned and retained long-term can be studied using adaptation tasks by asking which of the learning components in adaptation are responsible for savings.

To address this question, my advisors, John Krakauer and Adrian Haith, and I devised and conducted a set of experiments. In one study, presented in Chapter 3 of this dissertation, we asked how much prior experience with a perturbation was necessary to instill savings. Were savings supported by recall, for instance of actions or of an explicit strategy, very minimal prior experience should be sufficient to obtain savings. If savings required prolonged practice with the perturbation, it would have appeared that a procedural mechanism was responsible, and that any explicit component that might have been active was not retained. In another study, we used a method to manipulate the preparation time prior to movement in order to more directly measure implicit adaptation and observe whether it was responsible for savings, in a similar way to Ferandez-Ruiz, et. al¹⁶. This study is addressed in Chapter 4.

In addition to our studies, a few other recent studies have attempted to address these same questions about the nature of savings in adaptation. A consistent conclusion has been that savings is primarily supported by recall of some explicit representation of actions or of strategies^{44,45} (Morehead; Hadjiosif). In a third study, we recognized that some motor skills require prolonged practice to consolidate and shed any potential reliance on declarative processing or memory⁴⁶⁻⁴⁹, and so we extended the amount of practice that we provided participants during an adaptation task to see if the mechanisms supporting savings changed. This study is presented in

Chapter 5, and is to our knowledge the first that addresses the question of consolidation of the multiple components in adaptation over longitudinal learning.

Visuomotor adaptation is only one model for motor learning, and has its limitations and drawbacks as a model. For instance, it only considers learning to counteract the effects of an imposed perturbation to otherwise over-learned behaviors, especially simple reaching. Many behaviors most associated with skilled movement, on the other hand, require the formation of novel actions that may require continuous feedback and arbitrary associations. Other tasks that serve as models for skill learning, such as sequence learning^{14,18,50,51}, or arbitrary visuomotor associations^{52,53} do not necessarily encapsulate each of these features. In particular, these tasks typically build up longer movements from pre-existing abilities, such as finger tapping or reaching, and are usually discrete rather than continuous. While all of these models are helpful for answering particular questions and gaining certain insights, their limitations make it difficult to address other profound questions and to gain a broader perspective on the nature of skill learning. A task that attempts to address these limitations is the motor acuity task⁵⁴ (Bioarxiv paper), where participants must learn a novel, continuous control strategy.

The fourth study described in this dissertation, in Chapter 6, investigates learning of a continuous feedback controller longitudinally with practice. Certain properties of learning can be informative for inferring the underlying mechanism. For instance, measuring changes in mean behavior^{55,56}, stereotypy^{18,55-58}, feedback responses⁵⁴,

and the covariance structure of movement⁵⁶ can give clues as to the mechanism of learning. This is particularly true when assessing the response to perturbations⁵⁴, or measuring the transfer of behavioral characteristics under different conditions than those encountered during learning⁵⁹⁻⁶². For instance, measuring the extent of generalization of behavior provides information regarding whether learning involved model-free or model-based mechanisms⁶³. In Chapter 6 of this dissertation, I present a study that uses a novel task implemented in a custom-designed driving simulator video game (Max & Haley, Inc., Baltimore, MD) to study continuous-action learning longitudinally. The task tests for generalization at four different times throughout learning to assess how the underlying mechanisms involved in learning may have changed over the course of practice. While this study does not directly measure or evaluate the implicit-versus-explicit nature of learning, it makes an important first step in expanding the tools, methods, and concepts for studying motor skill learning. This study expanding beyond discrete, overlearned behaviors into a model that is more consistent with the behaviors that make us most human.

2 General methods

In contemporary psychology and behavioral science, empirical experimentation and quantitative analysis has supplanted the introspective analyses of the early philosophers⁶⁴. In accordance with this strong tradition, I have investigated the questions I proposed in the Introduction through controlled experiments, recorded observation, and quantitative analysis.

In the empirical investigation of any phenomenon, the scientific approach is typically to begin with a hypothesis for a model that includes the factors, objects, and modes of action for how a phenomenon may emerge. The hypothesis must be tested in some way, contingent on available methods and possible control over the phenomenon. Tests vary in the validity of their conclusions. For example, a simulation may be done to test the plausibility of a model, comparing the pattern of results from the simulation with that observed in nature. For some questions and hypotheses this method is the only one available, such as for testing many phenomena in climate and earth sciences. This approach is also popular in human behavioral science to test whether a given model or algorithm can plausibly reproduce behavioral results. Other tests may come in the form of “natural

experiments”, in which natural variation or serendipitous circumstances of nature allow for observation of the consequences of certain conditions and the comparison with other, more normal conditions. For example, in sociology, it might be possible to study the consequences of certain public policies by comparing localities that instituted a certain policy versus others that did not. In psychology and neuroscience, this approach has been widely used and highly influence. For instance, studies of the consequences of naturally occurring or incidental brain lesions or diseases have been the incipient evidence for highly influence theories of memory. Finding that having bilateral lesions to the medial temporal lobe results in debilitating memory deficiencies has led to theories for the independence of declarative versus non-declarative memory. However, studies of these forms are potentially confounded, because it remains possible that the reasons for a condition emerging naturally may correlate with consequences of that naturally occurring event. The most powerful and convincing form of evidence is generally through randomized control studies, in which a manipulation or condition is applied selectively to a randomly selection sample of a population of interest and compared against members who did not receive the condition. This approach allows the establishment of causality, and although there are potential hazards and pitfalls of drawing conclusions from the results of such studies, they remain the most powerful tool in an empirical scientists’ arsenal.

Each of the studies presented herein take this latter approach, using randomized control studies to investigate the mechanisms of movement and learning. In

addition, in forming conclusions and attempting to place the raw findings in a broader context, I draw from other evidence from simulation studies and incidental lesion studies.

Visuomotor adaptation

One popular experimental model for human learning is the visuomotor adaptation task⁶⁵⁻⁶⁷. One manifestation of this model is the visuomotor rotation task, in which a cursor that serves to represent the position of a participant's hand is perturbed through the application of a rotation of a certain angle from the actual direction of reach⁶⁷. Evaluation of behavior in this task usually comes in the form of measuring the angle at which participants launch their movement on each reaching attempt. Evidence for learning in this task comes in the form of observing that participants adjust their reaching direction so as to cancel the effect of the rotation. This effect is robust and has been reproduced many times.

This basic model of learning has been coopted to study many other aspects of learning. For instance, it has been used to study memory of adaptation, or savings, in which learning is faster during subsequent exposures to similar perturbations^{38,39,68-72}. This task has also been subject to additional modification in order to decompose the underlying components to adaptation learning, for instance through the use of dual-tasking⁷³, manipulations to the reaction time^{16,72,74}, or explicit instructions³⁵.

Continuous-movement learning

I will argue that a neglected characteristic of human learning is learning novel continuous movements. Typically, learning tasks involve discrete decisions, like forced choice tasks (e.g. Decker, et. al.⁷⁵), and discrete movements, such as sequence learning tasks (e.g. Diedrichsen, et. al.¹⁸), which may include learning changes to the value of stimuli or choices. Most learning tasks can be distilled down to a choice, if even among continuous options, such as adaptation learning. It is far less common to study the way that continuous movements are learned, such as in⁷⁶. One approach for the study of the kinematics of movements and how they change with learning is to introduce a novel behavior and measure the kinematics of movements throughout learning⁵⁴. I will introduce a new model for continuous-movement learning that uses a custom-built video game implemented on a tablet computer. I will also introduce novel methods to analyze the behavior from this task, both in terms of task success and movement kinematics.

3

Recall of actions supports memory for adaptation

Long-term memory for adaptation is established following minimal initial practice, which is consistent with an action recall mechanism.

Adaptation learning in humans occurs in response to changes in movement dynamics or changes in the environment and serves to maintain movement accuracy^{66,67,77,78,79}.

One theory for the information processing that occurs during adaptation is that an internal model that assists in generating motor commands for a given movement is updated in proportion to the sensory-prediction error observed as a result of the movement perturbation^{23,66,67}. More recently, theories and empirical data have suggested that in addition to an error-based mechanism, another mechanism is simultaneously active during adaptation that may be explicit in nature, such as choosing to reach in a direction other than directly toward the target^{23,74,80-83}.

One important observation related to adaptation is that human subjects adapt to a perturbation in fewer trials when they have previously experienced that perturbation, a phenomenon referred to as 'savings'^{37-39,41-43,84}. How savings occurs is a matter of debate. There have been a number of theories for savings that can be

broadly categorized as recall, modulation of error sensitivity, and representational redundancy. Recall refers to a mechanism for converging on an action that had previously been successful in countering a rotation^{42,85}. The error sensitivity theory suggests that prior experience with a given perturbation durably changes the future response of the apparent error-driven mechanism to similar perturbations, resulting in savings^{60,70,86-88}. A third theory for savings suggests that, although subjects may behave similarly at baseline from one day to the next, re-adaptation is faster during the second exposure because adaptation begins from a different underlying state^{78,89-92}. Although all of these explanations differ in important ways, they all assume that periods of prolonged prior exposure to a perturbation are necessary in order to elicit savings.

Recent work has shown that savings is attributable to a single component of learning^{45,93,94}, which appears to be the component that may be driven by explicit processing⁹⁵. This mechanism may involve, for instance, choosing to aim in a direction other than the one towards the target when adapting to a rotation⁸³. Thus, savings may plausibly result from recall of this explicit component of prior learning, rather than modulation of the implicit one. If so, savings may be obtainable following far less prior practice than has typically been thought, assuming that an explicit memory can be acquired rapidly.

To investigate this hypothesis specifically, we conducted an experiment to determine the minimum amount of initial exposure to a perturbation that is sufficient to obtain

savings. To do this, we varied the duration of initial exposure to a visuomotor rotation, and tested for savings a day later.

Materials and Methods

Subjects

80 right-handed, neurologically healthy subjects participated in this study (18 – 40 years old, 49 women), which was approved by the Johns Hopkins School of Medicine Institutional Review Board.

Experimental Setup

Subjects were seated at a glass-surfaced table with their right forearm supported by a splint equipped with air-vents allowing near-frictionless planar arm movements. Subjects' arms were obstructed from their own view by a mirror, on which was projected a graphical interface from a downward-facing LCD monitor installed above the mirror (60 Hz refresh rate; LG). A cross-hair cursor presented on the screen represented the position of a subject's index finger, as reported by a Flock of Birds (130 Hz; Ascension Inc., Shelburne, VT) magnetic sensor placed under the finger.

Task

Subjects were instructed to make rapid “shooting” movements from a home position (a green circle, diameter 0.7 cm) through a target (blue and grey concentric circles,

diameter 1.0 cm) located 8 cm away (Figure 1A). After reaching to the target, subjects were instructed to return their hand and cursor to the start position again. The cursor indicating their hand position was not visible during this time, unless it was within 1 cm of the start position. On a specific predefined subset of trials, the cursor's instantaneous position was manipulated by imposing a rotation (30° in all but one condition) of the cursor location about the start position in either the clockwise or counter-clockwise direction, depending on the condition (Figure 1A). Any perturbation was turned off in the inter-trial interval. The target location was fixed for each subject but was randomized across subjects in order to mitigate any biomechanical biases that may have been present at any individual target location.

50 subjects were randomly assigned to one of four "principal" groups or a control group (Figure 1B). The principal groups differed only in the number of trials of the initial rotation: 2-, 5-, 10-, and 40- trials ($n = 10$ subjects per group). Note that subjects in the 40-trial group actually only received 39 trials of the rotation due to an implementational error; we nevertheless maintain the "40-trial" notation throughout. All subjects in each group made 59 reaching movements under "null" rotation conditions in which the cursor accurately reflected the location of the subjects' index finger. Both the initial and subsequent perturbations were 30° counter-clockwise rotations for these principal groups. The training durations of the first rotation were chosen to vary the amount of adaptation achieved across groups during the initial exposure. We refer to these groups as ROT₂, ROT₅, ROT₁₀ and ROT₄₀, respectively. The control group, ROT₀, did not experience a perturbation on the first

day and thus served as a baseline against which to establish the existence of savings in the principal groups. ROT₀ practiced reaching to the target under null-perturbation conditions (no rotation) on Day 1, and then first encountered the rotation on Day 2. 10 subjects who had never experienced a rotation were assigned to this group. All subjects in each group returned the next day to complete 65 trials of a 30° counter-clockwise rotation.

Three additional groups, ROT_{15DEG}, ROT_{COUNTER} and ROT_{5MIN}, were tested to further explore the conditions sufficient to achieve savings. Each group was composed of 10 new, naïve subjects. Group ROT_{15DEG} tested whether the magnitude of the first and second rotations must be the same to bring about savings. For the first rotation, subjects experienced a 15° counter-clockwise rotation for 39 trials in order to match the conditions experienced by group ROT₄₀. The second rotation was identical to that for the principal groups. A further group, ROT_{COUNTER}, was tested in order to determine whether the sign of the first and second rotations must be the same to observe savings. For the first rotation, subjects in this group received a 30° clockwise rotation for 5 trials and were tested for savings the next day by experiencing 65 trials of the opposite rotation, which was the same savings probe as in all the other groups. In the last group, ROT_{5MIN}, we tested whether savings requires an overnight period between exposures or can be achieved with only a short break between sessions on a single day. Subjects in this group received 5 trials of a 30° counter-clockwise rotation and then started Session 2 five minutes later, which again consisted of the same savings probe as all other groups.

Data analysis

All data were analyzed offline using Matlab (The Mathworks, Natick, MA). Kinematic data were sampled at 130 Hz. These signals were filtered with a 3rd-order Savitzky-Golay interpolation filter with half width 35 ms. Reach direction was determined by computing the angle at which each movement passed a circle centered on the start position with a radius of 8 cm (the distance to the target). Each subject's reach direction bias, determined by taking the mean reach direction during a 59 trial practice block without a rotation was subtracted from the reach directions measured during the rest of the experiment to mitigate any potential biases due to biomechanical differences across subjects and target locations. Analysis results were qualitatively unchanged if the initial reach direction (the angle at which each movement was launched, measured at 200 ms after movement initiation) was used instead of the angle that the cursor passed the target radius.

There are at least three ways in which prior experience with the rotation can influence behavior in subsequent exposures. First is retention of adapted behavior, expressed as a reach direction bias on the first trial of the second exposure ^{96; 97}. Second, and of primary interest to us, is savings, in the form of a faster relearning rate ⁴¹. Third is an asymptote effect, in which the mean steady-state reach direction after adaptation is closer to the direction that would fully cancel the rotation ⁸⁴. We quantified each of these aspects of behavior as follows: The initial bias was defined as the measured reach direction on the first trial of the second rotation. Adaptation

rate is reflected in subjects' average amount of learning early in adaptation, which was defined as the mean reach direction on trials two through six on Day 2. This range of trials was chosen *a priori* as it encompasses the period during which learning progresses most rapidly in prior studies^{42,36}. Alternative trial boundaries for this measure (possibly including the first trial or later trials) did not qualitatively alter the results. Finally, asymptote was defined as the mean reach direction over the last 40 trials of the second rotation.

The control group, ROT₀, served as a basis of comparison for bias, savings, and asymptote effects measured in the other groups. Three one-way ANOVAs were conducted with group as the main factor and the relevant measure (i.e. initial bias (Trial 1), early learning (Trials 2-6), and asymptotic learning (Trials 31-65)) as within group factors. In the event that the outcome of a test returned a significant main effect, we planned *post-hoc t*-tests between group ROT₀ and each of the other groups to detect which groups were significantly different from naïve, correcting for multiple comparisons using the Tukey-Kramer method. Additionally, a one-way ANOVA was used to test for differences in these three behavioral measures (bias, savings, and asymptote) among the four principal groups.

A single-trial analysis was also used to more closely examine behavior at the very beginning of re-exposure to the rotation. This "single-trial learning rate" was defined as the change in reach direction from the first to the second trial of a rotation. The reason for including this alternative analysis was that if a subject had a larger single

trial learning rate at the start of their second exposure compared to their first, they must have formed a memory for how to counteract that rotation. The use of a single trial to determine an estimate for learning rate has been employed by others^{70,88,98,99}. To formally test this difference, a paired *t*-test was conducted for each group comparing the single-trial learning rate between the first and second rotation exposures within each subject.

Analysis for the three additional groups (ROT_{15DEG}, ROT_{COUNTER}, ROT_{5MIN}) was the same as that described for the above groups with respect to quantifying bias, savings, and asymptote. All additional groups were compared against ROT₀ with respect to the mean initial adaptation measure (using a *t*-test) and groups ROT_{COUNTER} and ROT_{5MIN} were compared against ROT₀ with respect to the difference in the single-trial learning rate. For the single-trial learning rate analysis, we reversed the sign of the reach direction for ROT_{COUNTER} for Day 1 in order to compare across rotation sessions. The single-trial-learning-rate analysis was not performed for the ROT_{15DEG} group because of the difference in perturbation magnitudes across sessions.

An additional analysis was conducted to measure how closely the initial few trials of the second rotation exposure matched to the best performing trials from the first exposure. This analysis was conducted to determine plausibility of the recall hypothesis of savings. In this analysis, we tested for correlation between the best trial from Day 1 (the reach direction closest to canceling the rotation, at 30-degrees) and the reach direction during the first two trials of Day 2 (excluding the very first trial,

which regressed back to baseline given the overnight break) that best matched that value reached on Day 1.

Group sizes of 10 were chosen based on a power analysis conducted using pilot data. Specifically, we used an estimate for the effect size of the initial adaptation measure of 6.5° and an estimated standard deviation of 6° , with a probability of a false negative result of 0.8. This results in an estimated minimum of 8 subjects per group.

Results

Participants in this study engaged in a reaching task, moving their right hands from one target to another on each trial (Figure 1A). A 30° counter-clockwise rotation was introduced on Day 1 of the study, and on Day 2, the same perturbation was given to test for savings. The number of rotation trials on Day 1 was varied across four different groups so that the effect on savings of differing amounts of prior practice could be measured (Figure 1B).

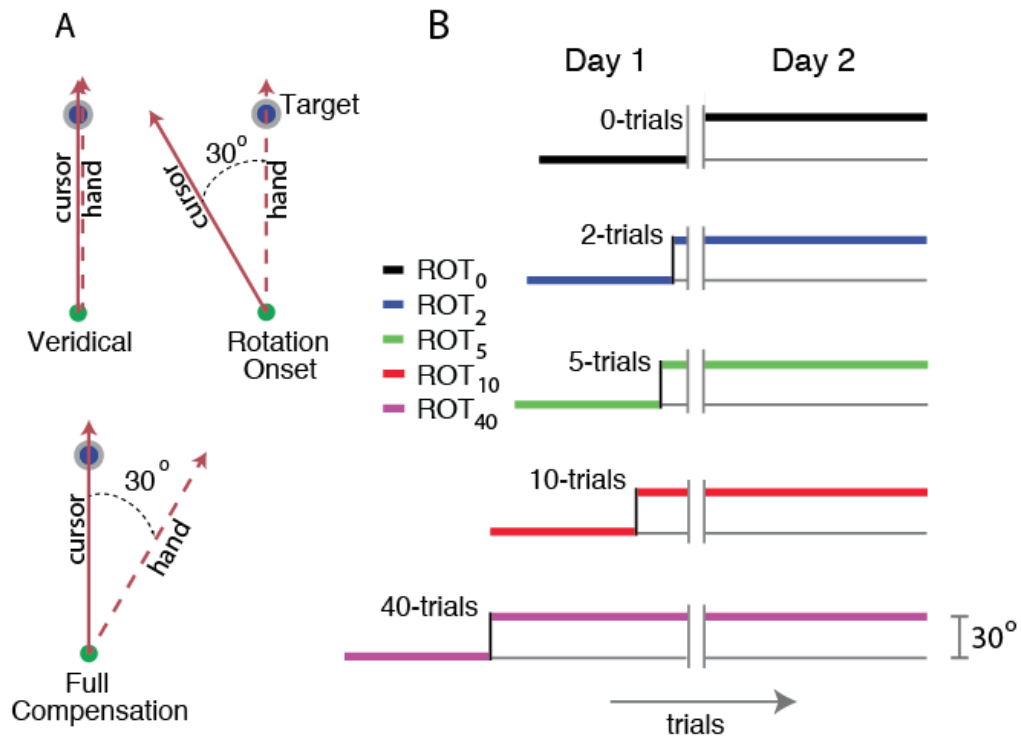


Figure 1: Visuomotor rotation experimental setup. (A) During baseline movements, cursor feedback accurately reflects the position of the subject's hand (veridical, 0° rotation). With onset of the 30° rotation, cursor feedback is rotated about the origin (the start position) by 30° . Dashed line: hand path, solid line: cursor path, green circle in isolation: movement start position, blue circle with grey ring: target. (B) Perturbation schedule for principal groups and the control group ($n = 10$ per group). Double gray vertical lines indicate a break across days.

Varying the amount of prior practice with the rotation had the effect of varying the compensation achieved during that time so that groups different in the extent of compensation that they achieved on the first day. On average, ROT₂ adapted 3.8° , ROT₅ adapted 17.0° , ROT₁₀ adapted 23.0° , and ROT₄₀ adapted 26.8° (Figure 2). Thus, the pre-defined groups spanned a wide range of experiences during the initial exposure to the rotation.

Savings was observed even when initial adaptation was brief and incomplete

Despite having differing amounts of adaptation during the first session, groups ROT₅, ROT₁₀ and ROT₄₀ all showed savings during Day 2; each group adapted faster compared to the rotationally-naïve group ROT₀ (Figure 3). There was a significant difference across the five groups according to mean performance during early learning (the average reach direction on trials 2 – 6; ANOVA, $F(4, 45) = 6.0$, $p = 0.0006$). *Post-hoc* tests comparing early learning in each group that experienced a rotation on Day 1 to that for the control group, ROT₀, revealed that each group except ROT₂ exhibited significant savings (ROT₀ vs. ROT₂: $p = 0.49$; each other comparison: $p < 0.01$). An ANOVA revealed a marginal difference across the four principle groups (ANOVA, $F(3,36) = 2.76$, $p = 0.056$).

In addition to savings in the rate of adaptation, we examined how other characteristics of performance (i.e. bias and asymptote) in the second session varied with the duration of exposure in the first session. The initial bias across all of the groups was not detectably different (Figure 3; ANOVA, $F(4,45) = 1.88$, $p = 0.13$; ANOVA excluding ROT₀, $F(3,36) = 2.08$, $p = 0.12$), and nor was the asymptote during the second session (Figure 3; ANOVA, $F(4,45) = 1.37$, $p = 0.26$; ANOVA excluding ROT₀, $F(3,36) = 1.80$, $p = 0.17$).

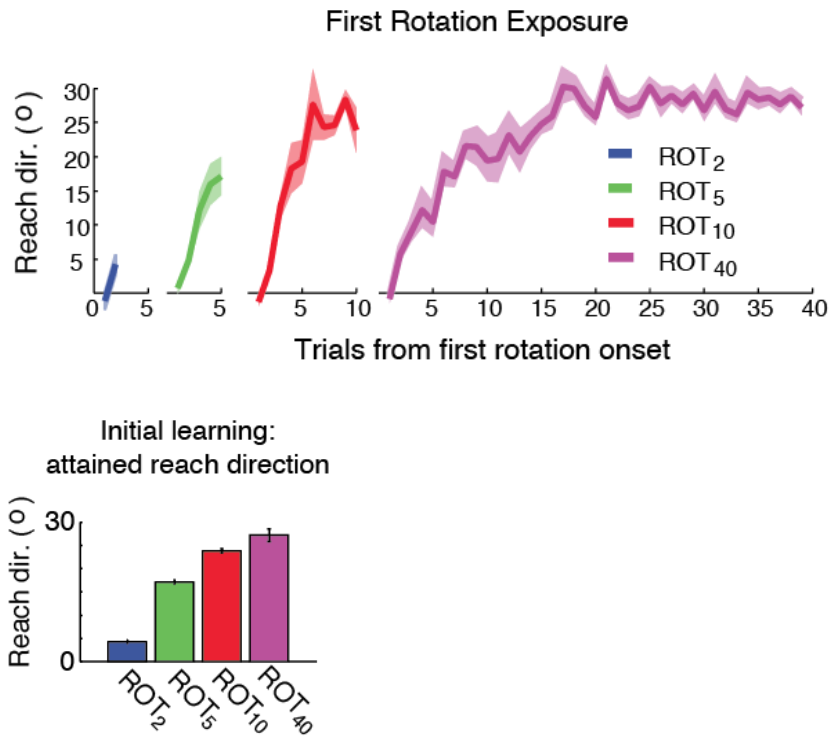


Figure 2: Rotation learning curves. *Subject-averaged learning curves from the initial rotation session for the four groups that experienced a rotation on Day 1. Shaded regions indicate \pm s.e.m. Reach direction is abbreviated as “Reach dir.” Right panel: The mean attained reach direction for each group at the end of their initial exposure to the rotation. Values represent the mean reach direction across subjects on the last trial of adaptation within each group. Error bars indicate s.e.m.*

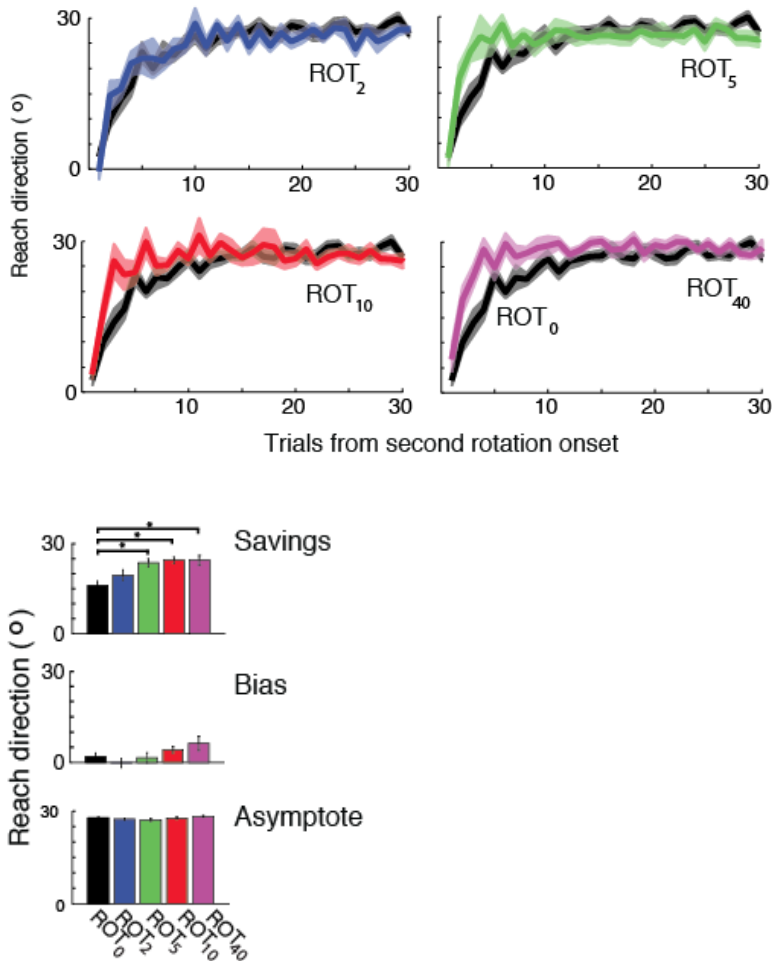


Figure 3: Savings in adaptation. Left panel: *Re-learning data for the principal groups. Adaptation curves for the second rotation exposure are shown for each principal group with group ROT₀ superimposed in black.* Right panel: *Mean performance across groups. (Top) Adaptation rate (Day 2, Trials 2-6) (Middle) Initial bias (Day 2, Trial 1) (Lower) Asymptote performance (Day 2, Trials 26 - 65)*

Any amount of prior practice was sufficient to alter single-trial learning

Each group exhibited a similar increase in compensation early during learning in the second rotation compared to compensation from the naïve group, ROT₀. This was

apparent as an increase in the difference in reach direction between each group's compensation on Day 2 and the compensation of group ROT₀ (Figure 4). Positive values in Figure 4 connote savings. This accelerated learning was transient for ROT₂ and ROT₅, lasting just a few trials, but was sustained for more trials for ROT₁₀ and ROT₄₀. Thus, apparently, savings was sustained only in groups that had reached asymptote on Day 1. Notably, however, the additional 30 trials on asymptote completed by ROT₄₀ did not lead to stronger savings, compared to ROT₁₀.

In summary, group ROT₂ appeared to have faster re-learning transiently, but did not register savings through the early learning measure presented above. This contradiction prompted us to perform a finer-grained analysis of the differences in re-adaptation among the groups. Specifically, the amount of learning from the first trial (the difference in reach direction between trials 1 and 2) was analyzed to test for a difference between Day 1 and Day 2. Since each group aside from ROT₀ performed at least two trials on both days, this measure of learning rate yielded a within-subject measure of single-trial savings. Each group had a greater single-trial learning rate in the second rotation exposure compared to the first exposure (Figure 5; paired *t*-tests, $p < 0.05$ for each group with Bonferroni correction). Moreover, the magnitude of this effect was comparable across groups (ANOVA, $F(3,36) = 1.08$, $p = 0.37$). This analysis established that even very limited (as few as 2 trials) prior experience with a perturbation could lead to single-trial performance improvements during re-exposure. This effect is clearly illustrated by plotting the reach direction on Day 2 as a function of the reach direction on Day 1 (Figure 5) and noting that all groups follow

the same pattern of faster learning on day 2, at least for as many trials as had been experienced initially.

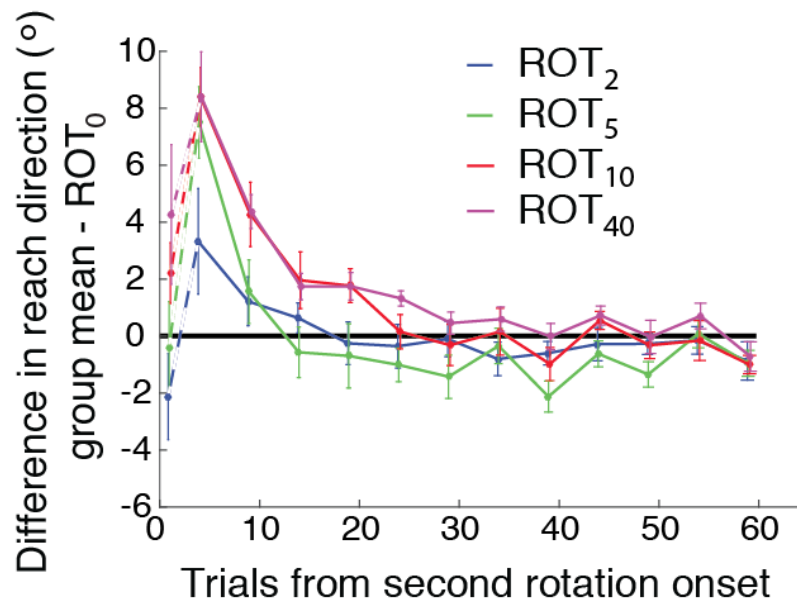


Figure 4: Differential savings. *Difference in adaptation curves of each group from that of group ROT₀, binned by trials of 5 (except the initial trial, which is connected by a dashed line).*

In summary, although all the principal groups exhibited some degree of savings, there was a difference in the pattern of savings across groups. Savings was equally strong at the single-trial level in all groups, but was sustained for just a few trials in groups that had very limited initial exposure (i.e. ROT₂, and ROT₅). Only the groups in which subjects reached or nearly reached asymptote during the first session showed sustained savings (i.e. ROT₁₀ and ROT₄₀).

What kind of mechanism might be responsible for this pattern of results, where relearning is faster up to the point that adaptation initially reached, but then appears no faster thereafter? Figure 6 may help to clarify; here, the adaptation curve for each group was aligned according to the total number of rotation trials experienced. The figure reveals that participants appear to rapidly re-acquiring the reach direction attained at the end of the initial exposure, and then adapt at a naïve rate thereafter. Critically, there was no evidence of performance on Day 2 surpassing that of naïve learners who had experienced a comparable number of rotation trials in total. There also did not appear to be a gradual exponential convergence towards the behavior of naïve subjects, as might be expected from a change in sensitivity to error. Instead, participants appeared to rapidly reacquire the position on the adaptation curve they had attained during adaptation to the initial rotation. This view of the data suggests that savings represents a process of rapid retrieval, or recall, rather than a change in the learning rate of the same initial acquisition process.

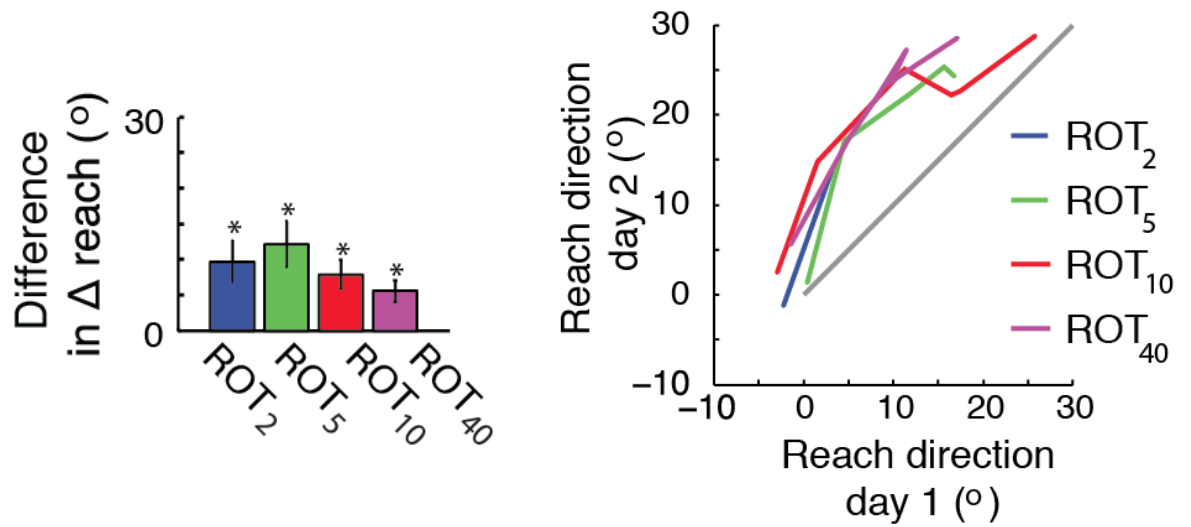


Figure 5: Similarity of savings. (Left panel) *Difference in single-trial learning between Day 2 and Day 1.* (Right panel) *Reach direction on Day 2 vs. that on Day 1. Grey line represents the unity line where data would be expected to lay if adaptation were unchanged from one day to the next.*

Another way to test the idea that, upon re-adaptation, participants recall the best attained adapted state from their first experience is to check for a correlation between the reach direction on the last trial of the first rotation, and the closest matched reach direction between the second and third trials of the second rotation (it appears the recall mechanism may require a few trials to re-acquire the previous state, which is why this analysis allowed for comparing the best of two trials). This correlation was seen to be significant, comparing data from all subjects across groups (Figure 10; $r^2 = 0.45$, $p < 0.001$).

Savings was sensitive to the direction but not the magnitude of the rotation

The results above showed that experiencing even a small number of trials of a perturbation is sufficient to create some form of memory leading to savings. To further explore the conditions necessary to bring about savings, three additional groups were tested. ROT_{15DEG} experienced a 15° rotation on Day 1 for 39 trials and was assayed for savings with a 30° rotation the next day, ROT_{COUNTER} experienced five trials of a clockwise rotation and then was tested the following day with a counter-clockwise rotation, and finally, ROT_{5MIN} experienced five trials of a counter-clockwise rotation and was tested for savings with the same rotation just five minutes later. The purpose of including these group was to further test the conditions which form a memory associated with savings; i.e. is the memory only associated with a specific perturbation, and is a break required for some form of consolidation to occur.

Savings was detected for group ROT_{15DEG} (Figure 7); early learning (mean reach direction measured during trials 2-6) was faster than that for naïve participants (t -test, $p < 0.01$). The behavior of group ROT_{15DEG} was compared with that of groups ROT₅ and ROT₄₀ because these were the principal groups matched for attained reach direction on Day 1 (ROT₅), and for number of rotation trials on Day 1 (ROT₄₀). An ANOVA comparing these three groups revealed no difference in savings (ANOVA, $F(2,27) = 1.14, p = 0.34$). Bias and asymptote measures also failed to show a difference across these three groups (bias: ANOVA, $F(2,27) = 1.46, p = 0.24$; asymptote: ANOVA, $F(2,27) = 1.56, p = 0.22$). The single-trial learning rate analysis was not applicable for ROT_{15DEG} because the rotations on Days 1 and 2 differed in magnitude.

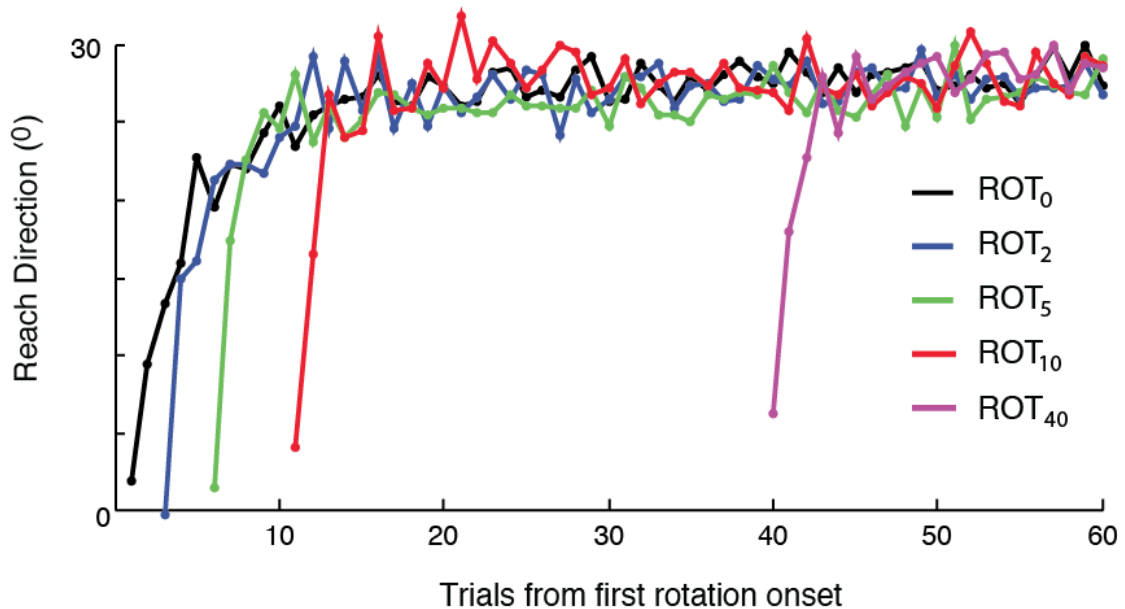


Figure 6: Savings as recall. Day 2 learning curves aligned by total number of perturbation trials experienced. Curves represent mean across subjects; error bars not shown for clarity. All error bars and shaded regions indicate ± 1 s.e.m. across subjects.

ROT_{COUNTER} was added to test whether the perturbation needed to be in the same direction during the first and second rotation exposures in order to observe savings. A comparison of performance during early learning (trials 2-6) in this group with that of group ROT₀ revealed no evidence for savings (Figure 8; *t*-test, $p = 0.84$). Thus, the direction of the two rotations seems to matter for the formation of the memory supporting savings. Confirming this finding, a comparison of groups ROT₅ and ROT_{COUNTER}, which is the group that is matched in number of initial adaptation trials, did show a significant difference (*t*-test, $p < 0.05$). Finally, an analysis of the single-trial learning rate further supports the conclusion that there is no change in response to the perturbation from the first to the second rotation (Figure 8; paired *t*-test, $p = 0.46$) in this group. These groups (ROT₀, ROT_{COUNTER}, and ROT₅) also failed to show a significant difference in bias and asymptote between the two days of testing (bias: ANOVA, $F(2,27) = 2.54$, $p = 0.10$; asymptote: ANOVA, $F(2,27) = 1.51$, $p = 0.24$), and thus cannot account for the findings from the analysis of savings.

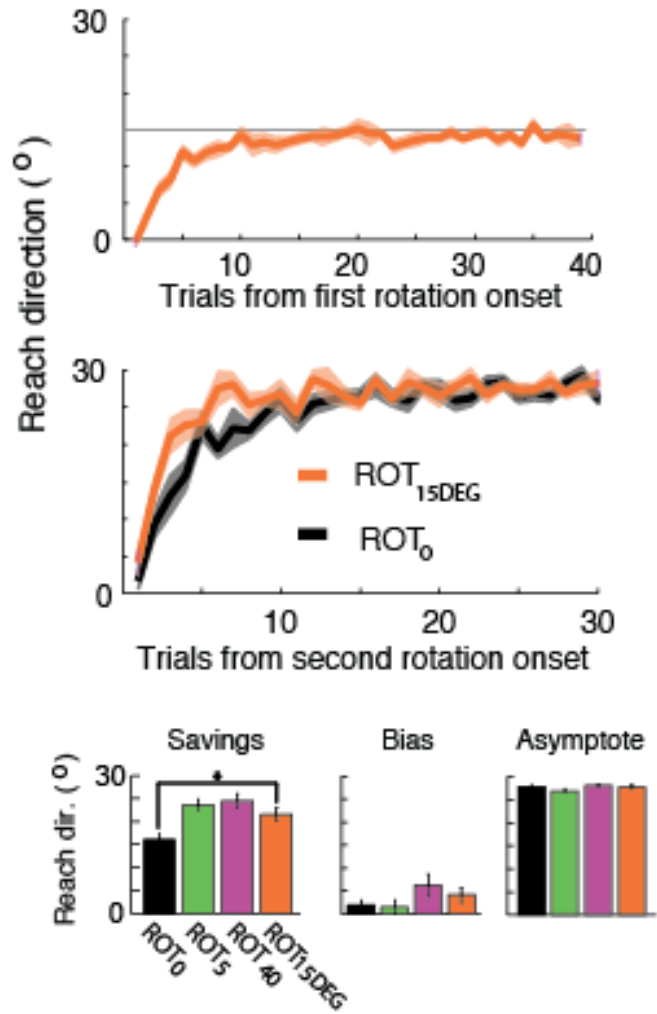


Figure 7: Magnitude generalization. *Top panel: initial adaptation for ROT_{15DEG}. Middle two panels: re-adaptation. Lower panel: early learning (Day 2, Trials 2 - 6), initial bias (Day 2, Trial 1), and asymptote performance (Day 2, Trials 26 - 65).*

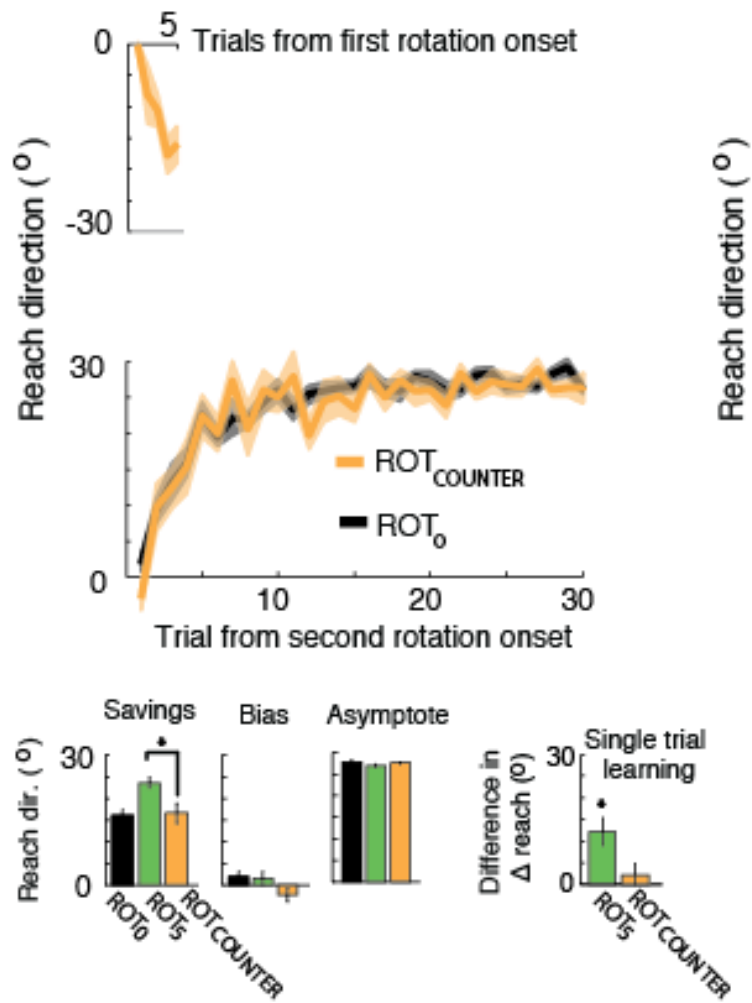


Figure 8: Direction specificity. Top panel: initial adaptation for ROT_{COUNTER}. Middle panel: re-adaptation. Lower panel: early learning (Day2, Trials 2 - 6), initial bias (Day 2, Trial 1), asymptote performance (Day 2, Trials 26 - 65), and difference in single trial learning.

Savings was insensitive to the passage of time between the first and second exposures

Prior studies of savings in adaptation suggest that an overnight break might be necessary in order to establish the memory for savings⁸⁴. Thus, a final group was added, ROT_{5MIN}, that tested whether the overnight break given to all other groups was necessary in order for the memory supporting savings to have been established. Participants in this group experienced 5 trials of a 30° rotation and were re-exposed to the perturbation following a 5-minute break. There was savings for this group compared to the naïve group (Figure 9), based on comparison of performance during early learning (trials 2-6) (*t*-test; $p < 0.01$). This group also showed no detectable difference in early learning from group ROT₅ (*t*-test; $p = 0.88$), which is the group matched for all conditions except time between initial and final perturbation exposures. The single-trial learning rate was also greater during the second exposure compared to the first in this group (paired *t*-test; $p < 0.05$). Comparison of the biases across groups ROT₀, ROT₅ and ROT_{5MIN} did show marginal significance (bias: ANOVA, $F(2,27) = 3.37$, $p = 0.051$) (Figure 3C) likely due to the comparatively short interval between the initial and second adaptation sessions in ROT_{5MIN}⁹⁶. Asymptotic performance on either Day 2 or Session 2 was not significantly different among these comparison groups (ANOVA, $F(2,27) = 1.41$, $p = 0.26$). These results suggest that savings does not depend on an overnight consolidation period; comparable savings is evident even after a 5 min break.

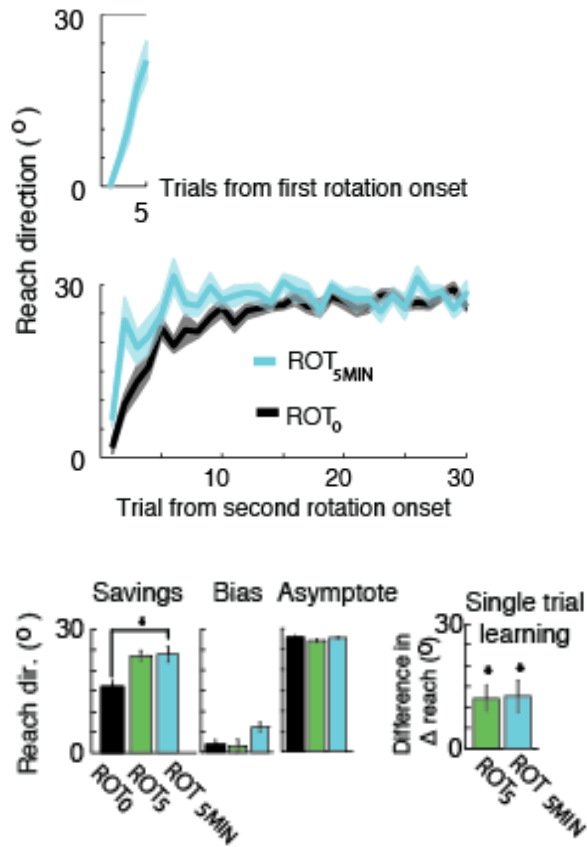


Figure 9: Passage of time insensitivity. *Top left panel: initial adaptation for ROT_{5MIN} . Bottom left panel: re-adaptation. Right panels: early learning (Day2, Trials 2 - 6), initial bias (Day 2, Trial 1), asymptote performance (Day 2, Trials 26 - 65), and single trial learning difference.*

To test the plausibility of the recall mechanism from the data, we conducted an analysis to test for a correlation between the best performing trial from Day 1 (i.e. the trial that reached closest to 30°, and the trial from the first two trial of Day 2 that most closely matched that best reach direction from Day 1. There was a significant correlation between these two quantities when pooling data across groups ROT₂ to ROT₄₀ (Figure 10; Linear regression analysis: $R^2 = 0.467$, $p < 0.001$).

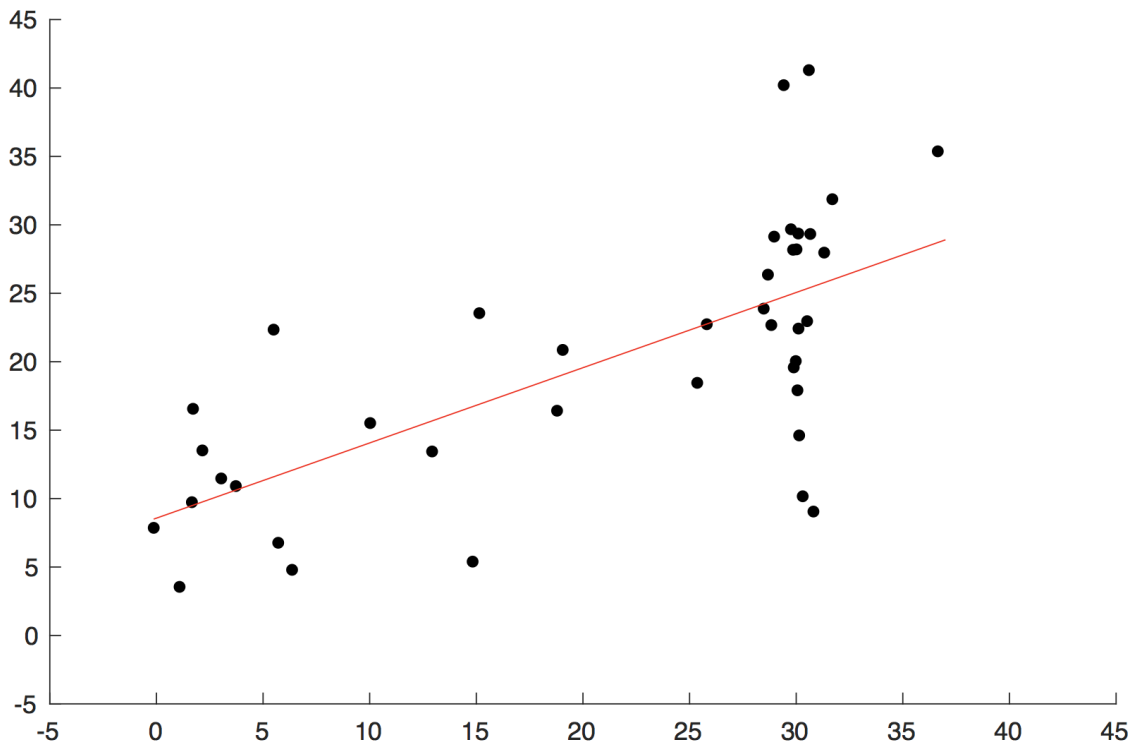


Figure 10: Recall of best reach direction. There was a significant correlation between the best reach direction on Day 1, and the direction reached on Day 2 within the first two trials of the rotation re-exposure, excluding the very first trial.

Discussion

Theories regarding the formation of savings in adaptation tasks commonly assume that extended practice is required to instill a memory^{38,90,60,42,96}. Knowing the lower bound on the duration of initial experience with a rotation required to obtain savings could provide important insight into the nature of this phenomenon. We therefore sought to determine the minimum amount of exposure of a rotation that is sufficient to form a long-term memory for adaptation by varying the number of trials of initial exposure across four groups of subjects and assaying for savings a day later.

Notably, savings was present even after only two trials of initial exposure to a rotation. The specific pattern of savings differed, however, across groups: they all showed a similar benefit of prior experience according to the amount they learned from the first trial of re-exposure, but this advantage over naïve learners was only sustained all the way until asymptote was finally reached in groups that had initially reached asymptote during their first exposure. These differing patterns are most starkly illustrated by group ROT₂. Depending on the analysis used, we could either conclude that ROT₂ showed strong savings (based on single-trial learning rate) or no savings (based on mean reach direction during early learning) because this group rapidly jumped to the position on the adaptation curve it had previously acquired, but then adapted as if naïve thereafter.

Further experiments revealed that the duration of the break between the first and second rotation exposures had little bearing on whether or not savings would be

observed; participants exhibited the same amount of savings whether that break was overnight or only 5-minutes. Additionally, in order for savings to be observed, the direction of the rotation had to be consistent across exposures, but the magnitude could differ.

Savings as recall

How can a long-term memory for adaptation be established if not via gradual processes requiring practice at asymptote? Recent evidence showing that explicit processes contribute to initial adaptation^{83,80,74,16} may provide a possible explanation. Specifically, since an explicit aiming component is present early in adaptation⁸³, subjects might form a memory for this aiming strategy early during the initial exposure and recall it once they have identified that the rotation is present when tested again later.

Alternatively, subjects may form a memory for action^{42,85}, as opposed to a memory for an aiming direction⁸³, or a memory for the perturbation⁷⁰. We have previously suggested that this may occur through an implicit reinforcement learning mechanism that is established through experience⁴². Specifically, repetition of a successful action on asymptote might be necessary in order to reinforce and remember it. Our new data suggest, instead, that subjects remember something about their prior rotation exposure even in the absence of such repetition on asymptote. That said, it is still possible that other latent mechanisms may be active in parallel with a recall

mechanism when experimental conditions promote them, and thus either phenomenon or both may be active depending on the experimental conditions.

Potential mechanism supporting savings as recall

Why would one remember an action or aiming direction that was ultimately unsuccessful (i.e. led to a target miss), as is often the case given the bias toward baseline often exhibited at asymptote^{36,100,101}? It is plausible that a memory for action could be formed because of strong positive reward prediction errors experienced by subjects during the initial course of adaptation. However, as was just mentioned, performance is typically worse under a perturbation than during baseline. Thus, nominally, the reward prediction errors during adaptation would be negative (i.e. reward is less than expected), because performance is worse under the perturbation compared to at baseline. Whether subjects interpret a given action as an improvement (a positive reward prediction error) or continued failure (a negative reward prediction error) may depend on whether they detect that a change-point had occurred in the experiment following the rotation onset¹⁰². If the imposed rotation is interpreted as a change, actions and/or strategies that reduce the initially large errors experienced after the onset of the perturbation may be associated with a positive reward prediction error, and thus may be remembered even though they are ostensibly worse.

Recall as a general mechanism of meta-learning in adaptation paradigms

Other studies have also observed behavior that is consistent with the idea of recall as a mechanism for savings. For instance, two recent experiments have shown that if experience with a particular perturbation (e.g. a force field perturbation or a visuomotor rotation) is followed by a single episode of a novel perturbation, the first few actions under the new perturbation are directed in accordance with cancelling the previously experienced perturbation^{88,95}. These findings are consistent with the idea that such actions were stored in memory and retrieved (albeit inappropriately) when another perturbation was experienced. Retrieval of actions previously used to counter a perturbation can even be triggered by withholding an expected visual reward¹⁰³, suggesting that reward prediction error, rather than re-experiencing the same or a similar perturbation, may be the key trigger for retrieval.

A recent study suggested that savings may not be due to recall of prior actions, but rather might be due to an underlying sensory error-driven learning process increasing its sensitivity to previously experienced errors⁷⁰. The authors of that study showed that experiencing a particular error at one time leads to a durable change in response to the same or similar errors in the future. These findings, however, can also be interpreted under a recall hypothesis if we posit that errors of a specific magnitude can augment reward prediction error to act as a cue for retrieval of an existing memory.

The sensitivity-to-error model proposed by Herzfeld and colleagues⁷⁰ cannot account for all of our results, however. In particular, it predicts that adaptation rate upon re-

exposure to a given perturbation will steadily increase as the duration of the initial exposure to the perturbation increases, even after one reaches asymptote. In our data, however, the duration of initial exposure had little effect on the overall magnitude of savings. In particular, having just reached asymptote (as in ROT₁₀) is sufficient to exhibit nearly identical savings behavior as having experienced nearly 30 trials on asymptote (as in ROT₄₀). Similarly, only reaching halfway to asymptote (as in ROT₅) produces nearly the same amount of savings as having reached asymptote (ROT₁₀ & ROT₄₀), as subjects rapidly re-acquire the state of adaptation they had previously attained. Furthermore, the pattern of learning in all of the conditions we tested was different from that expected by a modulation of rate: participants rapidly reacquired the position they had previously attained during adaptation, rather than showing exponential convergence with an increased rate. We therefore suggest that savings is, in general, driven by recall of prior behavior rather than modulation of learning rate, but that this recall process can potentially be cued by the observation of a specific error.

A further piece of evidence in support of the recall hypothesis is that Parkinsons Disease (PD) patients are typically unimpaired in initial adaptation to a perturbation¹⁰⁴⁻¹⁰⁷, but show impaired savings during re-adaptation^{106,108,109}. This dissociation suggests that initial adaptation and savings depend on different processes. Models that posit that savings is due to up-regulation of the rate of adaptation processes would need to explain how initial adaptation would be unaffected in PD but modulation of adaptation rate would be impaired. Alternatively, the model proposed

here, in which savings is attributable to a separate recall mechanism, is entirely consistent with observed memory impairments in PD, in which deficits in the acquisition and/or retrieval of cognitive information have been observed ^{110,111}.

Conclusions and implications for motor skill learning

Here we have suggested that savings in adaptation after just a single exposure can be entirely accounted for by rapid retrieval of a component of learning that is acquired within a few trials, and that this component may be subserved by explicit memory. This might suggest that savings actually reflects formation of declarative memory ¹¹², rather than formation of a motor memory. In particular, it has been shown that savings is absent under constrained reaction time, a condition that likely omits explicit or strategic components to adaptation ⁹³. It is also thought that long-term motor learning requires extended practice over days and weeks to acquire ^{113; 114; 115; 116}. What, then, does adaptation serve as a model for: motor skill, or some other form of memory that is possibly declarative? The idea that initial acquisition and savings both have an explicit component is congruent with recent theories that contend that cognition and explicit knowledge are factors critical to learning and performing any motor task ^{28; 57}. Adaptation may therefore serve as a suitable model for how cognition and knowledge together may play a role in the formation of long-term motor memories.

The link between explicit processes and motor memory might be that long-term motor memory takes the form of a persistent explicit memory. Alternatively, long-term motor memory might be mediated by an implicit or procedural memory for a

component of learning that was initially explicit or declarative. This process of transition from one type of memory to another has been suggested as a general mechanism for skill acquisition ^{117,118}. If visuomotor adaptation serves as an example of the initial, explicit stage of this process, one task that may serve as a model for this process following more practice is adjusting grip and load forces for lifting objects of unusual densities. This task is ostensibly similar to visuomotor adaptation, given that both show signs of long-term memory formation following only brief periods of initial practice ^{25,119,120}. However, visuomotor adaptation is known to be subserved by both explicit and implicit processes ^{23,83}, while adjustment of grip and load forces during lifting seems to be largely implicit, evidenced by the fact that the size-weight illusion persists after appropriate motor adjustments have been made ¹¹⁹. These tasks also differ in their dependence on the cerebellum; patients with cerebellar degeneration are impaired in adapting to visuomotor rotations ¹²¹⁻¹²⁶, but show no deficit in adjusting grip and load forces to objects of unusual densities ¹²⁷.

We suggest that the core difference between visuomotor adaptation and grip/load force adjustments is in the duration of prior practice, given that subjects have a lifetime of experience lifting objects whose weight is difficult to predict, but generally do not have much prior experience with unusual visual manipulations like a cursor rotation. It might be that given prolonged experience with adapting to rotations, adjusting to novel visuomotor mappings would begin to more closely resemble adjusting grip and load forces for novel size and weight combinations, including no longer relying on explicit or cerebellar-mediated adaptation processes. This prediction has yet to be tested.

This work and text appeared previously in (Huberdeau, Krakauer, Haith. J Neurophys., 2015). I would like to thank the Journal of Neurophysiology and my co-authors for allowing its reproduction here.

4 Memory for adaptation is supported by deliberate processes

The availability of planning prior to movement during adaptation learning modulates the speed of compensation, and savings is only achieved when deliberate processing is permitted.

Following a change in the environment or motor apparatus, human subjects are able to rapidly compensate their movements to recover accurate performance. This ability to adapt is thought to be achieved through multiple, qualitatively distinct, learning processes acting in parallel. It is unclear, however, what the relative contributions of these multiple processes are during learning. In particular, long-term memories for adaptation have been extensively studied through the phenomenon of savings – faster adaptation to a given perturbation the second time it is experienced. It is unclear which components of adaptation contribute to this effect. Here, I present a study that showed that distinct components of learning in an adaptation task can be dissociated based on the amount of preparation time they require. During adaptation, subjects were forced to generate movements at very low preparation times. Early in learning, subjects expressed only a limited amount of their prior learning in these trials, though performance improved gradually with further practice. Following washout, subjects exhibited a strong and persistent

aftereffect in trials in which preparation time was limited. When subjects were exposed to the same perturbation twice in successive days, they adapted faster the second time. This savings effect was, however, not seen in movements generated at low preparation times. These results demonstrate that preparation time plays a critical role in the expression of some components of learning but not others, and suggests that savings for visuomotor adaptation is achieved primarily through the contribution of explicit, cognitive components of learning.

Introduction

Motor learning is commonly studied through adaptation tasks, in which subjects must learn to compensate for an imposed perturbation that disrupts their movements (for instance a distortion of visual feedback⁷⁷). An important characteristic of behavior in these paradigms is that subjects re-adapt faster the second time they are exposed to a perturbation. This phenomenon, referred to as savings, is thought to reflect the formation of a long-term motor memory^{40,69} and thus potentially provides a critical link between learning in adaptation paradigms and other forms of motor skill acquisition.

Learning in adaptation tasks is known to depend on an implicit²³, cerebellum-dependent^{125,128-130} learning process that is posited to reflect updating of an internal forward model¹³¹⁻¹³³ driven by sensory prediction errors^{23,125,128}. In addition to this implicit, error-driven process, multiple additional processes are thought to contribute to learning in adaptation paradigms^{35,42,90,134}. In particular, explicit

cognitive strategies can account for a significant amount of learning, particularly during early exposure^{16,34,35,74,80}. Characterizing the properties of individual components of adaptation is challenging, since only the summed contribution of all of these components can typically be observed.

Here, we sought to dissociate components of learning based on their preparation time requirements. Reaction times are known to increase during visuomotor adaptation^{16,135}. Furthermore, this increase is causally related to adaptation rate¹⁶ and is thought to reflect additional time required for cognitive contributions to influence movement. Previous work has also shown that movements released at low reaction times through startle¹³⁶ show reduced expression of prior motor learning^{137,138}.

We show how carefully controlling the amount of time available to subjects to prepare their movement on a trial-to-trial basis allows us to decompose their learning into constituent components. We identified one component of learning that is expressible at minimal preparation time and appears to reflect implicit learning driven by sensory prediction errors. A further component of learning could only be expressed given prolonged preparation times. We speculate that this process reflects cognitive contributions to learning. This precise trial-by-trial control over the expression of different components of learning allowed us to directly test which component of learning is responsible for savings upon re-exposure to the same perturbation.

Materials and Methods

A total of 24 human subjects (11 women, 13 men; aged 24.6 ± 7.5 years) participated in this study (10 in Experiment 1 and 14 in Experiment 2). All participants had no known neurological disorder and provided written consent prior to participation. All procedures were approved by the Johns Hopkins University School of Medicine Institutional Review Board. Participants sat in front of a glass-surfaced table with their right arm supported on an air sled to allow frictionless planar movement. A mirrored display presented targets and a cursor controlled by the hand in the plane of movement. Hand position was tracked at 130Hz using a Flock of Birds magnetic tracking device (Ascension Technologies). Subjects began each trial by moving to a central start location. A target then appeared in one of two possible locations, $\pm 82.5^\circ$ from the straight-ahead direction, at a distance of 8cm from the start position (see Figure 11a). A sequence of four tones, each spaced 500ms apart, was initiated as the target appeared. Subjects were instructed that, synchronously with the fourth tone, they should initiate a rapid movement of the hand in order to move the cursor through the target. When the cursor passed the target radius, it was extinguished and re-appeared when the subject's hand came within a 2cm radius of the start position when returning to begin the next trial. Subjects were provided feedback about the timing of their movement initiation relative to the fourth tone. Successfully timed movements had to be initiated within ± 100 ms of the fourth tone. On-screen text informed subjects if they had initiated their movement "Too Early" or "Too Late". Other than observing the trajectory of the cursor, subjects did not

receive any overt feedback about whether their movement successfully hit the target.

Initial Training

Prior to the main experiment, subjects completed 400 trials of training (200 to each target, over 2 blocks) in the basic task in order to practice accurate timing of their movement initiation. After this initial training, subjects performed a calibration block. In this block the target occasionally (30% of trials) switched from one location to the other at a random time before the onset of the fourth tone, chosen uniformly between 200ms and 500ms. Subjects were instructed to prioritize the timing of their movement initiation but at the same time to also make an effort to hit the target when possible. Based on subject performance in this block, we estimated the minimum response time each individual subject would require in order to successfully compensate for the target switch. We used maximum likelihood estimation to fit a sigmoid to the relationship between reaction time (measured as the time between target jump and movement onset) and reach direction. This threshold was rounded up to the nearest 25ms to obtain a subject-specific switch time for all subsequent trials in which the target switched.

Adaptation Task

After completion of initial training, we imposed two trial types on subjects (Figure 11b). In 80% of all trials, the target appeared at the time of the first tone and

remained in the same place for the duration of the trial. Subjects therefore had 1.5 seconds to prepare their movement from the time of initial target presentation to the time of movement initiation. We refer to these trials as high preparation time (highPT) trials. In the other 20% of trials, the target switched locations shortly before movement initiation. The purpose of this late target switch was to force subjects to make a movement towards the new target with a minimal amount of preparation time. We refer to these trials as low preparation time (lowPT) trials. The timing of the target switch was determined based on each subject's individual performance in the earlier calibration block, such that subjects would only just be able to react to the target switch.

Experiment 1 examined the effects of preparation time on subjects' ability to compensate for an imposed visuomotor rotation. Ten subjects participated in Experiment 1. Following initial training and calibration, each subject performed three blocks: *Baseline*, *Adaptation*, and *Washout* (Figure 11c). Each block consisted of 100 trials to each target. The trial order was organized as a series of 10-trial sub-blocks, with each sub-block containing 8 highPT trials (four to each of the two potential target locations) and 2 lowPT trials (one to each target), arranged in a pseudorandom order. Each subject received a different, randomly-generated sequence of trials (using the `randperm` function in Matlab). All trial numbers reported henceforth refer to trials *to a particular target*, rather than to the actual trial number within the block.

During the *Adaptation* block, a 30° clockwise rotation of the cursor position was imposed on the left half of the workspace at the start of trial 11. The rotation remained on for the rest of the *Adaptation* block and for the first 20 trials of the *Washout* block. The perturbation was switched off at the start of trial 11 of the *Washout* block and remained off for the rest of the experiment.

Experiment 2 examined whether learning expressed in either highPT or lowPT trials would be faster upon a second exposure to the perturbation (i.e. whether savings would occur). Fourteen subjects participated in Experiment 2. This experiment was conducted over 2 days. On Day 1, subjects performed initial training plus two experimental blocks: *Baseline* and *Adaptation1*. On Day 2, subjects performed 2 further blocks: *Adaptation2*, and *Washout* (Figure 12a). Each block consisted of 100 trials to each target, and the sequence of trial types was structured in the same way as in Experiment 1. In a preliminary study (data not shown), we found that subjects had persistent aftereffects ($\sim 10^\circ$) when returning after 24 hours. This partial retention of learning across days means that baseline behavior is poorly matched across days, making it difficult to assess changes in the *rate* of learning across exposures (savings). We therefore introduced a brief period of washout at the end of Day 1 (last 20 trials). On Day 2, the perturbation was switched off during the first 10 trials and was re-introduced at the start of trial 11 of *Adaptation2*. As in Experiment 1, the perturbation was on for the first 10 trials of the *Washout* block, and was then switched off for the remainder of the experiment. The sequence of trial types (i.e. left/right, highPT/lowPT) in *Adaptation2* was identical to *Adaptation1*; these blocks

differed only in that the cursor rotation was switched off toward the end of *Adaptation1*. Finally, in order to ensure that the effects observed in Experiment 1 were not the result of biomechanical asymmetries, the overall experiment was reflected across the midline such that a 30° *counterclockwise* rotation was now introduced in the *right* half of the workspace.

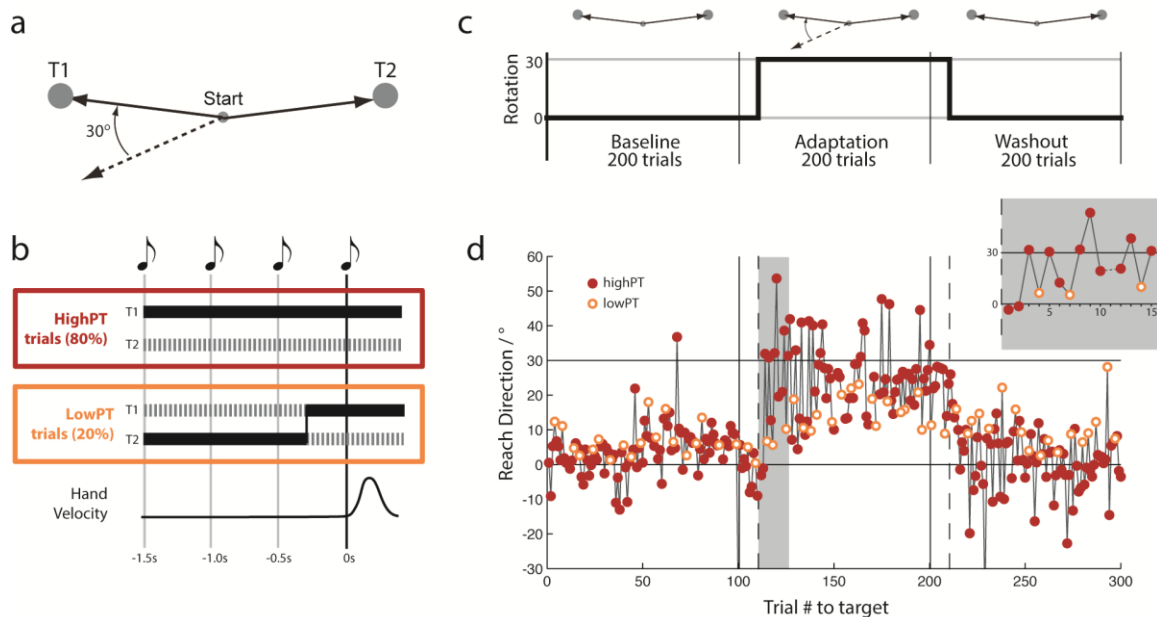


Figure 11 Timed response with rotation. **A)** Target layout. Two possible targets are located 8cm from the start position and $\pm 82.5^\circ$ from the straight-ahead direction. **B)** Trial timeline. Subjects heard 4 tones spaced 500ms apart. A target appeared with the first tone and subjects were trained to initiate movement toward it synchronously with the fourth tone. In 80% of trials (highPT trials), the target remained in place throughout the trial. In 20% of trials (lowPT trials), the target was switched shortly (~ 300 ms) prior to movement onset. **B)** Perturbation schedule. Subjects performed one block of trials with no perturbation, one block in which a 30° clockwise visuomotor rotation was imposed on the leftward target, followed by one block in which the perturbation was switched off. **D)** Trial-by-trial reach direction for a representative subject. Filled, red circles indicate highPT trials, open, orange circles indicate lowPT trials. Inset shows the first 15 trials after perturbation onset (grey shaded region) in greater detail. Note that this subject failed to make an accurate movement on several trials, including the 11th trial after perturbation onset.

Data Analysis

Position data were filtered using a Savitzky-Golay filter (2nd order, half-width 54ms) and differentiated to obtain velocity. We identified the time of movement onset as the first time at which the tangential velocity of the hand exceeded 0.02m/s. The initial reach direction was calculated as the direction of the smoothed tangential velocity vector 100ms after movement onset.

We compared behavior between lowPT and highPT trials with paired, two-tailed *t*-tests on the mean reach direction for each trial type across subjects within a particular window of trials. We averaged performance over a window of 15 trials to a specific target (12 highPT, 3 lowPT) (with one exception: we considered a window of just 10 trials to assess washout at the end of block *Adaptation1* in Experiment2). To assess savings in Experiment 2, we quantified the rate of initial learning as the difference between behavior in the last 5-trial bin before the onset of the perturbation and the first 5-trial bin after the onset of the perturbation. We quantified savings as the difference in this learning rate between days. The specific trial windows used for each test, which were determined *a priori*, are described in the results and are indicated by shaded grey regions in each figure.

In lowPT trials, subjects occasionally failed to move to the correct post-switch target. We deemed a trial to be a 'miss' if subjects moved more than 2cm in the direction opposite the target. Such miss trials were an inevitable consequence of

switching the target as late as subjects could cope with. These 'miss' trials were excluded from further analysis. One subject in Experiment 1 and two subjects in Experiment 2 missed the target switch in more than half of the lowPT trials. Data from these subjects were excluded from subsequent analysis. In addition, the remaining subjects were excluded from specific statistical comparisons if they missed the target switch on all trials of interest for that particular comparison. At most one subject was excluded from each statistical comparison on these grounds (though it was not necessarily the same subjects that were excluded from each comparison). Of the remaining (retained) subjects, 14.1% of pertinent lowPT trials (i.e. those that would have contributed to a statistical analysis) were unavailable due to 'misses' in Experiment 1. This figure was 11.5% for Experiment 2. Miss trials were uniformly distributed across (retained) subjects, trial windows, and locations within each window. Since the learning rate analysis necessarily included a smaller number of trials, a greater number of subjects (4) had to be excluded from this analysis. The basis for excluding data – that subjects missed the switch in target locations on these trials – is independent of their exact reach direction when they moved towards the correct target. Therefore our analysis is unlikely to be biased by considering only a subset of the data.

Shapiro-Wilk tests on data from 34 subjects across all experiments confirmed that mean reach directions used in statistical tests were normally distributed across subjects in both trial types, during both early learning (trials 1-15) and at asymptote (trials 51:75) ($p > 0.2$ in all cases). Variability across subjects was approximately

similar across trial types at all points during learning, although slightly larger in highPT than lowPT trials during early learning (5.8° versus 3.3° std. dev.). The variances could be equalized through a log-transformation of the data, in which case the outcome of all statistical tests remained similar to the analysis of the untransformed data (not all shown).

Results

We sought to dissociate components of motor learning based on the amount of time available for subjects to prepare a movement. Subjects made fast reaching movements to guide a cursor through a target that was presented either to the left or right of a central start location (Figure 11a). We varied preparation time by using two distinct types of trial (Figure 11b). In 80% of trials, subjects were allowed a high preparation time (highPT trials). In these trials, the location of the target was revealed 1.5s before subjects were required to initiate movement and remained there for the duration of the trial. In the other 20% of trials (lowPT trials), a target was displayed at the start of the trial but the location of the target unexpectedly switched sides shortly (~300ms) before movement onset (Figure 11b).

Selective expression of a distinct component of learning at low preparation times

In Experiment 1, we tested the effects of preparation time on the amount of learning expressed during adaptation and, subsequently, during washout. Ten subjects participated in this experiment. After an initial baseline period, a 30° clockwise

rotation of the cursor was introduced in the left half of the workspace so that it only affected movements to one of the two possible targets (Figure 11a,c).

Figure 1d illustrates the main features of behavior in this paradigm by means of a representative subject. This subject showed little difference in performance during the baseline phase given different amounts of time to prepare their movement (red, filled circles (highPT) versus orange, open circles (lowPT)). After 110 baseline trials, a rotation of the visual cursor position was introduced. This subject was able to successfully counter the perturbation within 3 trials of its onset (Figure 11d, grey shaded region + inset). In the fourth trial, a lowPT trial, the subject was unable to maintain this compensatory behavior and their reach direction reverted back towards baseline. In the fifth, highPT trial, the subject was again able to compensate for the perturbation. This pattern continued through the next 100 trials: the subject was largely able to compensate for the perturbation in highPT trials, but exhibited poorer performance in lowPT trials. Performance in lowPT trials, did, however, gradually improve throughout the course of the block. During washout, the pattern of behavior was reversed: the subject reverted to baseline behavior in highPT trials, but displayed a persistent aftereffect in the lowPT trials.

The key features of this representative subject's behavior were consistent across all subjects who participated in the experiment (Figure 12a-d). The movements subjects made at baseline were not distinguishable between highPT and lowPT conditions: There was no significant difference in initial reach direction between lowPT and highPT trials to either the adapted target (trials 51-100,

difference= $1.02 \pm 3.7^\circ$; $t(8)=0.82$; $p=0.43$) or the non-adapted target (difference= $1.44 \pm 3.21^\circ$; $t(8)=1.347$; $p=0.22$). Peak velocities were comparable across highPT and lowPT trials (trials 51-100, highPT: $1.04 \pm 0.36 \text{ms}^{-1}$, lowPT: 1.014ms^{-1} ; within-subject difference: $0.028 \pm 0.063 \text{ms}^{-1}$; $t(8)=1.355$; $p=0.212$).

When a 30° clockwise rotation of the cursor was introduced in the left half of the workspace, subjects rapidly adapted their initial movement direction to compensate (Figure 12c). Average behavior in highPT trials reached an asymptote after approximately 30 trials. Behavior in lowPT trials, by the same subjects in the same block, changed much more gradually. Subjects exhibited significantly greater error in lowPT compared to highPT trials during early learning (trials 11-25, $t(8)=2.548$; $p<0.05$). Performance in this period was uncorrelated between lowPT and highPT trials ($r=0.097$; $p=0.80$) (Figure 12d), suggesting that poorer performance in lowPT trials was not simply due to a fixed fraction of overall learning being expressed in those trials. Notably, performance in highPT trials during this window appeared to be considerably more variable across subjects than behavior in lowPT trials (highPT std = 13.4° ; lowPT std = 6.2°). Although performance in highPT trials quickly reached an asymptote, behavior in lowPT trials continued to improve gradually and was comparable to highPT trials at the end of the *Adaptation* block (trials 86-100, $t(8)=1.35$; $p=0.22$). The perturbation was removed early in the next block (*Washout*). In highPT trials, subjects' reach directions rapidly returned to baseline. Behavior in lowPT trials, however, revealed a significant aftereffect (trials 86-100,

$t(7)=-5.92; p=0.001$) which persisted until the end of the experiment 90 trials later (Figure 12f).

Critically, the overall pattern of behavior we observed, across initial learning and washout, cannot be explained in terms of a single component of learning expressed to differing degrees. Although a single-component model could plausibly explain the pattern of behavior during initial learning (e.g. if subjects gradually become better at expressing this component at low preparation times), such a model, however, necessarily predicts that a return to baseline in highPT trials during washout would generalize fully to lowPT trials. Instead, we found that subjects exhibited a clear and persistent aftereffect in lowPT trials.

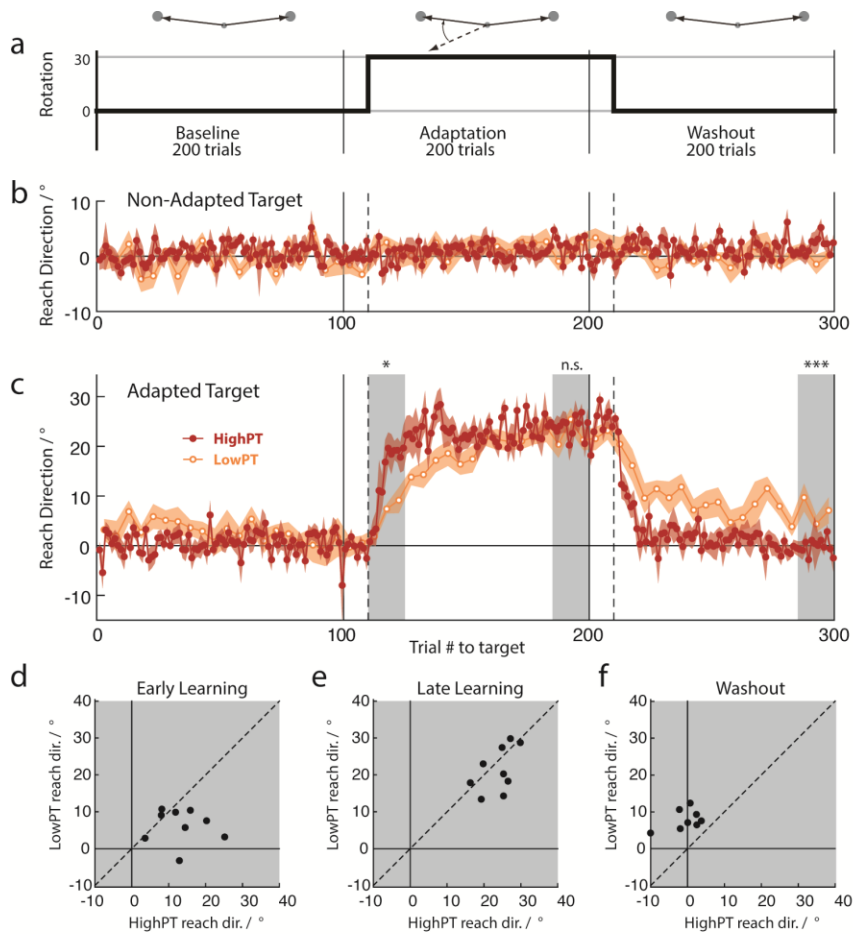


Figure 12 Preparation time modulates adaptation. A) Perturbation schedule(see also Figure 1c). **B-C)** Mean initial reach direction across subjects throughout the experiment to **B)** the unadapted target and **C)** the adapted target. Filled red circles show highPT trials, open orange circles show lowPT trials. The x axis reflects approximate trial number within session. Shaded regions indicate \pm s.e.m. **D-F)** Scatter plots showing individual subject behavior during **D)** Early learning, **E)** late learning, and **F)** late washout. Data points reflect average reach direction across the relevant shaded regions in panel C). **G)** Estimated contribution of the additional process recruited on highPT trials, obtained by subtracting lowPT from highPT performance.

This overall pattern of data is instead better explained in terms of *two* components of learning acting in parallel: one that can be expressed regardless of preparation time, and one which can be expressed only at high preparation times. These processes act in the same direction during initial learning, but in opposing directions during washout. We estimated the influence of the component of learning that was expressible only at long preparation times by subtracting performance on lowPT trials from the average performance on adjacent highPT trials (Figure 2g). The contribution of this process was large early in learning but slowly declined to near zero with practice. It was re-engaged during washout and remained in effect throughout the remainder of the experiment, apparently compensating for a persistent aftereffect in the component of learning expressed in lowPT trials.

Savings for adaptation can only be expressed at high preparation time

In Experiment 2, we sought to determine which of the two components of learning identified in Experiment 1 is responsible for savings, i.e., faster re-learning upon re-exposure to the same perturbation at a later time. We recruited 14 new subjects for Experiment 2. Experiment 2 followed a similar design to Experiment 1, except that subjects were exposed to the perturbation twice on successive days (Figure 13a). The perturbation was applied to the rightward target, rather than the leftward target, to rule out any potential effects of limb biomechanics in the results of Experiment 1. In order to minimize carry-over of any aftereffects of learning to Day 2^{40,96}, initial learning on Day 1 was briefly washed out with 20 non-perturbation trials (to the adapted target) at the end of the session.

Initial behavior on Day 1 of Experiment 2 reproduced the results of Experiment 1 (Figure 13b,c): we found significantly greater compensation for the rotation in highPT trials than in lowPT trials during early learning (trials 11-25, $t(13)=4.131; p=0.001$). This difference disappeared later in learning (trials 66-80, $t(13)=1.44; p=0.16$). During washout at the end of Day 1, lowPT trials exhibited a greater aftereffect than highPT trials (trials 91-100, $t(13)=-2.26; p<0.05$).

On the second day, subjects exhibited a small aftereffect from the previous days' learning in lowPT trials (*Adaptation1*, trials 1-10, vs *Adaptation2*, trials 1-10; $t(12)=-2.290; p<0.05$). This aftereffect was, however, very small in size ($2.9\pm 4.7^\circ$, $\sim 14\%$) relative to the overall change in behavior on Day 1. During adaptation, behavior on Day 2 was qualitatively similar to that on Day 1 (Figure 12c). After onset of the perturbation, subjects exhibited rapid adaptation in highPT trials but only expressed a limited amount of this learning in lowPT trials (*Adaptation2* trials 11-25, highPT vs lowPT, $t(13)=4.34; p=0.001$). Late in learning on Day 2, performance became comparable across trial types (*Adaptation2* trials 85-100, $t(13)=0.18; p=0.86$). At the end of washout on Day 2, a clear difference in reach direction remained between highPT and lowPT trials (*Washout* trials 85-100, $t(11)=-2.209; p<0.05$).

The critical question, however, is how learning compared across days within each trial type. We analyzed savings in terms of learning rate, taking into account the potential biases present at baseline, particularly in lowPT trials. We quantified the learning rate based on the change in behavior immediately before and after the

perturbation was introduced (trials 11-15 - trials 6-10). We found that learning rate in highPT trials was significantly greater on Day 2 compared to Day 1 (highPT, *Adaptation1* learning rate vs *Adaptation2* learning rate, $t(12)=-4.398$; $p=0.001$). This savings effect was, however, absent in lowPT trials (lowPT, *Adaptation1* learning rate vs *Adaptation2* learning rate, $t(9)=-0.260$; $p=0.801$). Power calculations (assuming an effect size of 6°, around half that seen in highPT trials, and variability estimated based on data in Experiment 1) suggested that 8 subjects would be a sufficient sample size to achieve a power of 0.8 at a significance level of 0.05, whereas our sample contained 10 subjects after exclusions for missing switch trials. The difference in the extent of savings between lowPT and highPT trials was further supported by a significant Learning Rate × Trial Type interaction (*Adaptation1* learning rate vs *Adaptation2* learning rate, highPT vs lowPT, $t(8) = 3.503$, $p<0.01$). Savings, therefore, could only be expressed when sufficient preparation time was available.

The results of all of our analyses did not change substantially if we log-transformed the data in order to control for differences in variability across subjects between lowPT and highPT trials. In particular, reach direction during early learning was closer to baseline in lowPT than highPT trials (Expt 1: trials 11-25, $t(8)=2.232$; $p=0.056$; Expt 2: trials 11-25, $t(13)=4.073$, $p=0.001$). This analysis also confirmed that savings was stronger in lowPT than highPT trials (trial window (6-10 vs 11-15) × type (lowPT vs highPT) interaction; $t(8)=2.315$, $p<0.05$).

In summary, savings was found only in components of learning expressed at high preparation times. Behavior at low preparation did not show any change in learning rate across days. The only evidence for long-term memory in this component was a small ($\sim 3^\circ$) directional bias that persisted throughout the second session.

Figure 13 *Savings is limited to when PT is available: Experiment 2 Results.* A) Perturbation schedule. Subjects were exposed to the perturbation on Day 1, but adaptation was washed out in the last 40 trials of the session. Subjects were re-exposed to the perturbation the next day, then washed out again. B-C) Mean reach direction across subjects for B) unadapted target C) adapted target. HighPT trials are shown in red, lowPT trials are shown in orange. The x axis reflects approximate trial number within session. Shaded regions indicate \pm s.e.m.

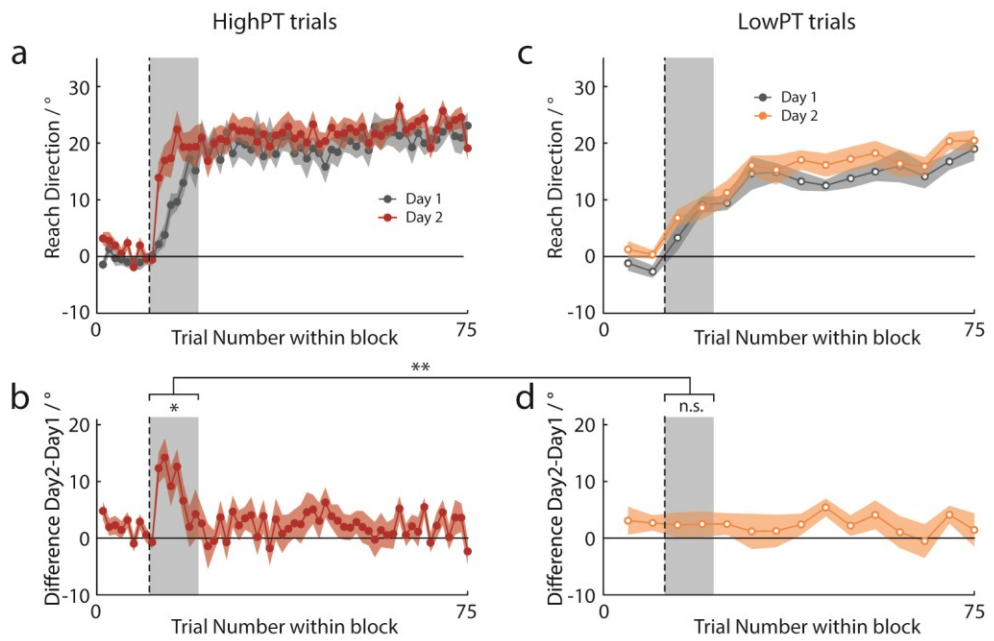
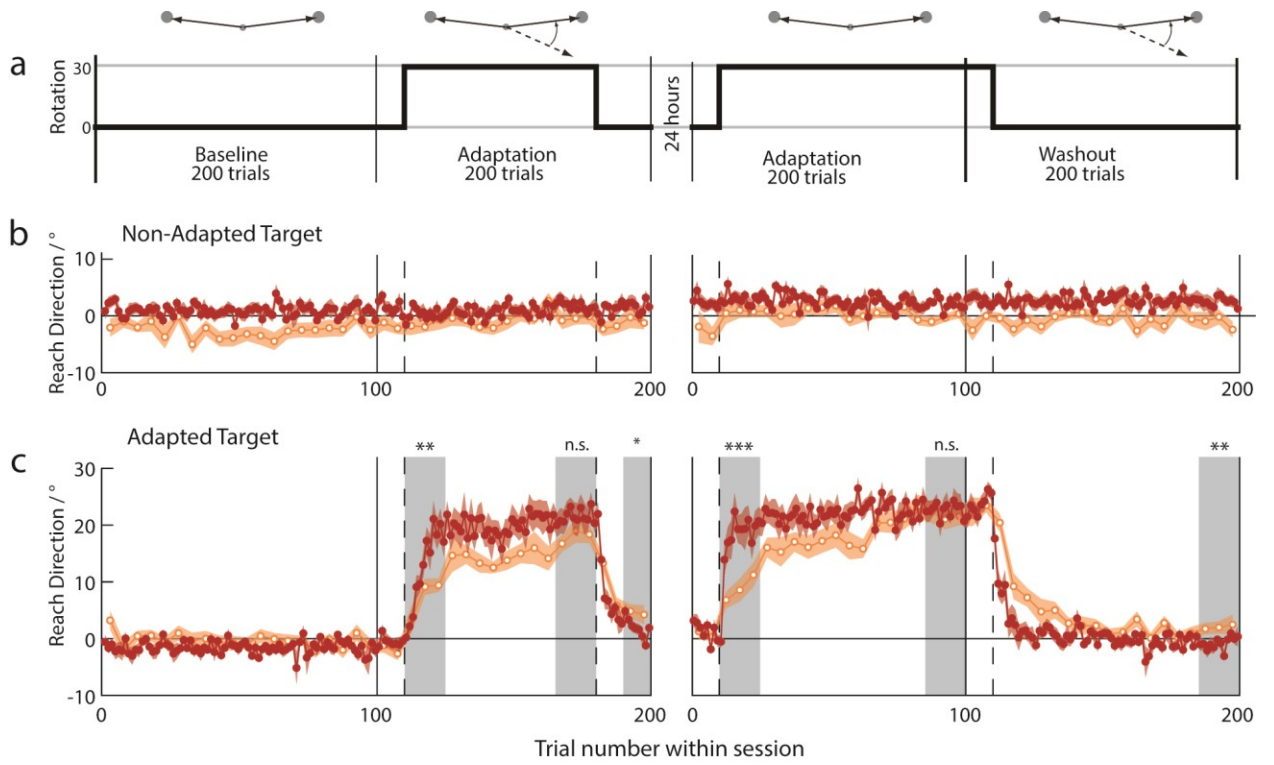
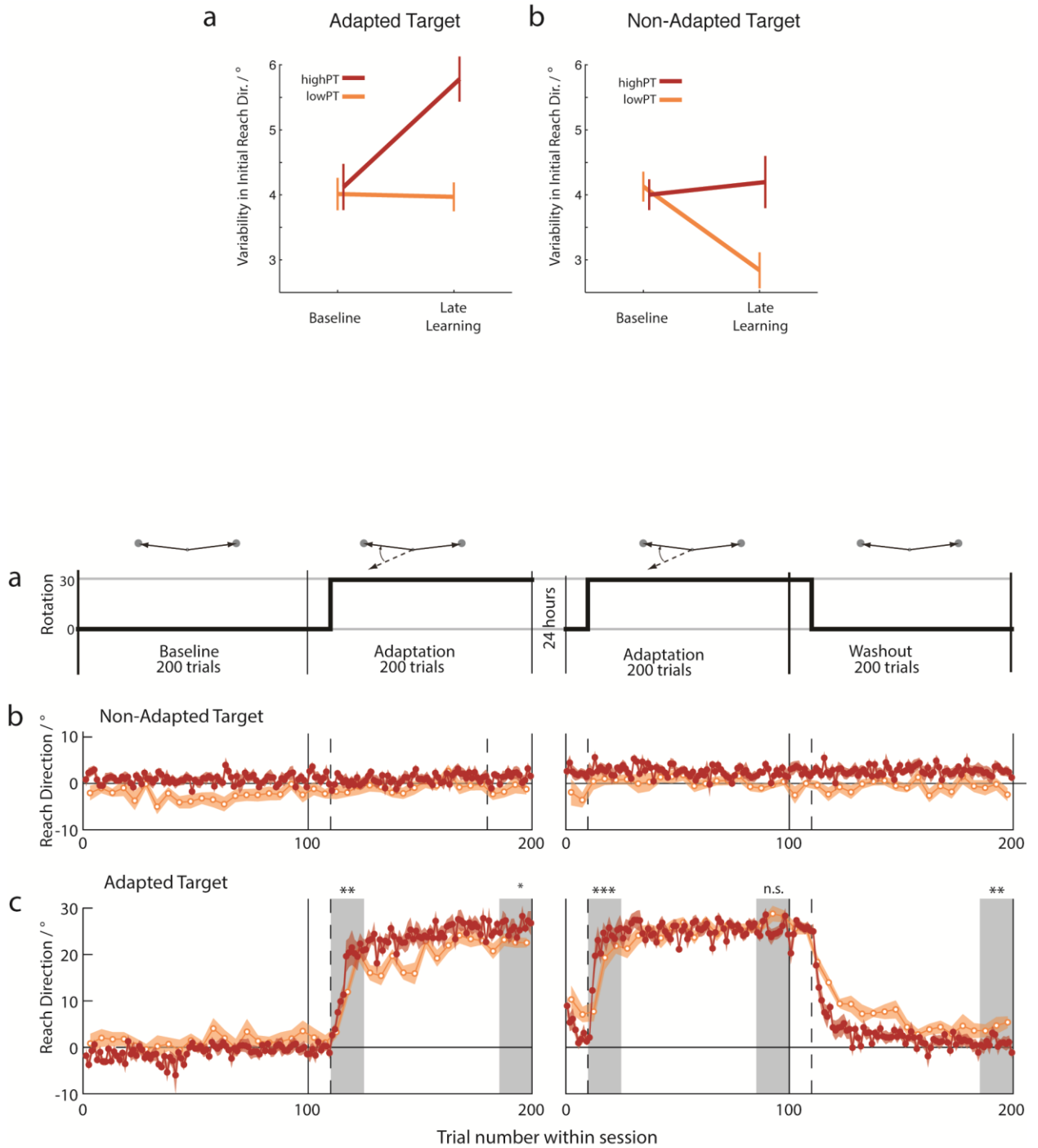


Figure 14 Comparison of learning across sessions. A) Mean reach direction in high-PT trials on Day 1 (gray) and Day 2 (red). B) Difference in state of learning expressed in high-PT trials across days. C) Mean reach direction in low-PT trials on Day 1 (gray) and Day 2 (orange). D)

Difference in state of learning expressed in low-PT trials across days. The x axis reflects approximate trial number within session. Shaded regions indicate \pm s.e.m.



Discussion

We have demonstrated the existence of two qualitatively distinct components of motor learning that can be dissociated from one another based on the amount of preparation time that they require. Our findings corroborate and extend previous work showing a relationship between preparation time and adaptation¹⁶. In particular, our target-switch paradigm allowed us to vary preparation time on a trial-by-trial basis, enabling us to assess the contribution of both components of learning in parallel in the same subject during a single exposure. Similar reduced expression of learning occurs for movements elicited through startle¹³⁷. Our results suggest that this effect is attributable to the effect that startle has on preparation time¹³⁶, rather than being a property of startle-elicited responses *per se*.

Importantly, startle is also known to affect behavior in a similar way following force field adaptation¹³⁷, showing that the effects of preparation time on expression of learning is a general property of adaptation.

A potential alternative explanation for our results is that there is only a single learning process, but that the target switch in lowPT trials served as a contextual label¹³⁹ which allowed learning to occur independently in the two different types of trials. The slow time course of learning in lowPT trials may simply be because of the lower frequency of those trials. This explanation, however, cannot easily explain the relative rates of learning in lowPT and highPT trials. Furthermore, it fails to account for previous work that observed similar effects of preparation time on expression of adaptation using either far more¹⁶ or fewer¹³⁸ trials in which preparation time was

limited. Furthermore, a contextual argument cannot explain the qualitatively characteristics of learning seen in the two different types of trials – in particular, the lack of savings in lowPT trials. Therefore, the difference in behavior we saw in different trial types does not reflect a contextual effect but rather a difference in expression of underlying components.

We exploited this effect to better characterize the nature of savings for visuomotor adaptation. We found that prior experience with a perturbation only affected the rate of subsequent learning in components that require a high preparation time in order to be expressed. In addition to this savings effects in highPT trials, we observed a small but persistent aftereffect of prior learning in the lowPT trials on Day 2, similar to effects that have been reported before^{43,96}. Although this aftereffect could be construed as a form of long-term memory, it was of limited utility to subjects facing a dynamically changing environment; the magnitude of the aftereffect ($\sim 3^\circ$) is too small to account for the savings seen in highPT trials ($\sim 10^\circ$). This bias effect therefore appears to be far more limited form of long-term memory in comparison to the more flexible behavior afforded by the memory that supports savings.

Characterizing preparation-time dependent components of learning

Learning behavior in highPT trials varied significantly across subjects and across learning sessions. By contrast, behavior in lowPT trials was relatively stereotyped across subjects (see Figure 11g) and across exposures (Experiment 2). The amount

of learning expressed in highPT and lowPT trials was uncorrelated; subjects who could compensate well for the perturbation relatively early in highPT trials did not necessarily exhibit faster learning in lowPT trials. Importantly, this implies that the component of learning expressed in lowPT trials is insensitive to task success. Such insensitivity to success is characteristic of implicit learning driven by sensory prediction errors^{23,35}. This learning is cerebellum-dependent¹²⁹ and is thought to reflect updating of an internal forward model¹³¹⁻¹³³. We suggest that the component of learning seen at low preparation time in our results corresponds to this implicit, cerebellum-dependent learning process, though further work will be required to confirm this claim.

The second component we identified, which could be expressed at highPT but not at lowPT, may reflect explicit cognitive contributions to learning^{16,34,35,74}. Explicit contributions to learning exhibit greater trial-to-trial variability, particularly early in learning³⁵. Behavior expressed at high preparation times displays similar elevated variability¹⁶ and this variability is associated with faster learning. The relationship between variability and learning rate is consistent with a learning process that is driven by scalar reinforcement rather than vector error^{55,140}.

Alternatively, learning that is selectively expressed at high preparation times could be based on a cognitive model of the perturbation¹⁶ that is distinct from the one computed by the cerebellum. Our preparation-time-dependent decomposition of adaptation may not, however, be entirely equivalent to an explicit/implicit

decomposition. For instance, it may be possible, given sufficient practice, to express an explicit strategy with minimal preparation time.

Motor learning and rapid motor responses

Our timed-response target-switch paradigm, inspired by the work of Ghez and colleagues¹⁴¹, was devised as a means to elicit movements at minimal preparation time. Low-latency motor responses can also be elicited through perturbations to the arm¹⁴², to a controlled cursor^{76,143} or to a target^{144,145} during or immediately before movement. Goal-directed responses following such perturbations emerge within 100-150ms^{76,142}.

Close examination of such rapid motor responses has found that behavior guided by explicit knowledge occurs at relatively long latency. If a cursor representing the hand location is displaced during movement, an implicit compensatory response is initiated in around 150ms^{76,145}. If subjects are instructed to override this natural response and instead move their hand in the same direction that they see the cursor move, they are able to do so only at much longer latencies (~350ms). The low-latency compensation for the initial cursor displacement still occurs and therefore seems to be involuntary. A similar pattern of behavior is found in object interception. Human and animal subjects possess an ability to rapidly (with a reaction time of around 150ms) select an appropriate hand and initiate a movement to intercept a moving object¹⁴⁶. If, however, subjects are asked to override their default hand choice and instead use a different hand, they can do so only at the

expense of a longer reaction time¹⁴⁶. Elevated reaction times also occur in the anti-saccade task in which subjects must initiate a saccade in a direction opposite to a presented target¹⁴⁷. In general, therefore, it appears that motor behavior is supported by a combination of implicit (perhaps procedural; see below) responses that can be executed at short latency, together with more explicit contributions that can only be expressed at longer delays. Thus these findings support our interpretation that components of learning expressible only at high preparation times, including savings, reflects the contribution of explicit components of learning.

Declarative versus Procedural Memory

A fundamental distinction in long-term memory is between *declarative* and *procedural* forms of memory. Although exact definitions vary, declarative memory is typically associated with knowledge that can be consciously recalled (though not necessarily verbalized²⁸), while procedural memory relates to knowledge that can only be expressed by doing something¹⁴⁸. The distinction between these types of memory rests largely on dissociations in amnesic subjects, who can acquire new perceptual⁴ (Cohen and Squire, 1980) and motor^{6,7} skills without having any conscious recollection of doing so. More concrete definitions of procedural memory have been proposed that appeal to the computational idea that procedural memory corresponds to a cached mapping or control policy relating stimuli to actions¹⁴⁹. According to this theory, procedural memories should correspond to memories that are expressible at minimal preparation times. Indeed, procedural memory is generally established through reductions in reaction time^{14,52,150-152}. In our results,

the long-term memory associated with savings could not be expressed at low preparation times and, therefore does not seem to reflect a procedural memory according to this more computational definition. Instead, the fact that savings required prolonged preparation time to be expressed is more consistent with it relating to a declarative memory.

The component of adaptation expressed at low preparation times appears to resemble implicit, error-driven learning of the kind that appears to be supported by the cerebellum^{35,89,125,153}. Although this component of learning could be expressed at low preparation time, the only long-term memory it exhibited was a weak overall bias of reach direction on Day 2. We question the degree to which this bias effect can be considered a model of procedural memory of the kind that supports more complex and dynamic motor skills such as driving, juggling or tying a shoelace. The concerns extend to the Cerebellum-dependent learning, at least as it is currently understood, might therefore play a very limited role in acquiring new skills, contrary to widely-held beliefs^{48,154,155}. Instead, cerebellum-dependent learning, might primarily serve to maintain calibration of control policies subserving existing skills⁴⁹.

This work and text appeared previously in (Haith, Huberdeau, Krakauer, 2015). I would like to thank the Journal of Neuroscience and my coauthors for allowing its reproduction here.

5

Memory for adaptation transforms from being deliberate to cached

Adaptation is initially supported by deliberate processing, but becomes cached with practice.

It is well known that the properties of visuomotor learning can be altered through experience. It remains unclear exactly how this meta-learning, often referred to as savings, is achieved. Two alternative theories have emerged, each relating to one of the qualitatively distinct mechanisms thought to be responsible for adaptation learning. One hypothesis is that the properties of a sensory prediction error-correcting mechanism change with experience so that similar errors are corrected for more quickly, leading to savings. Another model suggests that actions deliberately made to correct for task errors are remembered and recalled again later. We had previously shown that savings is limited to deliberate corrections when prior practice is limited, but it has also been shown that the properties of meta-learning continue to change with more practice, so it is possible that the mechanism supporting savings changes with experience. Here, we sought to measure the relative contributions of the adaptation components to the emergence of savings to discover their possibly changing contributions throughout practice. We found a qualitative change in the deliberative component of adaptation following practice with an alternating

visuomotor rotation, but could not detect any change in the implicit component of learning. These findings suggest that the properties of cerebellum-dependent implicit recalibration remain insensitive to experience and that, instead, practice induces a qualitative change in the nature of the memory retrieved during savings, ultimately enabling it to be expressed rapidly and automatically. The process of converting deliberate actions to automatic ones may be the foundation of more general motor skill learning in humans, and our results suggest that this process is mechanistically independent from implicit recalibration.

Introduction

Motor learning is commonly studied using adaptation tasks^{59,67}. In these tasks, a systematic perturbation is applied during a movement, and participants must learn to adjust their actions to cancel the effects of this perturbation to regain baseline levels of performance. The properties of adaptation are known to change with experience, a phenomenon known as savings or meta-learning^{37-39,41,43,69,156}.

The ability to adapt to an imposed perturbation appears to be supported by at least two underlying learning components⁷¹. One component is implicit, cerebellum-dependent, and driven by sensory errors^{23,35,129}. The other is more deliberate, may be driven by task-level success or failure^{16,35,44,72}, and does not appear to be cerebellum-dependent¹²⁹.

A critical question linking adaptation to more general human learning is which of these components is responsible for savings, as savings is one of the strongest signs of long-term memory for adaptation. The mechanisms by which savings emerges are thus likely to be the most relevant and relatable to more general motor learning in humans. It has been suggested that practice might alter the sensitivity of implicit learning driven by sensory prediction errors^{70,88}. However, several recent findings appear to show that savings after a single exposure to a perturbation is solely attributable to enhanced deliberate compensation rather than to implicit recalibration^{44,45,72}. This finding is consistent with the notion that savings occurs through retrieval of the actions or strategy that aided adaptation during the initial period of compensating for the perturbation^{71,156}.

However, it is also well-known that longer-term exposure to perturbations can continue to alter the properties of adaptation^{70,88,157}. It thus remains unclear what the nature of longer term savings is – whether it is qualitatively similar to savings after a single exposure (i.e., purely at the level of deliberate compensation) or whether it might eventually lead to plasticity in the properties of implicit recalibration.

Here, we assessed how repeated practice at adapting to a series of visuomotor rotations affected the properties of the multiple components of adaptation. We compared two distinct approaches to decomposing learning into subcomponents. First, we directly assessed implicit recalibration by instructing participants to halt any deliberate aiming strategy they may have adopted, and instead try to bring their

hand directly in line with the target^{35,44,74}. Second, we manipulated the amount of preparation time that participants were allowed between observing the target location and initiating their movement. This has been demonstrated to be an effective means of prohibiting the use of an aiming strategy^{16,72,158} {Haith; Fernandez-Ruiz; Leow}, owing to the lengthy computations involved in aiming towards a different spatial location^{30,34,159}.

Although it has been suggested that limiting preparation time might isolate the same component of learning as measuring aftereffects, it is also possible that the two might dissociate following more practice. In particular, existing theories of learning suggest that practice facilitates a transition from declarative control, which may require time-consuming computations to generate the correct action, to procedural control, which may be able to be generated more rapidly and automatically. We therefore hypothesized that practice might lead to a qualitative change in the nature of the memory retrieved during savings, enabling it to be expressed even when preparation time is limited.

Methods

Experiment Participants

61 right-handed, neurologically un-impaired participants took part in this study (18 – 40 years old, 37 women). The study was approved by the Johns Hopkins School of Medicine Institutional Review Board.

Experimental Setup

Participants were seated at a glass-surfaced table with their right forearm supported by a splint that allowed nearly frictionless planar arm movements. Participants' arms were obstructed from their own view by a mirror, on which was projected a display from a downward-facing LCD monitor installed above the mirror (60 Hz refresh rate; LG).

Participants' hand position was recorded by a Flock of Birds magnetic sensor (130 Hz; Ascension Inc., Shelburne, VT) placed under each participant's index finger. Hand position was reported to participants in near real-time via a cursor (a filled blue circle, diameter 0.5 cm) displayed on the screen. Visual feedback of the cursor had a delay of approximately 100 ms on account of an approximately 40 ms delay in the Flock of Birds and an approximately 60 ms delay in the visual display.

Experiment 1

21 participants took part in Experiment 1. Participants made rapid "shooting" movements using their right upper-limbs from a central start location (a solid green circle, diameter 1 cm) through a target (a solid light-blue circle, diameter 1 cm). The target could appear at one of two locations, positioned 8 cm either to the right or left of the start location (Figure 15A). Participants were trained to initiate their reaching movement coincident with the fourth of four audible tones. The tone sequence began 200 ms following stable placement of the cursor inside the start marker. Successive tones were played at intervals of 300 ms. On each trial, one of the two targets was

presented at the onset of the first tone, and remained on the screen until either the participant reached 9 cm radially from the start position, or 2.5 s passed from the time of the first tone (Figure 15A).

A visuomotor perturbation in the form of a 30° rotation of the path of the cursor about the start position (Figure 15B) was applied in repeating cycles (Figure 15C) throughout the experiment. Only movements directed to the right half of the workspace experienced the rotation. Seven cycles of cursor rotations were included across the experiment duration (the 7th cycle omitted the counter-rotation; Figure 15C). The experiment was divided into blocks of 100 trials each (grey vertical lines in Figure 15C). Rotation direction was counter-balanced across participants so that 11 participants in Experiment 1 had the leading rotation as [clockwise or counterclockwise] {rotation = 1 had 11 for E1}.

During trials designated as Long-Preparation Time (PT) trials, the target remained in its original location for the duration of the trial. During Short-PT trials, the target location abruptly switched to the opposite possible target position prior to the fourth tone (Figure 15A). The time at which the target switched locations was randomized for each Short-PT trial by sampling from a Gaussian distribution with a mean of 400 ms and a standard deviation of 25 ms. Short-PT trials were included among the more common Long-PT trials only during the first rotation and during the seventh and final rotation (Figure 15C). Within blocks where they were present, Short-PT trials were randomly interspersed among Long-PT trials such that for every 10 total trials, two

were Short-PT (one to each target) and eight were Long-PT (four to each target). No Short-PT trials were permitted as the first or last trial in each sequence of 10 trials.

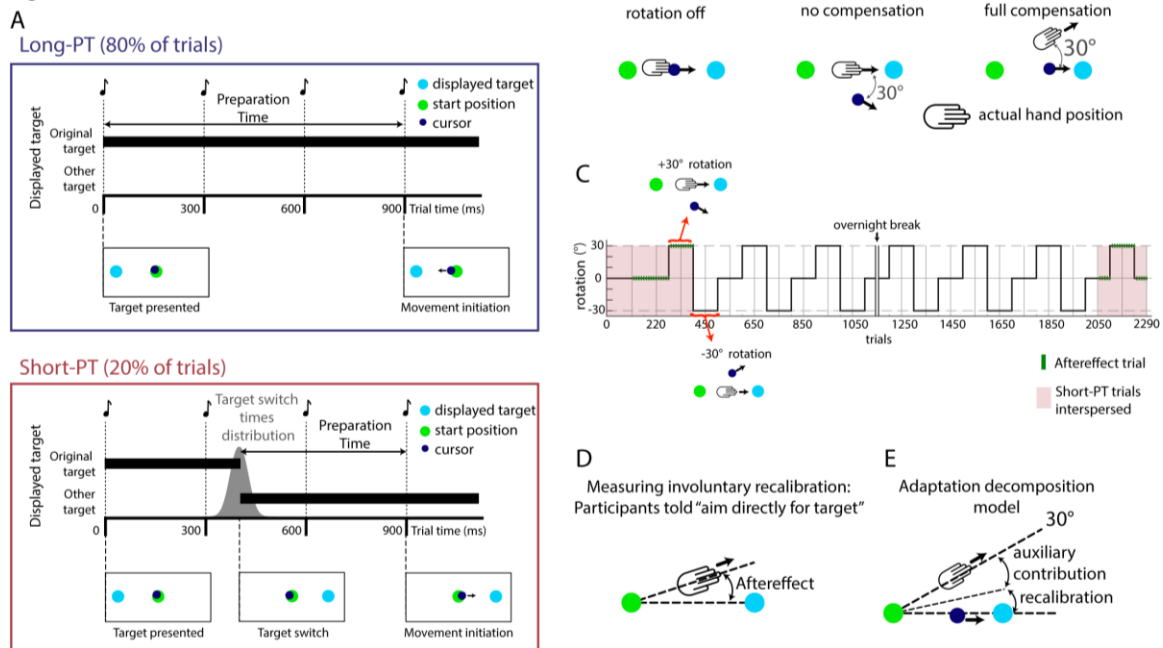


Figure 15: Experiment Design. Participants engaged in a reach task. (A) The amount of preparation time prior to movement was controlled by requiring movement initiation to occur coincident with the fourth tone of a metronome, and controlling the timing of target switches (lower panel). A rotation of the cursor path (B) was imposed in two opposite directions in repeating cycles (C) throughout the two-day experiment. Aftereffect trials (D) measured the amount of recalibration during adaptation, absent any overt aiming on the part of participants. The experiment was designed with a dual-process model of adaptation in mind (E).

Another trial type, the Aftereffect trial (Figure 15D), was used to measure participants' reach direction when explicitly instructed to aim for the presented target, rather than possibly applying a strategy or deliberately aiming in a direction other than towards the target. A similar method had been used before⁴⁴ to infer the extent of implicit adaptation. A pair of Aftereffect trials, one for each target direction,

followed each sequence of 10 Long- or Short-PT trials in blocks when they were present (Figure 15C). Aftereffect trials were included in each of the blocks for which Short-PT trials were present, except for the initial familiarization block. While Short-PT trials were randomly interspersed during the blocks in which they appeared, Aftereffect trials were instead clearly signified to participants and occurred in a consistent order both within and across participants. Prior to each Aftereffect trial, text appeared on the participants' screen for 4.5 seconds reading: "On the next trial / take your time / and aim directly for the target". All participants were literate in English. Participants were also verbally instructed at the beginning of each session of the experiment that during these Aftereffect trials, no cursor would be visible, no audible tone sequence would sound, no movement initiation time constraints were in place, and they were to reach for the target as if they wanted their finger to intersect with the target.

Participants were instructed that for Long- and Short-PT trial types they were to prioritize the timing of their movement initiation. They were instructed to be as accurate as possible in hitting the target with the cursor, and to reach with a speed between 4.5 cm/s and 13 cm/s. Feedback regarding movement timing and movement speed was provided following every Long- and Short-PT trial through visual displays on the screen (similar to Haith, et. al., 2015⁷²).

Cursor feedback during the movement was provided throughout each Long- and Short-PT trial. The cursor disappeared once participants reached 9 cm radially from

the start position. The cursor was not visible during the return movement, until the participants' hand was within 2 cm of the start position. Any cursor manipulations (i.e. the rotations) were turned off during the inter-trial period. During Aftereffect trials, no kinematic information or end-point feedback was provided.

Aftereffect trials and Short-PT trials were assumed omit any auxiliary component that may have contributed to overall adaptation during Long-PT trials, and thus should reveal only the recalibration component of adaptation (Figure 15E).

Experiment 2

20 participants took part in Experiment 2. Experiment 2 was conducted the same as Experiment 1, except that in Experiment 2, there were no rotations in between the first and final rotation cycles (Figure 18A). 20 participants took part in Experiment 2, and the entire experiment was conducted during a single session on one day.

Experiment 3

20 participants took part in Experiment 3. The reaching task and rotation schedule remained the same for Experiment 3 as in Experiment 1. Experiment 3 included Short-PT trials throughout the entire experiment, rather than just the first and final rotation cycles as in Experiment 1. No Aftereffect trials were included in Experiment 3. This experimental design was meant to give a measure of the evolution of savings under Short-PT conditions throughout the course of practice without the potential

influence of Aftereffect trials. Experiment 3, like Experiment 1, was conducted in two sessions across two consecutive days.

Data analysis

All data were analyzed offline in Matlab (The Mathworks, Natick, MA) and in R (The R Project, www.r-project.org). Kinematic data were smoothed with a 2nd-order Savitzky-Golay interpolation filter with half width of 54 ms. These smoothed signals were then differentiated to obtain velocity, the magnitude of which was used to detect movement initiation by searching from the peak velocity backwards in time to find the last time at which velocity exceeded a threshold of 2 cm/s. Reach direction was determined by computing the angle of the instantaneous velocity at 100 ms after movement onset. Trials during which participants either failed to reach or abruptly altered their initial reach direction after having reached 2 cm from the start position were excluded from analysis (on average, 5 trials were excluded per participant for this reason). This type of error was particularly prevalent during Short-PT trials where extra vigilance was needed on the part of the participants to recognize the target switch and alter behavior appropriately while also maintaining movement-initiation timing accuracy.

The initial learning rate during a given rotation cycle was quantified as the average compensation over the first few trials of that cycle. We assessed initial learning during Long-PT trials based on the mean reach direction over the initial 12 Long-PT trials (excluding the first trial following rotation onset and post-Aftereffect trials). For

Short-PT trials and Aftereffect trials, the average reach direction in the initial three trials of each type during the rotation cycle was taken as the initial learning rate. These measures are here referred to as the “early learning” measure for each trial type. Similarly, the final 12 trials (for Long-PT trials), and three trials (for Short-PT and Aftereffect trials), in each rotation were averaged and used as a summary measure for asymptotic behavior (excluding post-Aftereffect trials).

Participants were excluded from any analysis if their Long-PT early learning measure during the first or seventh rotation cycles were more than 3 standard deviations from the mean of early learning measures, because this would have indicated that they did not behave in a “normal” way even in the baseline task. Five participants from Experiment 1 were excluded on these grounds, four from Experiment 2, and three from Experiment 3.

For Experiment 1, a linear mixed-effects model analysis was conducted on both early learning and asymptote measures, with trial type (Long PT, Short PT, and Aftereffect) and rotation cycle as fixed factors and subject as a random effect. Since there was a significant interaction between trial type and cycle, t-tests tests were conducted to detect any difference among groups in early learning or asymptote measures during the first and the final rotation cycle, and to detect for savings from the first to the final rotation cycle for each trial type. This linear correlation analysis was repeated for Experiments 2 and 3.

Results

Experiment 1

Savings during adaptation appears to be limited to circumstances when participants are permitted to engage in deliberate compensation for the perturbation^{44,45,72}. We conducted an experiment to test the durability of this finding, providing a total of seven cycles of visuomotor rotations across a two-day study (Figure 15c) to determine whether having more practice changes the nature of the memory that supports compensation. Early learning and asymptote measures were taken separately for each trial type and for every cycle of the rotation to assess the effect of additional practice on adaptation.

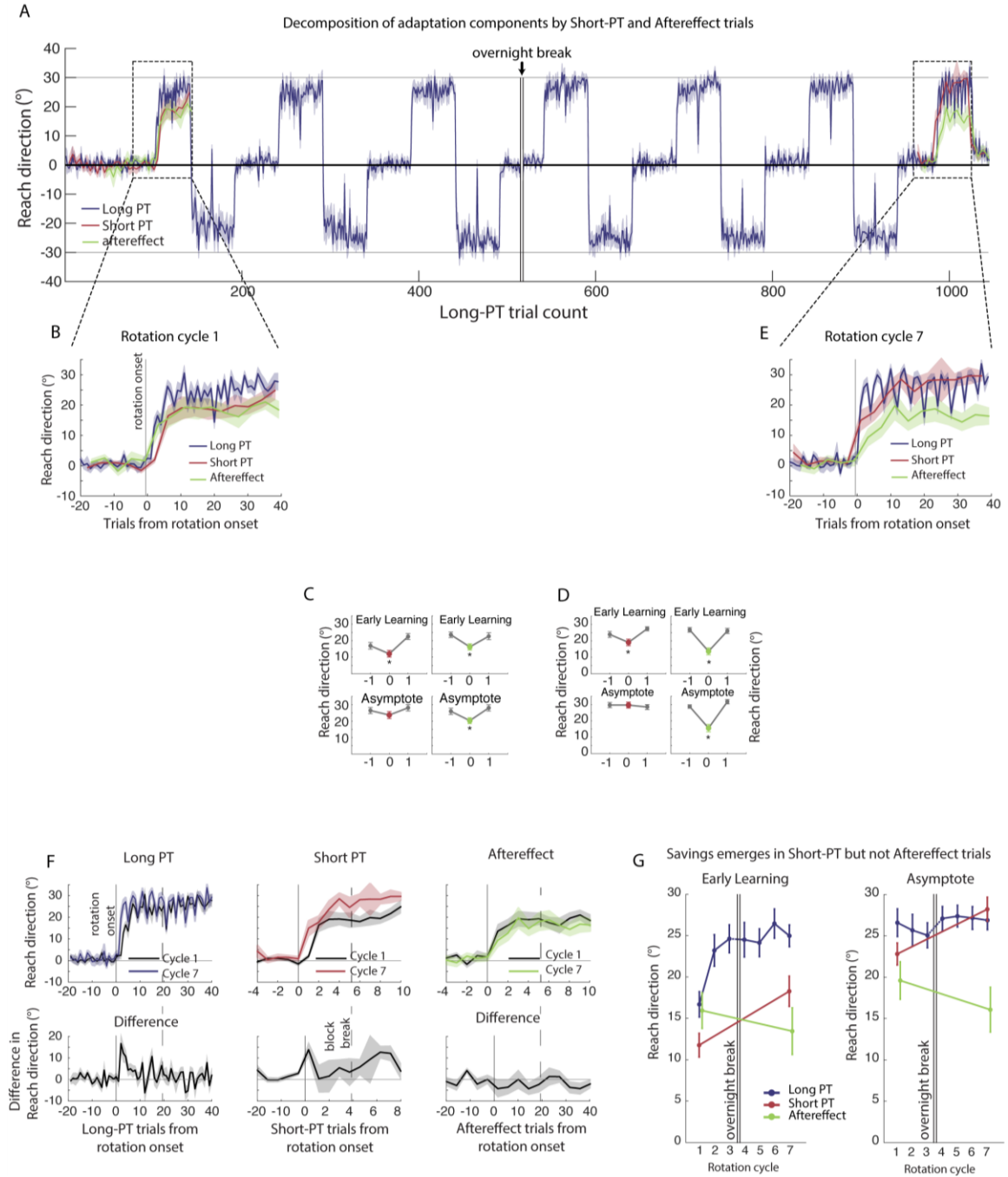
Short-PT and Aftereffect trials modulated the expression of learning during the initial rotation cycle

An experiment was conducted to test the effect of practice with visuomotor rotations on the nature of savings in adaptation. Adaptation during the initial perturbation cycle dissociated, so that under Short-PT and Aftereffect trials, adaptation was lower compared to during Long-PT trials (Figure 16A & B). During early learning, the amount of compensation differed across the three trial types (Long-PT trials, Short-PT trials, and Aftereffect trials; one-way ANOVA: $F(2) = 4.14$, $p < 0.05$). Post-hoc paired t-tests showed that Short-PT trials were significantly different from Long-PT trials ($p < 0.05$), but not detectably different from Aftereffect trials ($p = 0.36$), adjusting for multiple comparisons using the Tukey-Cramer method. There was no detectable difference between Aftereffect trials and Long-PT trials during early

learning ($p = 0.29$). At asymptote, there was also a significant difference among the trial types (one-way ANOVA: $F(2) = 4.33$, $p < 0.05$), with a significant difference between Long-PT and Aftereffect trials ($p < 0.01$) but not between Long-PT and Short-PT trials ($p = 0.093$) and not between Aftereffect and Short-PT trials ($p = 0.58$). Thus, during the first exposure to the perturbation, Short-PT conditions and the use of Aftereffect trials significantly modulated the expression of learning, consistent with previous findings^{35,44,72,160}.

One potential problem with the above analysis of the differences in adaptation rates and asymptotes among the trial types was that these measures may have been biased for Aftereffect trials, since Aftereffect trials consistently occurred later than Short-PT trials. An additional, finer-grained analysis was conducted to confirm the above findings by measuring the mean difference in reach direction between each Short-PT or Aftereffect trial from the average of the two nearest-neighbor Long-PT trials (excluding post-Aftereffect trials). This analysis revealed a significant difference in compensation between Short-PT and Long-PT trials early in learning ($t = 5.5$, $p < 0.01$), but not at asymptote ($t = 1.28$, $p = 0.213$; Figure 16C), confirming results from the above analysis. Aftereffect trials, however, were found to be significantly lower than neighboring Long-PT trials under this more nuanced analysis during both early learning ($t = 4.39$, $p < 0.001$), and asymptote ($t = 3.86$, $p < 0.01$; Figure 16C). Together, these analyses demonstrate that adaptation was significantly modulated during Short-PT and Aftereffect trials compared to during Long-PT trials.

Figure 16: Short-PT savings is not due to recalibration rate increase. Participants adapted (A) under the given rotation schedule. During cycle 1 (B) adaptation was lower for Short-PT and Aftereffect trials compared to neighboring Long-PT trials (C). During cycle 7 (D) adaptation remained lower for Aftereffect trials, but not for Short-PT trials at asymptote (E). Furthermore, there was significant savings for Long-PT trials and for Short-PT trials, but not for Aftereffect trials (F). There was a significant interaction in how adaptation early learning and asymptotes changed across the trial types (G), showing that practice affected the ability to express faster adaptation under shorter PT, but that such savings was not due to a change in the recalibration component to adaptation.



Regression toward baseline following Aftereffect trials

We noted that in Long-PT trials that immediately followed Aftereffect trials, the reach direction was on average lower, or less adapted, compared to the Long-PT trial prior to the Aftereffect trial (Figure 17, A & B; $t = 5.1$, $p < 0.001$). Previous studies have found that when adaptation is interrupted by an idle break in adaptation, the next reach following the interruption is closer to baseline than the reach prior to the interruption^{45,161}. For this reason, post-Aftereffect trials (which in this experiment were always Long-PT trials) were excluded from early learning and asymptote measures used to assess the amount of adaptation for Long-PT trials.

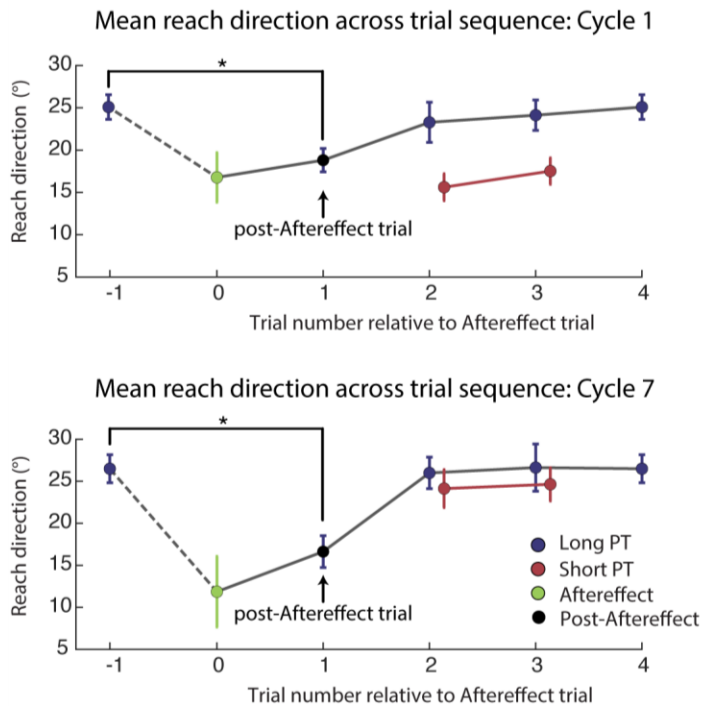
Savings in Long- and Short-PT, but not Aftereffect trials

Experiment 1 tested the effect of having more practice with adapting to a variety of rotations on adaptation measured through Short-PT and Aftereffect trials. There was a clear improvement in early learning between cycle 1 and cycle 7 in both Long-PT and Short-PT trials, but not in Aftereffect trials (Figure 16E & F). A linear mixed effect model that was fit to the early learning measure and that considering trial-type and rotation cycles as factors and subject as a random effect, found a significant trial-type by cycle interaction (Figure 16G; $\chi^2(2) = 9.88$, $p < 0.01$). Post-hoc t-tests confirmed that there was significant savings for Long-PT trials (t-test, $t = 4.39$, $p < 0.01$) and

Short-PT trials (t-test, $t = 2.73$, $p < 0.05$), but could not detect savings in Aftereffect trials (t-test, $t = -1.02$, $p = 0.32$).

The analogous analysis for asymptotic learning also yielded a significant interaction of cycle and trial-type (Figure 16G; $\chi^2(2) = 17.0$, $p < .001$). Post-hoc t-tests showed a significant difference in the asymptote measure in Short-PT trials between cycles one and seven (t-test, $t = 4.84$, $p < 0.01$), but no significant change with practice for Aftereffect trials (t-test, $t = -2.10$, $p = 0.11$), or Long-PT trials (t-test, $t = 0.917$, $p = 0.37$). Thus, practice led to a significant difference in participants' behavior in Long-PT trials, and also to their ability to express that behavior when preparation time was limited. Practice had no effect, however, on behavior in Aftereffect trials (Figure 16, F & G), suggesting that the properties of implicit recalibration remained unchanged by the additional rotation practice.

The problem of a potential bias in Aftereffect trial measures remained during cycle 7 (Figure 17B), so another analysis comparing the Aftereffect and Short-PT trials to the mean of the nearest two Long-PT trials (excluding post-Aftereffect trials) was again conducted and found that Aftereffect trials remained significantly different from neighboring Long-PT trials in both early learning and asymptote measures (Figure 16D; early learning: $t = 5.7$, $p < 0.001$; asymptote: $t = 6.9$, $p < 0.001$). Short-PT trials were significantly lower than neighboring Long-PT trials during early learning but not during asymptote (Figure 16D, early learning: $t = 2.7$, $p < 0.05$; asymptote: $t = 0.40$, $p = 0.69$).



*Figure 17: Post-Aftereffect trial regression. Trials immediately following Aftereffect trials (post-Aftereffect trials) were significantly less adapted compared to trials immediately prior to the Aftereffect trial. This was true during both the first (A) and during the seventh and final (B) rotation cycles in Experiment 1 and form the basis for excluding such trials from further analysis of early learning or asymptote measures. * indicates < 0.05*

Less practice resulted in less savings

A study we had previously conducted⁷² showed that savings was limited to Long-PT trials following only a single prior rotation exposure. That result, along with the

results from Experiment 1, point to a double-dissociation. With little practice, savings is limited to trials when PT is long, but following additional practice, savings is attainable even when PT is limited, but never, it is assumed, for Aftereffect trials. Experiment 2 (Figure 18A) was conducted to confirm this double dissociation. The same assays that were done for Experiment 1 were repeated in Experiment 2, but the six cycles of rotations and the overnight break were omitted (Figure 14A; see methods for details).

In Experiment 2, adaptation was significantly modulated during Aftereffect trials and Short-PT trials during the initial perturbation (Figure 17B). An analysis of variance was conducted on the early learning measure and found that the Long-PT, Short-PT, and Aftereffect trial types differed significantly (one-way ANOVA: $F(2) = 5.0, p < 0.05$). A post-hoc t-test between the Long-PT and Short-PT trial types was significantly different ($p < 0.01$), although there was no detectable difference between Long-PT and Aftereffect trials ($p = 0.51$) or between Aftereffect trials and Short-PT trials ($p = 0.11$). Another analysis of variance was not able to detect a difference among the trial types in terms of asymptote (one-way ANOVA: $F(2) = 1.87, p = 0.17$).

As in Experiment 1, there may have been a bias in the measure of early learning for Aftereffect trials since they always occurred a varying number of trials after Short-PT trials, so an analysis comparing Aftereffect trials and Short-PT trials to the nearest neighboring Long-PT trials (again, excluding post-Aftereffect trials) was conducted. This analysis revealed that there was a significant drop for Short-PT trials (Figure

18C) for both early learning ($t = 4.4, p < 0.001$) and for asymptote ($t = 3.4, p < 0.01$). Aftereffect trials (Figure 4C) were also significantly different during early learning ($t = 4.0, p < 0.001$), although not during asymptote ($t = 1.5, p = 0.14$). Together, these demonstrate a significant dissociation in adaptation among the trial types, as was found in Experiment 1 and in prior studies^{44,72}.

Experiment 1 demonstrated the emergence of savings under Short-PT conditions when additional practice with alternating rotations was done, however, it remains unclear how much practice was necessary to obtain that change. To determine whether there would be savings for each trial types without the amount of practice given in Experiment 1, the same analyses were done for Experiment 2 as were conducted for Experiment 1. These analyses revealed a main effect of trial-type ($\chi^2(2) = 31.3, p < 0.001$) and of adaptation cycle ($\chi^2(1) = 8.0, p < 0.01$), but no detectable interaction between trial-type and cycle ($\chi^2(2) = 0.80, p = 0.67$) for the early learning measure. Doing this analysis on the asymptote data revealed a main effect of trial-type ($\chi^2(2) = 12.3, p < 0.01$), but not of cycle ($\chi^2(1) = 1.0, p = 0.31$), nor of the interaction of trial-type and cycle ($\chi^2(2) = 3.32, p = 0.19$).

Thus, with less practice there existed savings marginally across trial types, although the effect was too weak to resolve differences among the trial types using this analysis (Figure 18F). However, an analysis to detect any drop in adaptation during Short-PT and Aftereffect trials compared to neighboring Long-PT trials found a significant difference during cycles two for Aftereffect trials during early learning ($t = 4.0, p <$

0.01), and during asymptote ($t = 3.2, p < 0.01$). Short-PT trials also showed a significant difference compared to neighboring Long-PT trials during early learning ($t = 3.1, p < 0.01$), but only marginally so during asymptote ($t = 2.0, p = 0.061$). These results suggests that far less practice may be sufficient to begin installing a durable change in the nature of savings, but that obtaining reliable savings under Short-PT conditions may require more practice than was given in Experiment 2.

Experiment 3

Experiments 1 and 2 together demonstrate that savings can be achieved under both Long-PT and Short-PT conditions, and possibly starting from the earliest amounts of practice tested. However, the time-course over which this savings emerges remains unclear. It is also unclear whether the presence of Aftereffect trials and the consequent regression of performance immediately following each such trial inadvertently introduced episodes of re-learning that might have affected the emergence of savings. Experiment 3 attempted to track behavior in Short-PT trials throughout learning, while eliminating the potential confounding effects of Aftereffect trials (Figure 19A).

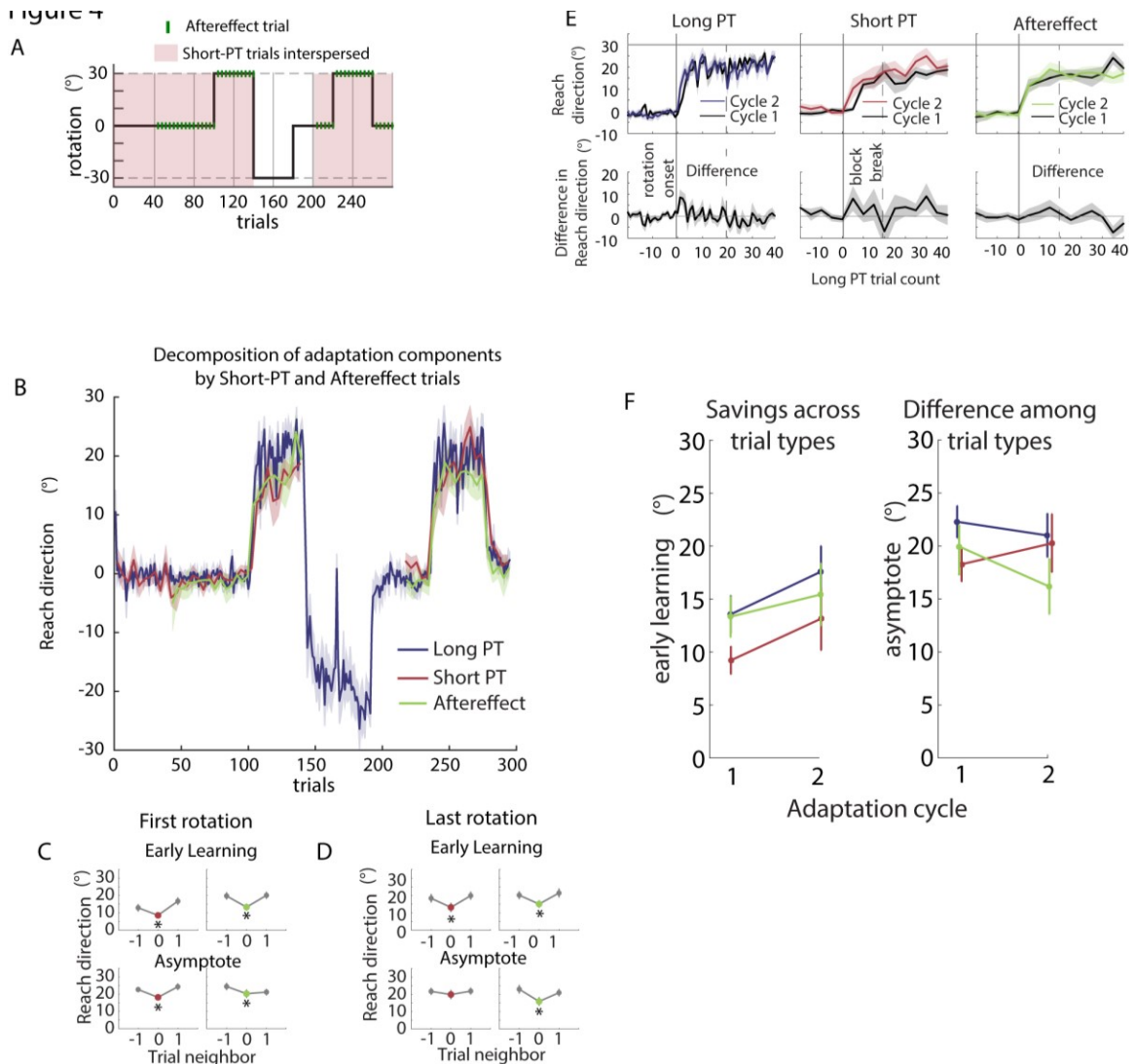


Figure 18: Testing the effect of prolonged practice. An additional experiment was conducted (A) to determine whether the additional practice provided during Experiment 1 was really necessary to obtain savings under Short-PT conditions. Participants underwent a shorter practice period compared to Experiment 1 (B). Short-PT and Aftereffect trials were lower than neighboring Long-PT trials during both the first (C) and the last (D) rotation cycles, except for Short-PT trials at asymptote during the second rotation. However, while savings was significant for Long-PT trials, it was not for Short-PT trials or Aftereffect trials (E). There was also no detectable interaction among the trial types (F) although there was significant savings marginally. * indicates < 0.05

In Experiment 3, early learning and asymptote measures for Short-PT trials significantly differed from Long-PT trials during the first rotation cycle (Figure 5B; Early learning: t-test, $t = 5.25$, $p < 0.001$; asymptote: t-test, $t = 3.00$, $p < 0.01$). Furthermore, it appeared that savings in Short-PT trials emerged gradually across multiple cycles of practice (Figure 19B). To test this statistically, a mixed-effect regression analysis was conducted, similar to that for Experiments 1 and 2, only this time including all seven cycles and considering cycle as a continuous factor. There was a significant effect of cycle on early learning (Figure 20B; $\chi^2(1) = 21.02$, $p < 0.001$), and asymptote (Figure 20C; $\chi^2(1) = 8.54$, $p < 0.01$), and an effect of trial-type (Figure 20B; early learning: $\chi^2(1) = 70.04$, $p < 0.001$; Figure 20C; asymptote: $\chi^2(1) = 13.37$, $p < 0.001$). There was no detectable interaction of trial type and cycle for early learning (Figure 19B; early learning: $\chi^2(6) = 4.02$, $p = 0.68$), although there was a significant interaction for the asymptote measure (Figure 20C; asymptote: $\chi^2(1) = 5.01$, $p < 0.05$). Post-hoc t-tests revealed significant savings (Figure 20A) in Short-PT ($t = 3.9$, $p < 0.01$) and Long-PT ($t = 2.3$, $p < 0.05$) trials between the first rotation cycle and the last for the early learning measure, although not for the asymptote measure (Short-PT: $t = 1.1$, $p = 0.29$; Long-PT: $t = 0.05$, $p = 0.96$). Thus, savings occurred gradually for Short-PT trials across multiple rotation cycles and emerged differently under Long-PT conditions.

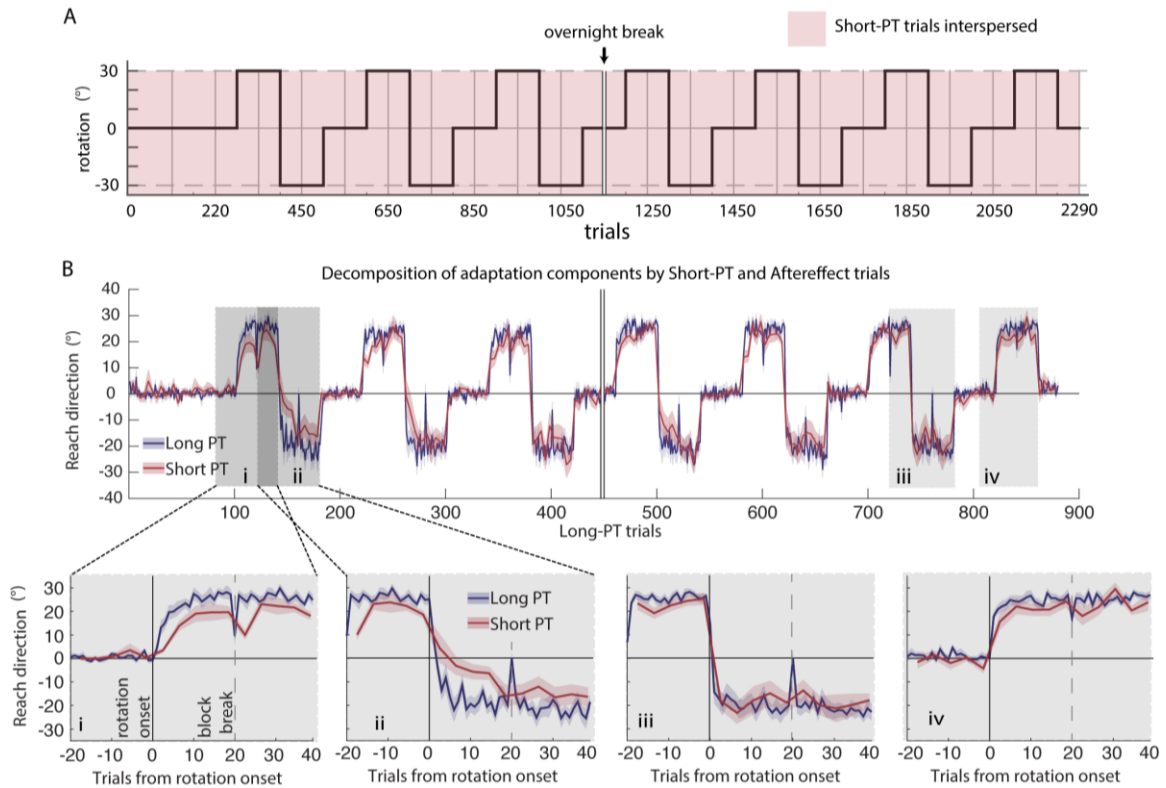


Figure 19: Measuring the emergence of Short-PT savings. Experiment 3 (A) sought to measure the time course of the emergence of Short-PT savings across the longer two-day experiment design. Participants adapted to the repeating cycles of rotations that included Long- and Short-PT trials throughout (B). Adaptation during Short-PT trials clearly became faster following practice.

Conducting the same analyses on the data from the opposite rotations, where the effect sizes might be expected to be larger on account of the larger change in rotation (60-deg, rather than 30-deg), results were even more dramatic. The mixed effects model analysis found significant interaction as well as significant savings and a significant effect of group (Figure 20F) for early learning (cycle: $\chi^2(1) = 21.6, p < 0.001$; trial type: $\chi^2(1) = 12.4, p < 0.001$), and for asymptote (cycle: $\chi^2(1) = 3.52, p = 0.061$, trial type: $\chi^2(1) = 16.2, p < 0.001$). Post-hoc tests confirmed

significant savings for Long-PT ($t = 3.21, p < 0.01$) and Short-Pt ($t = 2.88, p < 0.05$) trials as well (Figure 20E).

Furthermore, Short-PT trials were also lower than neighboring Long-PT trials during the primary rotation (Figure 20D) for both early learning ($t = 3.1, p < 0.01$) and asymptote ($t = 2.4, p < 0.05$) during the first rotation, and for early learning ($t = 3.1, p < 0.01$) and asymptote ($t = 2.4, p < 0.05$) during the last rotation. Finally, the same effect was found for the opposite rotation (Figure 20H), for the first rotation cycle (early learning: $t = -3.6, p < 0.01$; asymptote: $t = -2.1, p = 0.05$), although for the final rotation there was no detectable difference between Short-PT and Long-PT trials during either early learning ($t = -1.2, p = 0.26$) or asymptote ($t = -1.6, p = 0.13$).

Discussion

Visuomotor adaptation tasks have long been used to study human motor skill learning^{38,65,69,78}. Any model of skill learning should at least exhibit the characteristics that seem most relevant and prominent to learned motor behaviors, such as having durable improvements of performance following practice. Since behavior eventually regresses back to baseline in adaptation tasks³⁶, the most consistent sign of long-term retention of learned behavior is savings, or the property of re-learning similar perturbations faster during subsequent attempts. Were savings absent from adaptation paradigms, the relevance of adaptation learning as a model of more general motor learning would be limited.

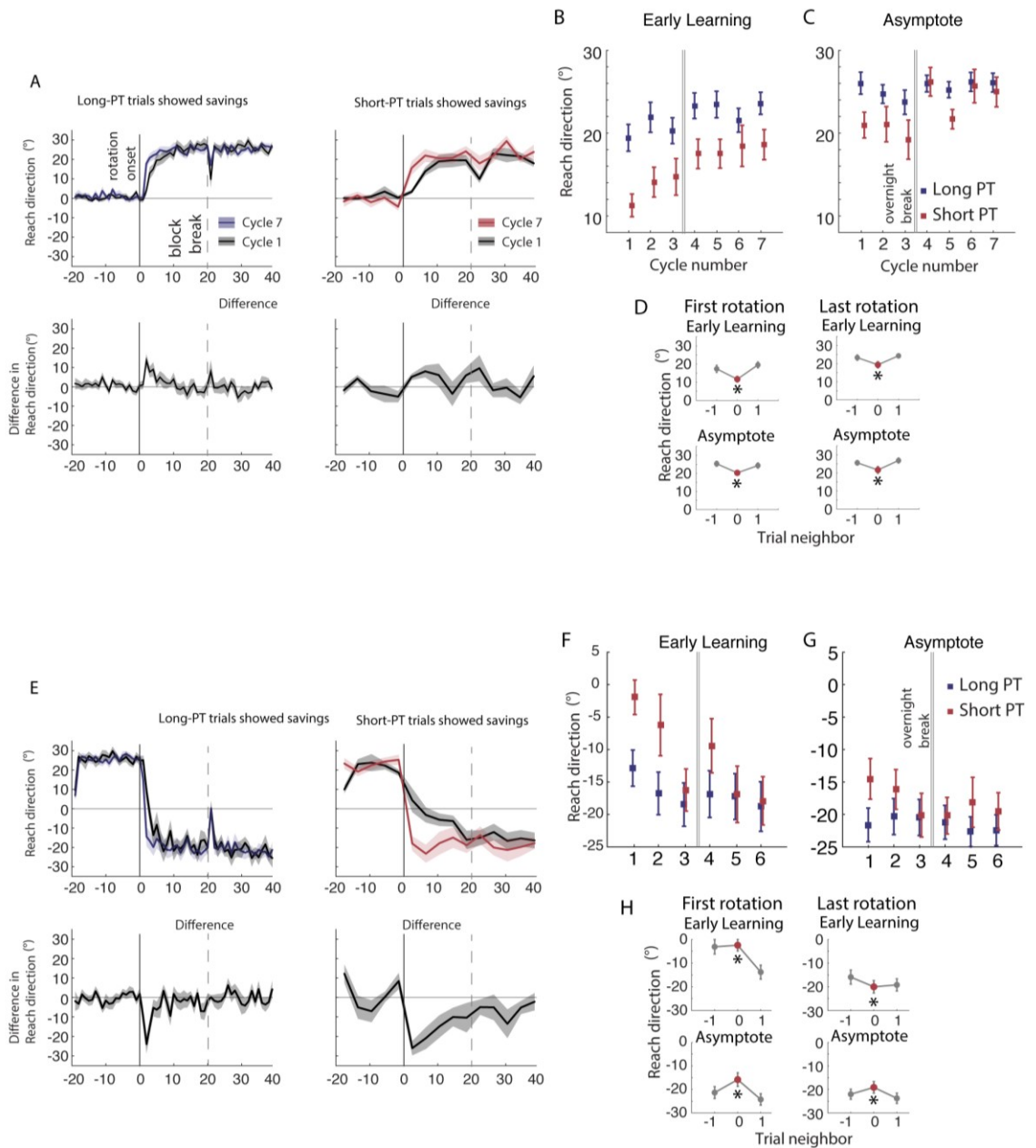


Figure 20: Caching occurs gradually with practice. Since Experiment 3 included both Long- and Short-PT trials for each rotation direction, analyses were possible in both directions. For the leading rotation, there was clear savings from the first to the last rotations in both Long- and Short-PT trials (A). The effect of savings was significant for both the early learning (B) and asymptote (C) measures, although there was a detectable interaction effect only for the asymptote measure. Short-PT trials were significantly lower than neighboring Long-PT trials for both early learning and asymptote during the first rotation cycle, but only during early learning for the last rotation cycle (D). The data for the rotation of opposite direction was even more stark (E). In that case, there was significant savings, effect of trial type, and an interaction in both early learning (F) and in asymptote (G). In the case of the counter-rotation, Short-PT trials were significantly lower than neighboring Long-PT trials for early learning and asymptote periods during the first rotation, but not during the last such rotation (H). * indicates < 0.05

Multiple hypotheses regarding the mechanisms responsible for savings have emerged. One suggests that the properties of the sensory prediction error-correcting mechanism change with practice, leading to increased error sensitivity and, ultimately, to savings⁷⁰. Another suggests that deliberate compensation for the perturbation is remembered and recalled⁷¹. One difference between these two models is what conclusions could be drawn about the nature of savings, i.e. whether it is an immutable process intrinsic to the sensory error-correcting mechanism, or whether it is more controlled and flexible. Understanding the nature of savings will contribute to understanding human learning more generally.

Recent work suggests that savings emerges from deliberate control through the application of intentional perturbation compensation^{44,45,72}. For instance, when forced to move with lower reaction time⁷², when instructed to reach without applying any deliberate compensation⁴⁴, or when given a short break leading to regression of behavior back to baseline⁴⁵, savings becomes undetectable. Instead, better performance during subsequent exposures to the perturbation is only achieved when participants are permitted to deliberately compensate. Thus, it appears that savings is limited to deliberate processing, implying that it may in fact be more related to memory and recall phenomena, such as remembering events from a week ago, than to motor phenomena, such as learning to ski. This would call into question the extent to which adaptation learning is a suitable model of more general motor learning, and would suggest that it may even be a better model for memory and recall phenomena.

Were this the case, many assumptions pervasive in the study of motor control and learning would need to be reevaluated, as conclusions based on the notion that adaptation tasks invoke “motor learning” would be potentially confounded. For instance, it would be unclear which component of adaptation was actually correlated to activity of brain regions such as the cerebellum. Additional steps would need to be taken to properly isolate the adaptation components to make non-confounded inferences about relationships to other phenomena and factors.

However, evidence also suggest that properties of adaptation change with additional practice^{70,88,157}. It is therefore possible that while savings appears to initially be supported by deliberate processes more reminiscent of declarative memory, another mechanism, possibly the sensory error correcting one, may eventually supplant the need for deliberate control and the additional processing that it requires. This question was the basis for the present study, where participants were given more practice than had been given in previous studies on the nature of savings^{44,72} to test whether the mechanism supporting savings changed as a result of the additional experience.

We found that savings under Short-PT conditions emerged with practice, but that Aftereffect trials remained insensitive to practice. This was evident in Experiment 1 as a significant interaction in the measures of learning rate (Early Learning) and extent (Asymptote) among the three trial types. Post-hoc tests confirmed that there was savings under Long- and Short-PT conditions following practice, but not during

Aftereffect trials. From this result we concluded that the sensory error-correcting, recalibration component of adaptation did not change with experience, and therefore could not be responsible for the savings observed in Long- and Short-PT trials. Instead, the deliberate component of adaptation that was initially computationally expensive (i.e. required more PT) transformed to being cached, or available without the need for additional processing. It underwent a transformation from computed to cached.

The implication of these results is that savings in adaptation is a model for motor learning in a way previously unconsidered. We suggest that the principle of human motor skill learning that savings in adaptation illustrates is that novel behavior is initially dependent on computationally expensive memory and recall phenomena (i.e. computed), but makes a transformation to relying on actions that are more mentally effortless following more practice (i.e. cached actions). These results redeem adaptation as a model of skill learning, but not necessarily in the way it was originally conceived. The sensory prediction error-correcting mechanism appears more incidental as it relates to human skill, rather than being the aspect of adaptation most relevant as it once was thought. The prediction error-correcting mechanism might even be considered a contaminant to adaptation learning as a model of long-term human motor skill learning because it changes behavior during the task but is apparently not responsible for any of the observed long-term changes in behavior, which is better modeled by the transformation of deliberate responses from being computed to being cached.

What aspects of practice caused the transformation from computed to cached?

We have argued that a mechanism of transforming initially computationally expensive deliberate behavior into cached responses accounts for the observation from Experiment 1 of the emergence of savings in Short-PT trials. We sought to further explore this mechanism to determine the time-course and nature of the emergence of this cached behavior. For instance, do responses become cached gradually with practice, or abruptly following some threshold event such as a minimum amount of experience, a minimum amount of time, or a night of sleep? And what form must the practice take: time on asymptote, or episodes of recall?

Evidence is mixed on how these factors (sleep, amount of practice, the passage of time, and the nature of practice) affect the transformation that was observed in Experiment 1. Part of the challenge in predicting the effect that any of these potential factors will have on the transformation that we observed lies in properly isolating that process that might be acted on. For instance, sleep appears to enhance the ability to recall declarative information, such as a list of words, as well as the ability to perform movements under novel visual mappings, such as mirror drawing¹⁶². Whether the transformation that we hypothesize to have occurred would be affected by sleep is unclear. Likewise, with respect to the nature of practice, it appears that, at least for certain types of tasks such as foreign language learning, practice with retrieval is more important than mere repetition¹⁶³, but it is unclear if the mechanism of transformation in that study is the same as we have observed.

Results from Experiments 2 and 3 from this study suggest that the transformation of deliberate responses from computed to cached requires practice, rather than merely the passage of time, and requires practice at asymptote, rather than with episodes of recall alone. Experiment 2, which assayed adaptation under Short- and Long-PT trials and Aftereffect trials, while omitting additional practice blocks, was not able to detect any difference in savings among the trial types. While savings was detected marginally, it was not clear which component saved and which did not, because a test for the interaction among them was not significant. Furthermore, savings appeared relatively muted in Experiment 2, even for Long-PT trials (Figure 18E) which should have shown robust savings (e.g. as in fig 2F). The conclusion we drew from this result is that the intervening rotation practice that was included in Experiment 1 but not Experiment 2 was necessary to invoke the kind of transformation that we observed through Short-PT trials in Experiment 1. Considering that our previous study⁷² included an overnight break but no detectable Short-PT savings suggests to us that the overnight break was not the important factor contributing to the transformation.

Experiment 3, which omitted Aftereffect trials but included Short-PT trials throughout a longer period of practice, appeared to show that savings under Short-PT conditions emerged gradually across practice, and differently than under Long-PT conditions. This was evident in the interaction of the change in asymptote from the first to the last rotation between Long- and Short-PT trials for the primary rotation, and in the interaction of the change in early learning from the first to the last rotation

between Long- and Short-PT trials for the counter-rotation. The results from Experiments 2 and 3 together suggest to us that the transformation that we conclude caused Short-PT savings requires some form of extended practice with the rotation.

Since Aftereffect trials, which were present in Experiment 1, caused reach directions during the Long-PT trials immediately following them to transiently regress towards baseline (as shown in Figure 17), these trial types may have acted as recall episodes since they would have required an abrupt correction in reach direction. Experiment 2 included these recall episodes but only limited time on asymptote and did not show a strong differential effect of savings among its trial types. Experiment 3 included both recall events and time on asymptote and did show a differential effect of savings between Long- and Short-PT conditions. We therefore conclude that the transformation of the deliberate component of adaptation from computed to cached likely requires practice with asymptote, although a more direct test of these possible practice types and a more thorough parameterization would be helpful in confirming this conclusion.

Interrelatedness of cognitive and motor phenomena

The idea that a deliberate behavior transforms from being computed to cached is not new, nor is it exclusive to motor learning. Theories developed under different experimental models and for different kinds of behaviors have made similar conclusions. For instance, at least as long ago as William James, the observation of seemingly automatic responses forming for behaviors that were often repeated led to

an action sequencing model for habit formation¹⁶⁴. More modern models of the observed difference between computed and cached behavior use language borrowed from reinforcement learning and artificial intelligence^{63,149,165}, including the description of rapidly expressible behavior as being model-free while slower, computed behavior as being model based. There is also evidence that a transition between these two general regimes of behavior occurs, either with practice^{118,166-172}, or through natural development⁷⁵.

The characterization of savings in adaptation learning as being initially computationally expensive before becoming cached is consistent with these models and suggests that cognitive processes, such as mental rotation^{30,159} or abstract reasoning¹⁷³, may underlying the computationally intensive component. Furthermore, we suggest that these kinds of cognitive processes may be intrinsic to motor learning more generally. For instance, were it not for cognitive processing, savings may not have been achieved in adaptation at all. Stanley & Krakauer argued this point as well in relation to learned human motor skills¹⁶⁸. This idea renders the labels “motor” or “cognitive” as they pertain to a behavior’s output almost inconsequential compared to their mechanistic similarity. This is because, if our model is accurate, the difference between a “motor” task (so labeled because it involves movement) and a “cognitive” task (so labeled because it involves inferred mental processes) may be smaller than the difference between two tasks, both involving movement, that lack other mechanistic similarity. For example, brushing one’s teeth, an overlearned movement task, seems to be more mechanistically similar

to reciting ones phone number than it is to a motor learning task such as learning to ride a bike, despite having the commonality of movement as the output.

Implications of the recall model for savings in adaptation to theories of motor learning

The results from this study may have theoretical implications across other areas of neuroscience. For instance, it has been hypothesized that a mechanism mediated in the cerebellum is responsible for learning novel skills⁵⁰, and sensory prediction error-based learning has been a key model under this hypothesis^{70,174}. If the role of the cerebellum in adaptation learning were limited to sensory prediction error-based mechanisms^{23,35}, then the present findings would present a challenge to the idea that the cerebellum is important in motor learning. However, the reality appears to be far more nuanced than this, as cerebellar involvement in normal movement control and recalibration is fairly indisputable^{125,175-177}. However, its role in skill learning *per se* might be different from that which is currently hypothesized^{70,174}. For instance, in addition to its role in allowing for the production of normal movement and for maintaining accurate calibration, the cerebellum is thought to have some influence on emotions and cognition¹⁷⁸, and it may be in these more abstract functions that its involvement is most critical for skill learning in particular. Furthermore, by demonstrating that adaptation is initially (i.e. before sufficient practice has been done) influenced by computationally expensive processing that may rely on the cerebellum in ways different from recalibration, these results force a potential reinterpretation of any result in systems neuroscience – behavioral,

neurophysiological, or otherwise – that rest on the assumption that adaptation is a “motor” behavior.

What is the nature of the representation that is transformed?

We have made the claim that a memory that is initially computationally expensive, and possibly dependent on cognitive processes, transforms to being cached following practice. What, precisely, has been cached, though? Are the steps in the computation itself cached so that they can be followed or executed more quickly or without the same resources or is the response, the action, that resulted from the computation what becomes cached and available without having to re-compute? In this rotation task, this would be equivalent to asking whether the process of selecting where in space to aim becomes cached or if the action that resulted from the selected aim becomes cached?

We speculate that it is the latter: declarative processing forms a scaffold that allows behavior to converge on a particular policy, but that the behavior itself becomes cached, rather than the processes that built the scaffold. One prediction of this hypothesis is that, provided that the actions taken were the same, there would exist many possible declarative scaffolds that would result in the same cached behavior. This model would explain how athletes can acquire a skill through many various means – a coach, trial and error, or their own creativity, - but end up with essentially the same behaviors. Another prediction would be that low-latency savings for adaptation would have limited generalization to other other rotation sizes. For

instance, if the response to a 30-degree rotation became cached, and then participants were given a 60-degree rotation, adaptation to the 60-degree rotation would be impaired compared to having previously done a 60-degree rotation.

If skill learning is initially declarative, how do amnesiacs learn?

Perhaps no result has influenced motor learning theory more than that of patient H.M: despite severe anterograde and retrograde amnesia, H.M. and other patients like him were capable of learning novel motor behaviors despite having no recollection of ever having done the practiced tasks^{4,5}. These results have led to the principle that motor skills are procedural while episodic memory is declarative, and that the two memory systems are independent¹⁴⁸. Here, we have argued that motor skills rely initially on declarative processing before becoming procedural through practice, a theory that has been proposed for the formation of habits and automatic responses in other, seemingly more cognitive domains as well as motor ones^{118,118,164,167,168,171,179,180}. How can the H.M. result and the declarative-to-procedural model co-exist? The answer, we suggest, is in the nuance of what actually is impaired in amnesiac patients like H.M. Amnesia leaves declarative processing *per se* intact¹⁸¹⁻¹⁸³; it is declarative memory or recall that is impaired. Specifically, amnesic patients are unimpaired at most cognitive tasks and basic reasoning abilities¹⁸¹⁻¹⁸³, provided the tasks do not require holding specific facts in memory beyond the capacity of their short-term memory. Thus, in principle, our model that declarative processing is initially involved in motor skill learning remains consistent with observations of learning in amnesiac patients. A better test to expose the actual consequence of impaired declarative memory on

motor learning would be one that involves movement instructions that are not discernable by affordances and that aren't explicitly communicated to patients on an as-needed basis, such as novel tool use²⁹. When these more specialized tasks are attempted, amnesic patients show no savings, i.e. no benefit of having done the task before. These findings are more consistent with our model that until sufficient practice has been done to cache a policy for a task, declarative-like mechanisms are needed as a substitute until the behavior can actually become procedural in nature.

Is there an advantage to having multiple representations linked by a transformation?

These results seem to confirm a more widely observed phenomenon that differentiates cached from computed behaviors: that procedural memory seems to require more experience while declarative memory can, in general, be formed with far less experience¹⁷². Speculatively speaking, one possible reason for this observation is that the assays used to evaluate whether or not and to what degree a memory has been formed for a particular policy may not match in terms of difficulty. That is, at least in our task, it may be that the task of recalling a specific reaching movement may be, normatively speaking, more difficult than the task of recalling a policy to, e.g., "aim to the left or right". Alternatively, the reason may be neurophysiological and anatomical: if, as has been suggested, there is a neuroanatomical difference in the regions where declarative vs. procedural memories are stored^{148,167,172}, synaptic alterations may occur at different rates in these different regions (e.g. the medial temporal lobe vs. the limbic system). These outstanding questions are ripe for further investigation.

6 Learning novel continuous behaviors resembles policy building

Performance on a novel continuous-action task generalizes to novel conditions requiring different actions, suggesting that a flexible feedback policy was learned.

How novel, continuous-action skills are learned is an important and relevant topic in human behavioral and neural sciences. Behavioral properties, such as movement stereotypy, the emergence of stable feedback responses, and the ability to generalize, can inspire or falsify mechanistic theories of learning. We sought to explore these properties throughout training in this category of human behavior, which includes skills such as skiing, serving in tennis, or riding a bike. We built a custom driving-simulator video game that was controlled by tilting a tablet computer to steer a virtual car along a narrow track. Participants' behavior changed throughout a maximum of ten days of practice through reduction in the risk of failure, increased movement stereotypy, and increased compliance with the state-dependent tablet tilt policy. We assessed generalization by testing participants' performance on a novel "Probe" track and found that they generalized almost completely. Movement stereotypy and policy compliance were unchanged during Probes. However, the risk of failure worsened by approximately 10%, but only after a few days of training. Given these results, we conclude that a flexible control policy was learned that can generalize under novel

conditions. The increase in the risk of failure appeared to be due to an increased probability of making aberrant actions, rather than a regression of ability back to a previous state of learning.

Introduction

Learning novel, continuous movement skills is a relevant and important topic in human neuroscience, medicine, industry, and sports. Theoretical and practical models for how novel continuous behaviors are learned can be used to devise more optimal training routines for athletes or better rehabilitation for patients that have suffered trauma or stroke. They may also assist in better understanding human and animal behavior more generally, or provide a better theoretical grounding for future neuroscientific investigation.

Defining what constitutes a “continuous movement” is not straightforward. One might consider as a definition any learned behavior whose velocity profile remains non-zero, which appears to be the operational definition that others have used^{184,185}. However, even behaviors for which any measure of velocity would be essentially zero, such as quietly standing, might be considered to require active control¹⁸⁶. In this chapter, continuous movement skills will be operationally defined as movements that require continuous active monitoring, whether in motion or not, such that corrective actions would be engaged in response to perturbations, such as noise or extraneous forces. Such movements are distinct from ballistic movements, like eye saccades, or binary behaviors, like forced choice decisions, in that they react

to continuous feedback. Tasks that require behavior to be continuously monitored to maintain stability present unique challenges for the nervous system to control and learn. Studies of learning movement of this type have found reliably consistent patterns of properties across many types of tasks. Practicing a particular task may cause movement kinematics to converge towards an optimal shape^{54,56}, adopt an optimal covariance structure^{56,187}, become more stereotyped¹⁸⁷⁻¹⁹⁰, experience a shift in the speed-accuracy function, or SAF^{54,115,191}, require less reaction time (RT) prior to movement initiation^{18,115,192,193}, and become more efficient¹⁹⁴. Finding consistent and reproducible properties such as these has helped to inspire theories for how motor skills are learned.

One theory is that, following practice and experience, actions can become sequenced and form into expanding representations of actions, or “chunks”^{17-19,21,195}. This theory is consistent with observations that movements become more stereotyped, have lower RTs, and have improved SAFs. It can also explain some forms of generalization, such as if a sequence of actions must be made in a different order, because chunks are thought to be permutable while still providing a performance benefit^{18,51,196}. However, if a novel action sequence is required that is not a subset of the learned sequence, i.e. not represented as a chunk, the theory would predict inferior performance. Thus, testing for generalization using a sequence of novel actions is one way to study the mechanism of learning of a particular task, and to potentially falsify the chunking model.

An alternative viewpoint of how novel continuous movements are learned is that a mapping from states to actions is learned, sometimes referred to as an internal model^{66,67,78,197}. This theory suggests that a mapping is established that dictates which actions, u , are executed based on a mapping, F , from states, x ; or $u = F(x)$. Many studies have investigated the learning properties of adaptation around existing mappings^{66,67,197-199}, but exactly how these mappings are formed in the first place is less well studied (though see⁴⁹).

We sought to experimentally explore the characteristics of learning a de novo continuous movement skill, including the generalization properties, and thus gaining some insight into the computational mechanisms that underlie learning. We decided to devise a novel task, as there are potential confounds inherent in some of the popular tasks used to study sequence learning and action chunking²², including the possibility that tasks such as sequential button-pressing are not even models of continuous actions, like skiing²². To do this, we created a novel video-game task that required continuous, wrist movements and active continuous monitoring of behavior to steer a virtual car along a narrow path at constant speed (Figure 21). We reasoned that if performance of this continuous movement skill generalized readily under novel required actions, it would be inconsistent with models of learning based on action-sequencing. On the other hand, if we found robust generalization, it would support the idea that learning continuous movement skills involve building a flexible feedback control mapping. We tested for these alternative hypotheses by probing for generalization using a track that was the mirror image of

the track used during training and that required a sequence of unique actions (see Supplement Figure 1). We assessed performance, both across learning and with respect to generalization, according to task success and kinematics. The use of this novel experimental design and the advanced analysis methods allow a uniquely detailed measurement of behavior and the effects of practice on learning.

Methods

Participants

81 human participants (47 Female) completed this study. All participants were 18 to 40 years of age, had no known neurological disorders, and were self-reported right (76) or left (5) hand dominant. The Johns Hopkins University School of Medicine Institutional Review Board approved this study and all of its procedures.

Experimental Procedure

The study was conducted using a custom-built video game (“the game”), developed by Max and Haley, Inc. (Baltimore, MD) for the Kata Project at The Johns Hopkins University. The game simulated a driving scenario. Participants steered a virtual arthropod (“the car”) along a constrained track by tilting (i.e. changing the pitch, yaw, and roll) an iPad (Apple, Inc., Cupertino, CA) computer (Figure 21A). The direction of the acceleration of the virtual car was obtained by projecting the vertical axis of a world-centered coordinate system onto the tablet’s surface, giving a magnitude and direction vector; which, by analogy, would be the direction and magnitude of acceleration of a marble rolling off of a flat surface if tilted. The

kinematics of the car in the game were obtained from a physics simulation that included the interaction of the multiple car segments, introducing nonlinearity. This transformation from the tablet tilt signal to the position of the car is thus not possible to write in closed form or to compute an exact optimal solution for. Nevertheless, these computations acted as a filter that introduced a delay of approximately 50 ms between the tablet tilt and the response of the car. The magnitude of the tablet tilt vector was set to a constant value, making the tilt magnitude a control null-space and effectively controlling the speed of the car in the game to a narrow range. The game's software recorded the magnitude and direction of the tablet tilt, and the path of the car along the track (Figure 21B) at 60 Hz.

The experiment included four groups of participants that differed in the number of practice trials on the Training track prior to testing for generalization on the Probe track (Figure 21C). The Probe track was the mirror image of the Training track, which guaranteed that the two tracks were matched in terms of difficulty but required different actions in a novel sequence to successfully navigate (Figure 26). Each group trained for different numbers of days before encountering the Probe (Figure 21D).

Each day included 200 trials and lasted approximately 30 minutes. Trials in which the entire track was completed lasted approximately 5s. A 4s delay was imposed if the car fell off of the track, which would happen if the track's edge was breached. Inter-trial-intervals lasted 3s on average and were self-paced; participants had to

tap a button on the device's screen to begin the next trial. The car's dynamics were invariant for the duration of the experiment including on the Probe track. Probes consisted of a block of 50 contiguous trials in which the Probe track was attempted instead of the Training track. Participants were not pre-warned that a Probe block would be experienced. 67 participants took part in the study in the BLAM laboratory at the Johns Hopkins Hospital, and 14 had the game downloaded onto their personal iPad devices and completed training for the study from home. All sessions that included the Probe track were conducted in the laboratory using the same individual iPad on which each participant trained.

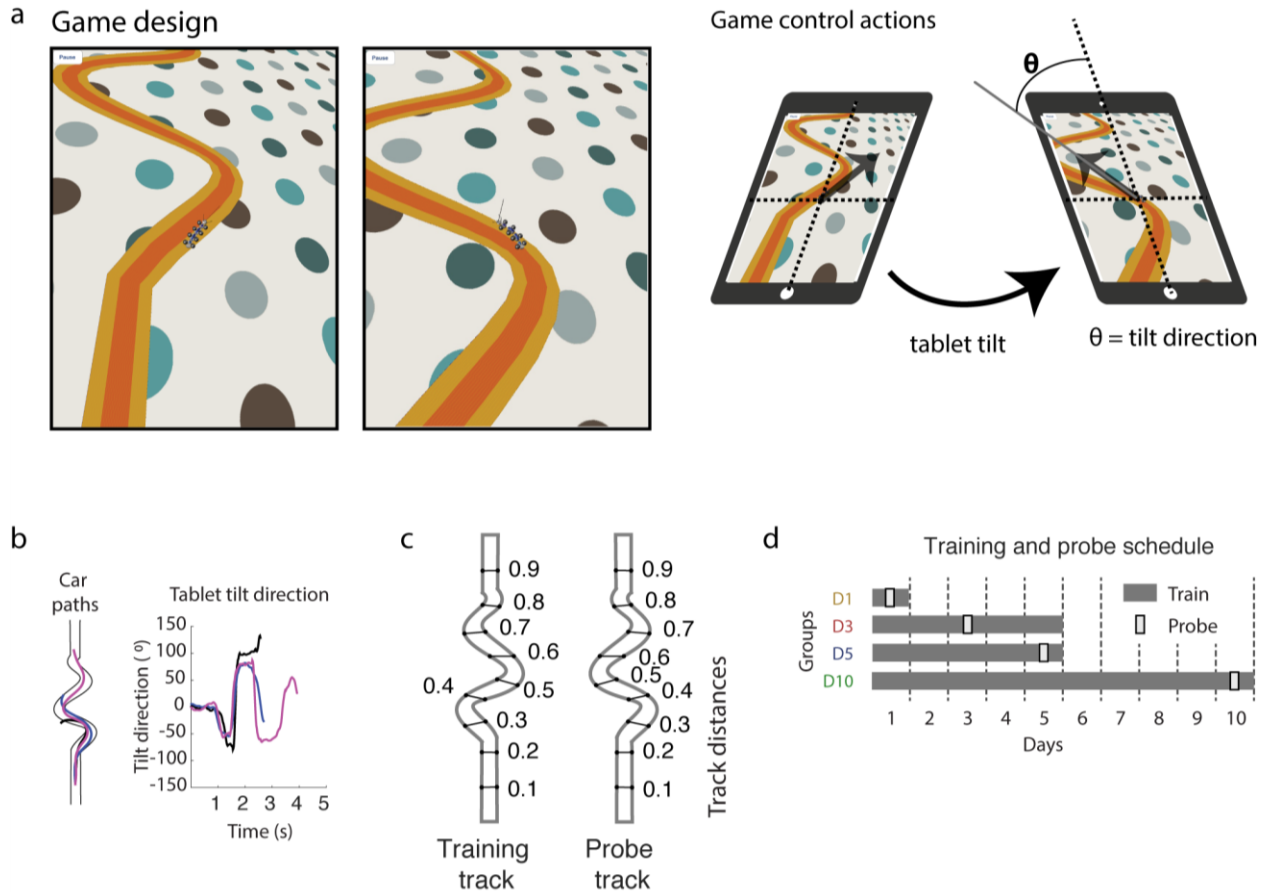


Figure 21: Video game experimental methods. *a*, The game design. The game required navigating a virtual car along a narrow winding path by tilting a tablet computer. The tilt direction was the angle of the vector that would result from projecting a plumb line onto the tablet surface. *b*, Recorded data from the game. The trajectory of the car and the direction of the tablet tilt were recorded for offline processing. *c*, Training and Probe tracks. The Probe track was the mirror image of the Training track. Track distances were taken as fractions of the total track length. *d*, Training and Probe trial assignments per group. Groups trained for varying numbers of days (grey bars), up to a maximum of ten days, and were probed for generalization at different times throughout learning (white boxes).

Data Analysis

Data were analyzed offline using Matlab (The Mathworks, Nadick, MA, 2013) and R (The R Project, www.r-project.org). For each trial, the position along the track at which the car fell off was detected by searching for breaches of the track boundary.

The length of track that the car reached by the fall off point was recorded in units of the fraction of the total track length, a quantity between 0 and 1. Trials in which the car did not fall off were assigned distance 1. The track-length travelled (referred to here as the “distance travelled”) measure was used to assess performance in the game for each trial, as well as to compare performance in the task between Training and Probe tracks.

A linear mixed-effect model was fit to distance travelled data using the window within a day (early vs. asymptote), the day of training (one through ten), and the interaction of window and day as fixed factors, and using subject as a random factor. A log-likelihood ratio test was conducted for each fixed factor to test for the significance of including it as a factor in the model. Separate models were fit to test for the effect of training within-days and for the effect of breaks across day. The initial 25 trials of each day were designated as the early window, and the final 25 trials as the asymptote window. Data was pooled across groups for this analysis.

To confirm results from the analysis of distance travelled, we analyzed the fall off hazard as a function of the length of the track. The hazard rate of car fall-offs, λ , as a function of track distance, t , is given by the conditional probability

$$\lambda(t) = \lim_{\Delta t \rightarrow 0} \left(\frac{\Pr(t < T \leq t + \Delta t | T > t)}{\Delta t} \right)$$

where T is a continuous random variable representing the track length at which a car fall off event occurred. Suppose that T has the *pdf*, or probability density

function, $f(t)$, and *cdf*, or cumulative distribution function, $F(t)$, then the hazard rate function is related to the *pdf* and the survival function, $S(t) = 1 - F(t)$, by the following equation.

$$\lambda(t) = \frac{f(t)}{S(t)}$$

Thus, knowing any one of λ , f , or S is sufficient to compute the others. An estimate of the survival function for each participant on each day of Training and during Probes was obtained using the Kaplan-Meier method {Therneau, Modeling survival data}.

Cox proportional hazard models {Therneau, R package} were used to represent the survival functions from the early and asymptote windows of each day of practice. Models were fit using day (one to ten) and window (early vs. asymptote, as before) as fixed factors, and subject as a random factor. Log-likelihood ratio tests were conducted to test for the effect of day, of window, and of the day-by-window interaction on survival. Separate models were fit to determine the effect of across-day breaks. Data was pooled across groups for this analysis.

For the analysis of kinematics, segments of the cars' paths were isolated by finding the time at which the car reached track length 0.25 and retaining car path data for 1 s thereafter. Only trials in which a fall off did not occur prior to or during this window of time were included in the analysis of kinematics. This window included the first turn in the track and the first major peak in the hazard rate. In order to compare kinematics across different track orientations, we flipped all car paths to

the orientation depicted in Figure 1 as the “Training track”, if they were not already in that that orientation.

To assess how kinematics changed with practice, we examined how the mean and variance of the car’s path across samples of trials changed with practice. To do this, a principal component decomposition was done separately for each individual using data from trials 51 to 150 of each day (excluding any Probe trials). Car paths from trials 1 to 50 (the early window) and from trials 151 to 200 (the asymptote window) of each day were projected onto the axis corresponding to the first principle component, and the mean and standard deviation of these samples were computed. Any windows of trials that had fewer than eight trajectories that had completed the track segment were excluded from further analysis. Linear mixed effect models were fit that included window, day, and the window-by-day interaction as fixed factors, and subject as a random factor. Separate models were fit to test for changes within a day and between days. Log-likelihood tests were conducted for each fixed factor to test for its significant toward the model fit.

Another form of kinematic analysis was done to measure compliance with the tablet tilt policy that resulted in successful track navigation. For this analysis, the Track was discretized along its length, across its width, and for different car direction headings to build an empirical state-dependent tablet tilt policy (Figure 25a). The policy consisted of the mean and standard deviation of the tablet tilt directions within each discrete bin among trials that were ultimately successful. Trials were

labelled "successful" if they reached track distance 0.5 and "unsuccessful" otherwise. The policy map was generated only for the region of track between track lengths 0.25 and 0.45, the region that matched that used in the analysis of car path kinematics and that corresponded to a peak in the hazard rate. This region of track was discretized into ten bins along its length, ten bins across its width, and 20 bins of car heading directions. Data from trials 51 to 150 from each day, excluding any Probe trials, were used to build a policy separately for each participant.

To assess how the tablet tilt policy changed with training, deviations from policy were computed for trials 1 to 50 and 151 to 200 for each day. The policy deviation for each trial was defined as the absolute value of the z-score of the tablet tilt at each discrete bin that the car visited along the length of the segment of track. This quantity measured the normalized difference in tablet tilt of a given trial from the average tablet tilt among successful trajectories, while controlling for the state (position and heading direction) of the car. There was no need to exclude from this analysis trials that fell off during the track segment, because the policy deviation signal could be computed at each discrete location of the track up to the point at which the car fell off. The mean policy deviation across the segment of track was obtained separately for those trial that fell off the track and for those trials that remained on the track throughout the segment. We tested for changes in performance according to this measure by fitting linear mixed effects models to the data separately for successful and unsuccessful trials. We tested for effects of days of

practice, within day differences, across day differences, and the interaction of day and within- and across-day differences using log-likelihood ratio tests.

A comparison of performance during Probe and Training conditions was done with respect to distance travelled, hazard rate and survival, across-trial mean and standard deviation of car paths, and policy compliance. These comparisons were done by testing for changes in each measure between the Probe and Pre-Probe windows of trials, which were, respectively, trials 26 to 75 and 76 to 125 of each day. For the analyses of kinematics (car path kinematics and policy compliance), the data that served as a basis for comparison, i.e. being used to compute the principle components and the empirical policy, were drawn from trials 1 to 25 and trials 126 to 200 from each day.

We sought a second way to analyze performance during Probes, so conducted an analysis to estimate the amount of practice with the Training track that most resembled behavior during Probes. This analysis was done for the car path, distance travelled, and policy deviation measures. Linear models were fit separately to estimate the mean and variance of each of these measures as they changed across days of training. We found the number of days of practice prior to the Probe that behavior during the Probe most resembled by finding the day during practice that had the maximum likelihood given the Probe data. A Kolmogorov-Smirnov test was used for each pair of measures to determine whether there were any differences in

the regression of behavior during the Probes across the three measures of behavior considered.

We sought to quantify the extent to which portions of the tablet tilt signal for the Training track might have been similar to segments of that signal for the Probe track, so we conducted an analysis to measure the difference between tablet tilt signals from the Training and Probe tracks. The difference between signals was taken to be the Euclidean distance between a segment from one signal to the best matching segment from the other signal. The maximum similarity between signal segments from trials in the post-Probe window and the best matched signal segment from trials in the pre-Probe window from group D10 were computed to obtain a measure of signal similarity. The window lengths used to isolate signal segments were 0.1s, 0.2s, 0.3s, 0.5s, 1s, and 2s. Only trials that had completed the track were included in this analysis. Segments of post-Probe trials was isolated using a sliding window with a step size that was 33% the width of the window. The procedure for measuring the maximal signal difference was repeated for the mirror-reversed versions of the pre-Probe signals. Since segment window size affects the Euclidean measure used in this analysis, relative signal differences was computed as the ratio of the Euclidean distance between the Training and Probe signals to the Euclidean distance between the post-Probe and pre-Probe Training signals.

Results

We created a video gaming task to assess properties of de novo learning of a continuous movement skill. The video game recorded task success and kinematics longitudinally with training (Figure 22 a-b), and included a test for generalization on one of four possible Probe days. The way in which behavior changed with practice and during the Probes can provide insight into the mechanisms responsible for learning this novel continuous-action task. If performance generalized to novel conditions, retaining movement stereotypy, better task success, and improved policy compliance, the evidence would be more consistent with a model of learning based on building a flexible feedback control policy. On the other hand, if learned performance was track- and action-specific, the findings would be more consistent with the sequence learning and chunking hypotheses.

Task success improved with practice

The distance travelled along the track increased across practice for all groups (Figure 22c; log-likelihood ratio test, $X^2(9) = 272.15$, $p < 0.001$). Performance improved within each day (log-likelihood ratio test, $X^2(1) = 88.7$, $p < 0.001$), but declined slightly from the asymptote of one day to the beginning of the next day (as in Figure 22d; log-likelihood ratio test, $X^2(1) = 15.0$, $p < 0.001$). Data was pooled across groups for this analysis (Figure 22e).

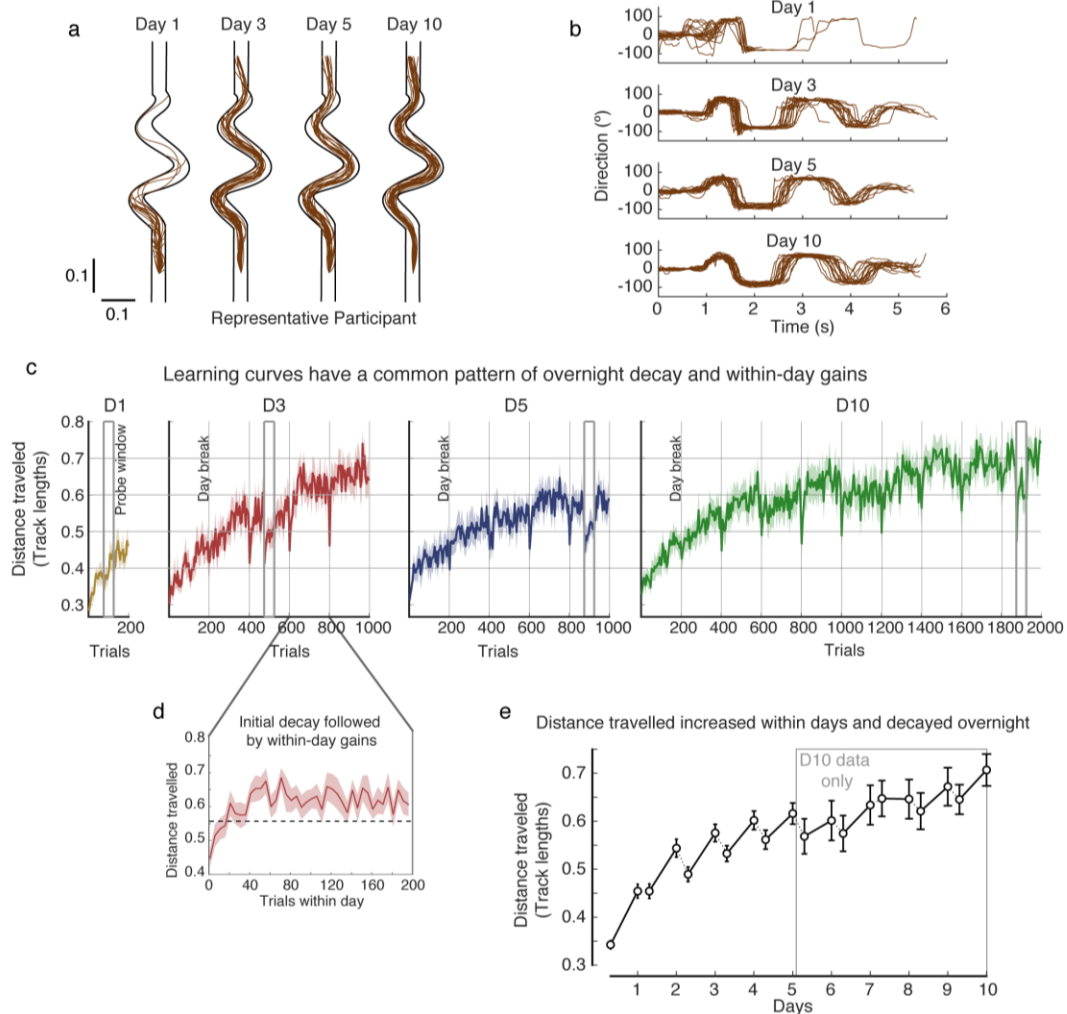


Figure 22: The distance traveled on the Training track increases with practice. A, Car paths and B, tablet tilt signals from a representative participant from group D10. The distance the virtual car travelled increased over days, had lower risk of falling off, and experienced increased stereotypy. C, The mean distance travelled along the path within bins of five trials and averaged across participants (mean \pm std. err.) for each group. Vertical lines indicate overnight breaks, horizontal lines included for comparison across groups. D, An example of the distance travelled in bins of five trials from one day of training. Performance dropped below the previous day's asymptote (the dashed line) but rapidly recovered to a higher asymptote. E, Distance travelled during early windows (first 25 trials, out of 200, within a day) and asymptote windows (final 25 trials within a day). Learning was significant within days but not across days.

We felt that an additional measure of task success, survival, was necessary to account for the potential sources of distortion in the distance travelled measure,

which were introduced by the fact that participants could not travel beyond the end of the track and the fact that the track was not uniformly difficult along its length (Figure 23a). The survival improved across days of practice (Figure 23b; log-likelihood ratio test, $X^2(1) = 355.1$, $p < 0.001$). Survival also improved significantly within days (log-likelihood ratio test, $X^2(1) = 1202.3$, $p < 0.001$), but declined from the end of one day to the beginning of the next (log-likelihood ratio test, $X^2(1) = 683.4$, $p < 0.001$). This analysis confirmed the results from the distance travelled measure. However, the analysis of survival also detected a significant interaction of within day gains and days of practice (log-likelihood ratio test, $X^2(1) = 35.5$, $p < 0.001$), which was not detected under the distance travelled measure (log-likelihood ratio test, $X^2(1) = 13.9$, $p = 0.13$). The median survival at each window (early and asymptote) was plotted to succinctly summarize these findings (Figure 23c).

Car paths became more stereotypical with practice

During learning, both the mean and the variability of behavior might change with experience^{56,58,76,187}. We assessed the mean and variability of segments of car paths (Figure 24A) chosen to correspond to a spike in the fall-off hazard (Figure 24B). Trajectory mean and variability were evaluated by performing a principle component analysis (PCA) decomposition and taking the mean and standard deviation of trajectories projected onto the axis corresponding to the first principle component (see methods for more details).

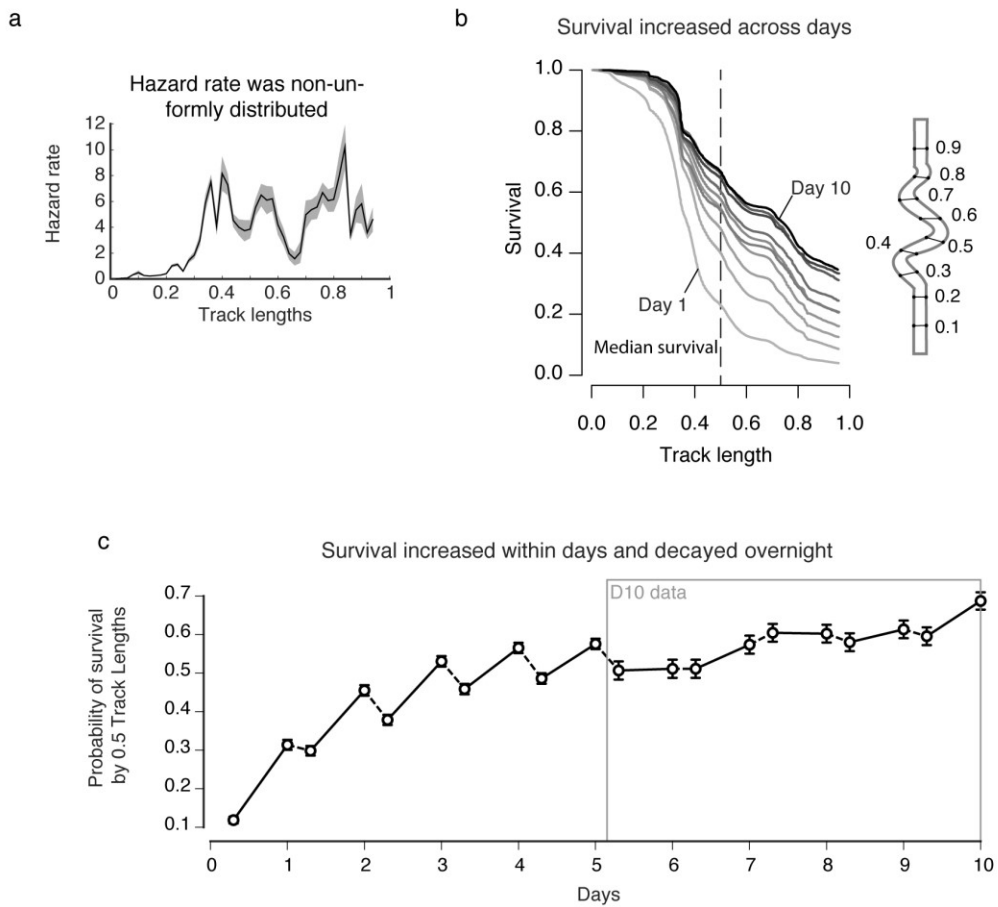


Figure 23: Falloff risk decreased with practice through within-day learning. A, The hazard rate (fall offs per 0.02 of track length) as a function of track length, pooling across all groups and days. B, The survival functions across days of training. Darker curves signify later days. The dashed line intersects the track half-way point and marks the median survival, used in C. The Track inset and the track lengths shown correspond to the azimuth of B. C, The median survival during early windows (first 25 trials within a day) and asymptote windows (final 25 trials within a day). Learning was significant within days but regressed significantly across days, according to Cox Proportional Hazard model analyses.

Kinematics became more stereotyped across days of practice (Figure 24C; log-likelihood ratio test: $X^2(9) = 85.5$, $p < 0.001$), and underwent changes in mean (Figure 24D; log-likelihood ratio test: $X^2(9) = 22.6$, $p < 0.01$). Variability decreased with practice within days (log-likelihood ratio test: $X^2(1) = 39.2$, $p < 0.001$) but the mean apparently did not systematically change within days (log-likelihood ratio test: $X^2(1) = 1.21$, $p = 0.27$). Variability increased across days (log-likelihood ratio test: $X^2(1) = 13.8$, $p < 0.001$), but the mean did not systematically change from the end of one day to the beginning of the next (log-likelihood ratio test: $X^2(1) = 0.33$, $p = 0.57$). These results are consistent with kinematics becoming systematically more stereotyped with practice, and drifting slightly towards what may be a more optimal mean path.

Tablet tilt became more compliant with the tilt policy following practice

An alternative way to assess kinematics was to compare the tablet tilt on each trial to an empirically determined, state-dependent tablet tilt policy (Figure 25a). We measured the compliance of tablet tilt signals separately for successful and unsuccessful trials from both the early and asymptote windows of each day to assess how compliance may have changed with practice and within and across days. Policy deviation among successful trials decreased across days of training (Figure 25b; log-likelihood ratio test: $X^2(1) = 63.8$, $p < 0.001$). There was significant change within each day of training (log-likelihood ratio test: $X^2(1) = 14.1$, $p < 0.001$), but not from the asymptote of one day to the early window of the next (log-likelihood ratio

test: $X^2(1) = 1.3$, $p = 0.26$). Among trials that fell off within the segment, policy deviation also decreased as a function of days of practice (Figure 25c; log-likelihood ratio test: $X^2(1) = 34.6$, $p < 0.001$), and decreased within days (log-likelihood ratio test: $X^2(1) = 8.7$, $p < 0.01$), but not from one day to the next (log-likelihood ratio test: $X^2(1) = 1.4$, $p = 0.25$).

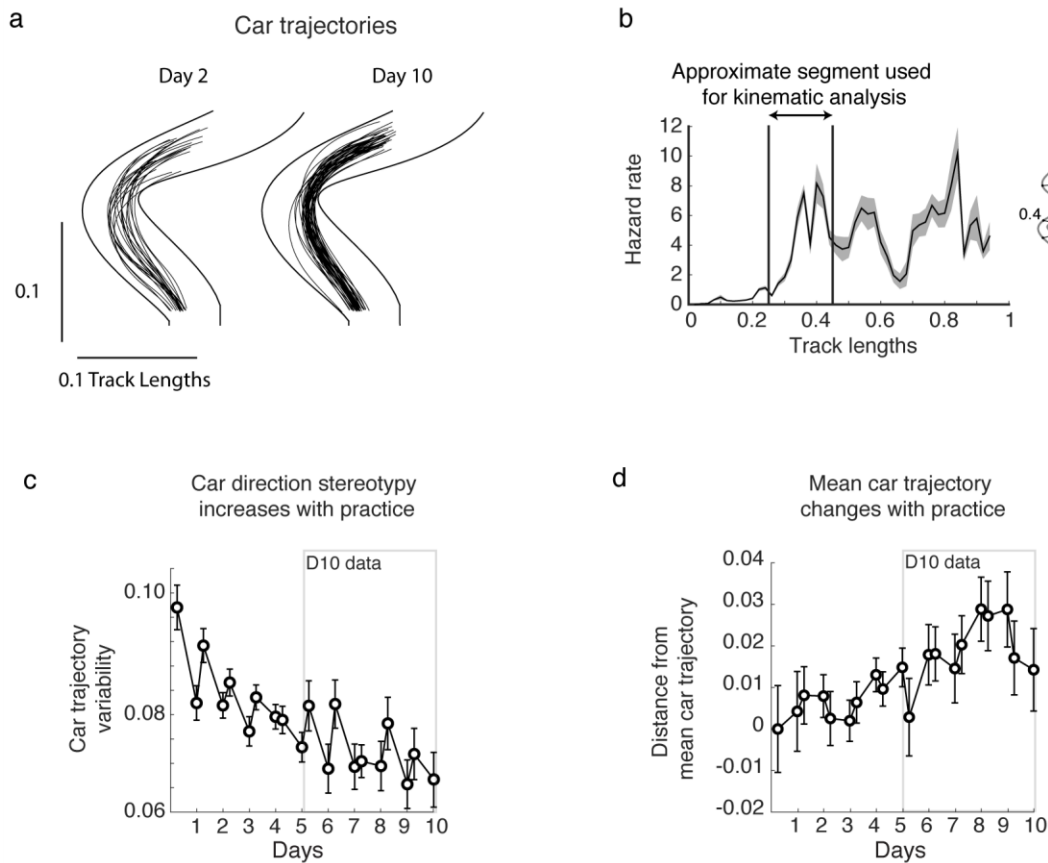


Figure 24: Trajectories became more stereotyped with practice. A, Sample trajectories from a representative participant on Days 2 and 10. Trajectories become noticeably more stereotyped (underwent a reduction in across-trial variance) with practice. B, Trajectories were analyzed over a segment of track that corresponded to a region with a spike in hazard rate. The segment of paths analyzed began at the time the car passed track distance 0.25 (marked by the first of two vertical lines) and extended for 1 s thereafter (approximately indicated by the second vertical line). C, Variability (the standard deviation of trajectories projected into the first principle component) decreased with practice, and decreased significantly within days, but regressed significantly between days. D, The mean trajectory (the mean of trajectories projected into the first principle component) changed with practice, but not reliably within or between days. Gray boxes in C and D signify that group D10 alone contributed data to the average for days after Day 5, since no other group practiced for longer than 5 days.

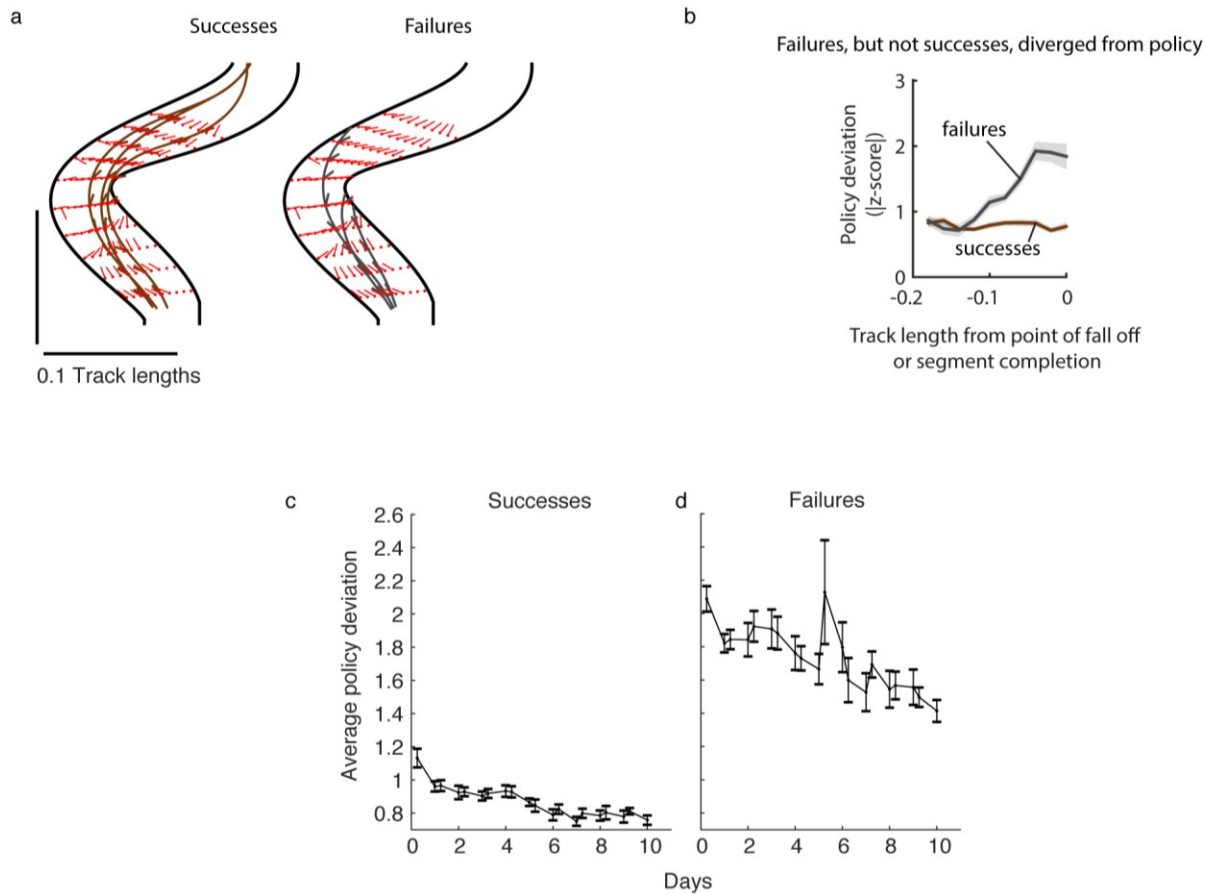


Figure 25: Deviations from the tablet tilt policy reduced with practice for both successful and unsuccessful trials. a, The tablet tilt policy consisted of the mean (red lines) and variance, among tablet tilt signals that successfully reached track length 0.5, at each discrete state. In a, the policy is shown collapsed across the multiple car direction states to show only the track discretization. The policy deviation for each trial was computed at each position along the track length by taking the absolute value of the z-score of that trial's tablet tilt at that state (grey bars) with respect to the empirically determined tablet tilt policy distribution. The deviation from policy among Successful, b, and failure, c, trials decreased with practice.

Measures of task success regressed during probes by a constant fraction from Day 3 onward

Performance on the probe track (Figure 21D) was tested at different times throughout training to determine whether learned behavior was specific to the actions and states experienced during training, or whether behavior would generalize to a novel track. The mirror image track was used to test for generalization because it matched the training path with respect to difficulty, but required entirely novel actions (see Figure 26 for more details).

The distance travelled dropped significantly during Probe trials compared to during the Pre-Probe window for each day, except Day 1 (Figure 27a). The distance travelled during the first five trials of the probe dropped significantly for groups D3, D5, and D10, but not for group D1 (Figure 25B; D1: $t = -1.09$, $p = 0.296$; D3: $t = -3.94$, $p < 0.01$; D5: $t = -5.77$, $p < 0.01$; D10: $t = -6.46$, $p < 0.01$; correcting for multiple comparisons using the Holm method). The mean distance travelled during the remaining 45 trials of each Probe window was also significantly different from the mean distance travelled in the Pre-Probe window (Figure 25D; D1: $t = 2.41$, $p < 0.05$; D3: $t = -2.58$, $p < 0.05$; D5: $t = -3.88$, $p < 0.01$; D10: $t = -4.02$, $p < 0.01$). The distance travelled was higher during the Probe window for group D1, while it was lower for groups D3, D5, and D10. Additionally, there was a significant difference among groups in the steady-state (final 45 trials of the 50-trial Probe window) drop in performance during the Probe (Figure 25B; 1-way ANOVA: $F = 8.41$, $p < 0.01$). Post-hoc analyses revealed that this effect was driven by the drop in performance on Day

1 being different from that of the other days tested, and that Days 3, 5, and 10 were not detectably different from one another (comparing for multiple comparisons using the Tukey-Kramer method). Thus, beyond a threshold of practice (i.e. by Day 3), there was a constant drop in performance as measured by the distance travelled that did not vary with the amount of additional practice. This can be seen by comparing the distance travelled during the Probe windows relative to the Pre-Probe windows for each group (Figure 27c).

We sought to confirm the finding from the distance travelled measure, so conducted an analysis to test for differences in survival between the Pre-Probe and Probe windows. Survival curves show a similar pattern as the distance travelled data; on Day 1, performance during the Probe matched that of the Pre-probe window, but on Days 3, 5, and 10, performance worsened during the Probe window (Figure 28a). Survival was significantly different marginally across the groups (log-likelihood ratio test: $X^2 = 5320.3$, $p < 0.001$), and during the Probe windows (log-likelihood ratio test: $X^2 = 285.42$, $p < 0.001$). There was also a significant interaction between group and probe (log-likelihood ratio test: $X^2 = 1117.1$, $p < 0.001$). This analysis confirmed that performance during Probes changed, and that the change differed significantly depending on the day. Since the interaction of probe and day was significant, additional analyses were conducted to test the effect of the Probe in each group individually. There was no detectable difference between Pre-Probe and Probes windows for group D1 (log-likelihood ratio test: $X^2 = 0.33$, $p < 0.57$), but there was a significant reduction in survival during the Probes for each other group (log-likelihood ratio tests: D3: $X^2 = 50.6$, $p < 0.001$, D5: $X^2 = 80.0$, $p < 0.001$, D10: $X^2 =$

123.8, $p < 0.001$). Furthermore, repeating the test for group, Probe, and their interaction for groups D3, D5, and D10, revealed a significant difference among the groups, marginally (log-likelihood ratio test: $X^2 = 9.8$, $p < 0.001$), a significant effect of Probe (log-likelihood ratio test: $X^2 = 166.5$, $p < 0.01$), but no detectable interaction (log-likelihood ratio test: $X^2 = 5.6$, $p = 0.06$). These findings are consistent with those from the distance travelled measure. Thus, it appears that generalization was complete during the probe window on D1, but that there was a significant drop in performance during the probe on each day tested thereafter that did not vary with the amount of additional practice.

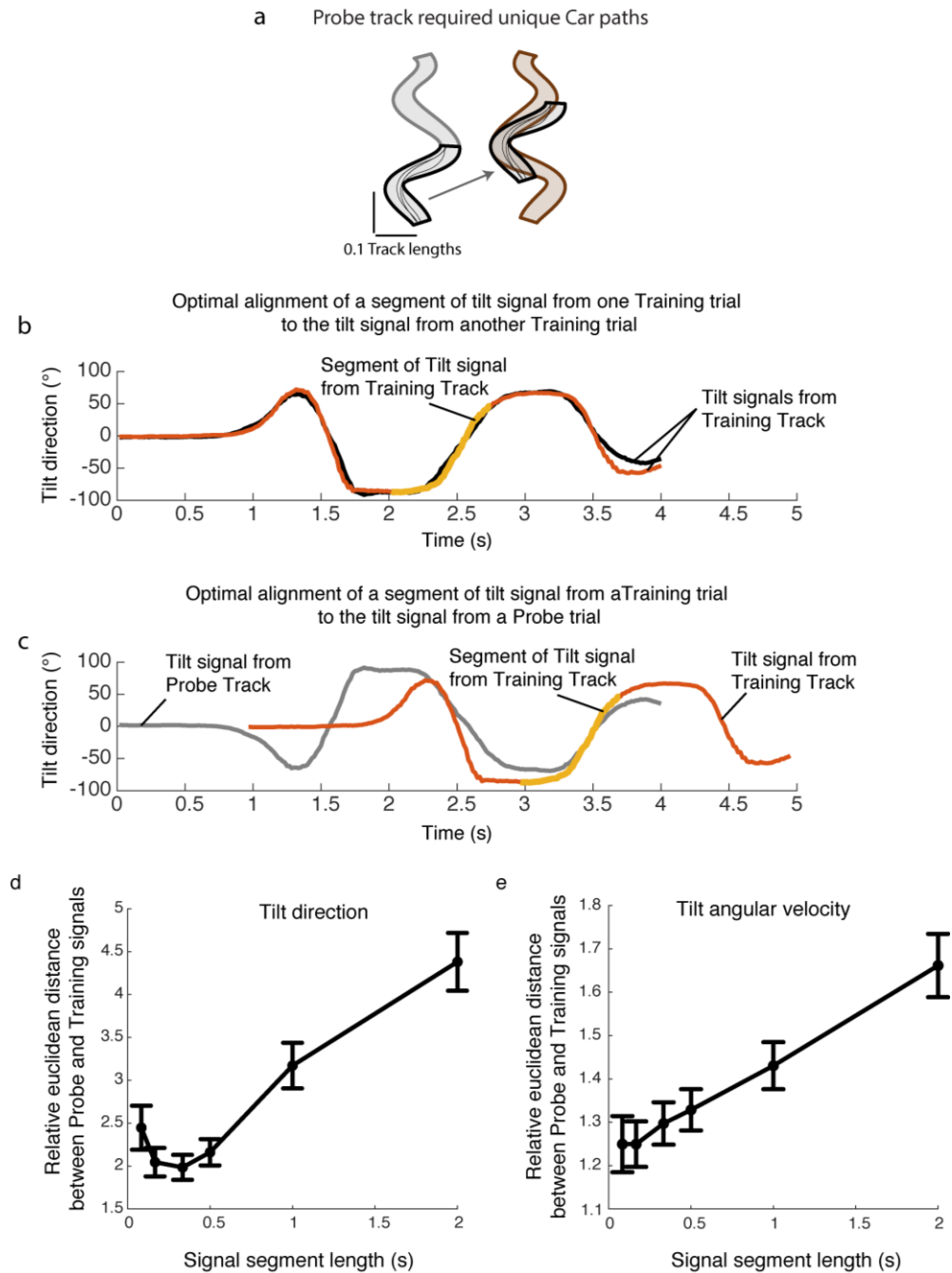


Figure 26: Training and Probe tracks required unique car trajectories and tablet tilt signals. a, Segments of the Training track resembled segments of the Probe track, but car paths from one would not generally be successful in the other. b - c, An analysis of tablet tilt signals measured the minimal distance between Probe and Training tracks for segments of trajectory. d, the best matched tilt direction signal segments between Training and Probe trials were twice as poorly matched as Training trials to each other. e, In the angular velocity domain, the best possible match between Training and Probe trials was better, but still 25% worse than expected from comparing Training trials to each other.

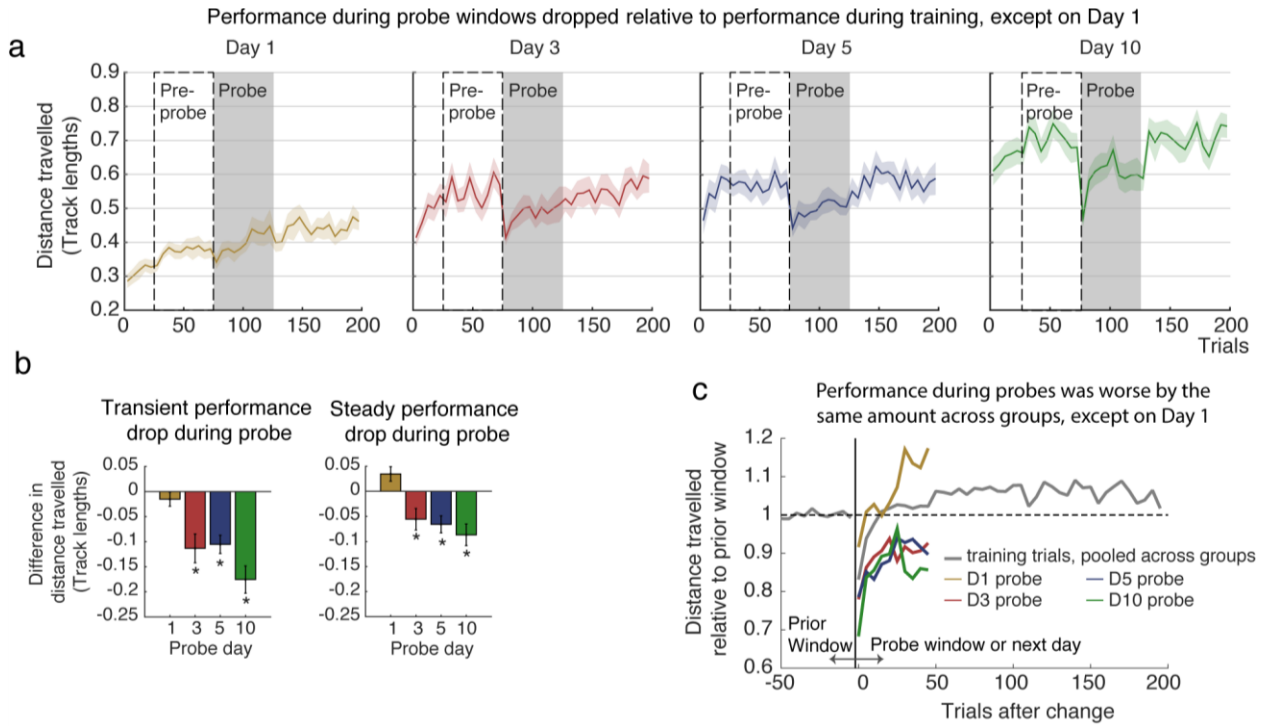


Figure 27: Distance travelled during probes compared to during training. A, The distance travelled on Day 1 continued to increase through the Probe, but on Days 3, 5, and 10, performance dropped during Probe trials. B, The difference in the average distance travelled over the first 5 trials of the Probe (left panel) and over the remaining 45 trials of the Probe (right panel). * indicates that a paired *t*-test determined the group's mean to be significantly different from zero, with an alpha of 0.05. C, Distance travelled relative to prior window of trials. Curves representing Probe days (D1, D3, D5, & D10) show the distance travelled relative to trials 26 to 75, the Pre-probe window. The curve representing Training days (the grey signal) shows the distance travelled relative to the prior day's asymptote, averaged over days 3 – 10, excluding any probe trials. Black vertical line: onset of probe or beginning of a new day of training. * = $p < 0.05$

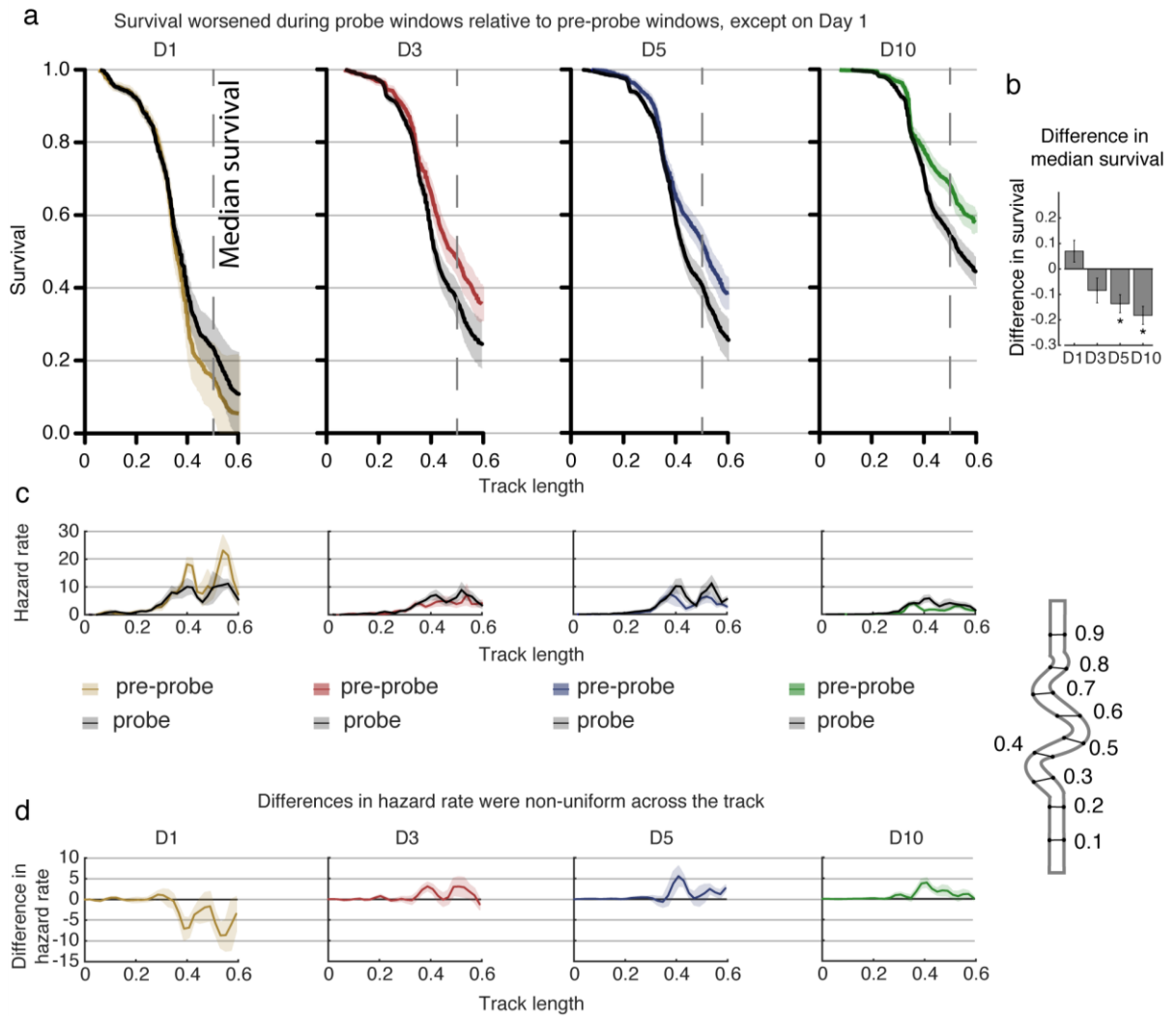


Figure 28: **Survival during probes compared to during training.** **a**, Survival curves for each group during pre-probe and probe windows. Shading indicates standard error as determined by fitting Cox Proportional Hazard models. Vertical dashed lines indicate the position of median survival, used to summarize the difference in survival for each group in the included bar chart. **b**, The Hazard rate (related to the slope of the Survival curves) for the pre-probe and probe windows. **c**, The within-participant difference in hazard rate (Probe – Pre-probe). The Path inset corresponds to the azithums in **a** – **c**. All error bars and shading represent standard error about the mean.

Why did task success (the distance travelled and the survival) change during the Probes in the way that it did – generalizing completely on Day 1, but dropping by a constant amount across all days tested thereafter? If the mechanisms responsible for learning were track- or action-specific, it would be expected that performance

would not generalize at all. The extent to which performance did generalize (i.e. by approximately 90% by Day 3 and thereafter, Figure 27c) could indicate that the mechanism of learning was partially general and partially specific, or that there were two mechanisms: one general and one specific. However, such models could not straightforwardly explain the invariance in the drop in performance during Probes, as these models would predict that the performance difference between Probe and Training conditions should increase with additional practice. Checking how the kinematics changed during the Probes may provide additional insights into why performance as measured through task success changed at all during the Probes. For instance, it could have been that the kinematics regressed to a previous state of learning, by undergoing a regression in mean or in variability to a previous level. On the other hand, if kinematics did not change commensurately with the drop in performance, it would suggest that learned behavior was in fact fully generalized under the Probe, but that some other non-skill-related factor affecting behavior was responsible for the drop in performance, such as a change in the probability of aberrant events leading to fall offs, a qualitatively different potential mechanism than regression in ability.

Kinematic mean and variability during the probes cannot account for the drop in task success

Kinematics may have changed, at least, through differences in movement stereotypy (trial-to-trial variation), or through changes in the mean movement. For instance, it is possible that since the mean movement and movement stereotypy changed

significantly across training, that one or both might have regressed to a previous state during the probes. However, this did not appear to be the case (Figure 29a). Even though the segment of track over which we analyzed kinematics included a peak in the hazard rate and a peak in the difference in hazard rates between the Probe and Pre-Probe windows for each group (Figure 29b), there was no detectable difference in either variability (Figure 29c, D3: $t(13) = -0.45$, $p = 0.66$; D5: $t(16) = 1.36$, $p = 0.19$; D10: $t(17) = -0.63$, $p = 0.53$), or in mean (Figure 29d, D3: $t(13) = -0.054$, $p = 0.96$; D5: $t(16) = -0.12$, $p = 0.91$; D10: $t(17) = 0.17$, $p = 0.87$). We corrected for multiple comparisons using the Holm Method²⁰⁰ (Holm). Nor was there a difference detected after pooling participants together from groups D3, D5, and D10 (Variability: $t(48) = 0.35$, $p = 0.73$; Mean: $t(48) = -0.026$, $p = 0.98$), which increased the statistical power to detect a significant change (power, with $n = 64$:).

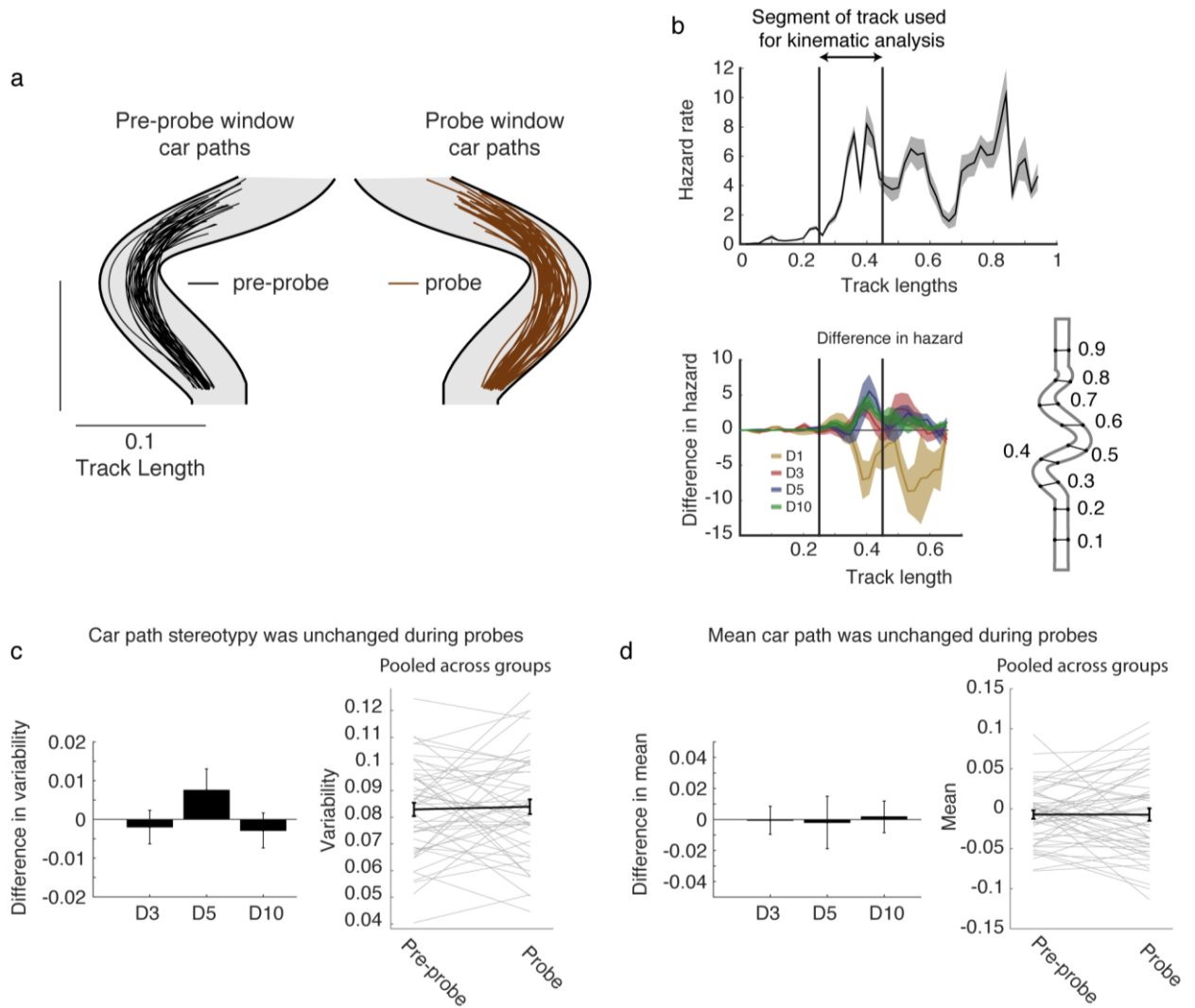


Figure 29: Movement mean and stereotypy did not change during probes. *a*, Car trajectories from a representative participant during the pre-probe window (grey traces), and the probe window (brown traces). *b*, Paths were analyzed within the same segment of Track as in Figure 24, indicated by the two vertical lines. *c*, The difference in the variability among Car Paths (Probe - Pre-probe) for the groups D3, D5, and D10 (Left panel) and for all participants pooled together (Right panel). *d*, The difference in mean Car Path (Probe - Pre-probe) for the groups D3, D5, and D10 (Left panel) and for all participants pooled together (Right panel). Group D1 was excluded from this analysis because too few participants had a sufficient number of trials that successfully navigated the Track for 1s after reaching track length 0.25. All error bars represent standard error about the mean.

This analysis introduced a paradox: how could performance drop during probes when measured with respect to task success (the distance travelled and hazard

rate), but remain unchanged with respect to movement kinematics? These findings are inconsistent with a learning mechanism that is action- or track-specific for several reasons. First, the decline in task success was invariant across practice from Day 3 onward, which would not be expected if separate task-specific and generalizable components were active in parallel. In such a case, both components would be expected to increase with additional practice and experience a practice-dependent divergence between performance under familiar conditions versus unfamiliar conditions. Second, the variability and mean of the car paths remained unchanged during Probes compared to during Training, which itself would lead to the conclusion that generalization during the Probe was complete.

What accounted for the drop in task success? Given that only those trajectories that successfully navigated the selected segment of track were included in the analysis of kinematics, it could be that the discrepancy lies in the excluded trials that terminated within the track segment. Since the survival was lower during Probes compared to during Training, it is evident that there were more fall offs during the Probes, but was there any qualitative difference in how trials failed? Trials might have terminated in a different way during the Probes than during Training, for instance, by deviating more from the established policy on the Probe track than on the Training track. Alternatively, failure trials might have deviated in qualitatively the same way, only having a higher probability of doing so. These two possibilities would support different conclusions as to the underlying reasons that task success dropped under the novel conditions. For instance, if failures were more deviant

during the Probes, it might suggest a problem retrieving or executing the policy that otherwise should be available, as was demonstrated on the successful trials. That is, it would suggest that some phenomenon that was not present during Training became a factor during the Probe on account of the change in track. On the other hand, if failures occurred in qualitatively the same way during Probes as during Training, it would be more parsimonious to conclude that the policy was being followed during the Probes just as it was during Training, but that factors that influenced performance during Training were modulated during the Probes, resulting in a higher fall off rate. Plausible factors that might do this include motivation or attention.

Fall offs occurred in qualitatively the same way on the Probe track as on the Training track

We conducted an analysis on tilt policy compliance to attempt to distinguish between these two hypotheses. Trials that were ultimately successful were analyzed separately from trials that fell off during the track segment (Figure 30a).

Trials that ultimately fell off diverged from the tilt direction policy, while those that were successful remained compliant (Figure 30b). This was true during both the Pre-Probe and Probe windows. The mean deviation and slope of the deviation along the track length was significantly higher during failed trials compared to successes (Figure 29D; stats). There was not, however, a significant change in the mean, or slope of the policy deviation between Pre-Probe and Probe windows. There was also no detectable interaction between the mean and failure status of slope and failure

status. Instead, the fraction of successful trials through the segment of track was higher during the Pre-Probe window compared to the Probe window (Figure 30d). These results demonstrated that, while fall offs may have occurred more often during the Probes, they proceeded in the same way during the Probes as during Training. This result suggests that some factor or factors that were not unique to the Probe condition influenced performance irrespective of the amount of practice and in the same qualitative way as it would have done during the more familiar Training condition; it just did so more often, or with a higher probability, during Probes.

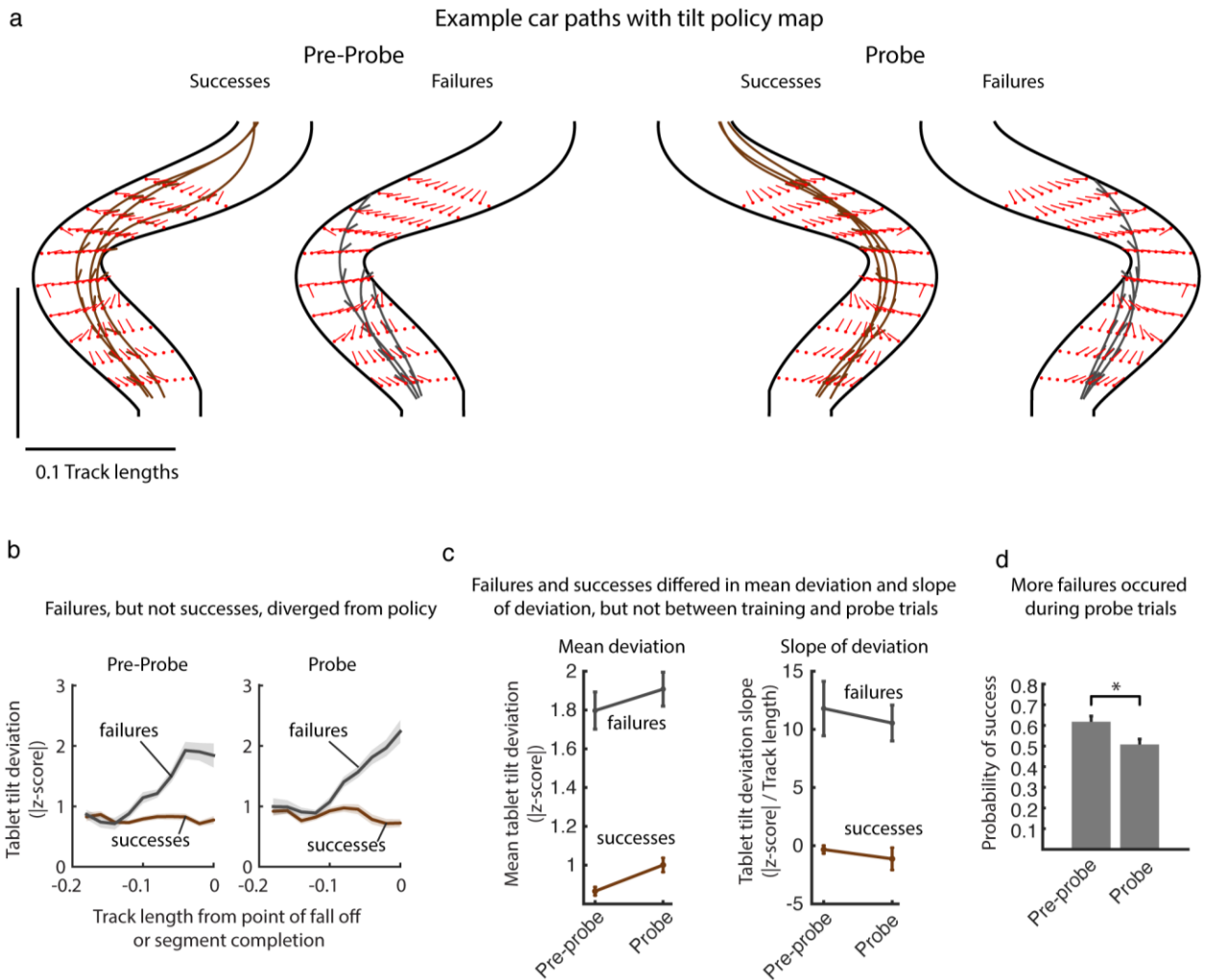


Figure 30: Analysis of terminal Car Paths. *a*, Car paths from a representative participant during the Pre-probe window (left half) and the Probe window (right half) for successful and unsuccessful trajectories (as labelled). The field of red lines indicates the mean tilt direction among successful Car paths at that position of track. Missing field lines indicate that an insufficient number of paths reached that position of track and successfully navigated the rest of the segment. *b*, The policy deviation aligned to the point of trial termination (for failures) or to the end of the track segment (for successes) for the Pre-probe and Probe windows. *c*, The mean (Left panel) and slope (Right panel) of the deviation signals for successful and terminal car paths during the Pre-probe and Probe windows. *d*, The fraction of successful trials during the Pre-probe and Probe windows. * indicates a significant difference at the $\alpha = 0.05$ level. For this figure and accompanying analysis, successful trials were those where the Car path reached at least Track length 0.5.

Car path and tablet tilt kinematics during Probes most resembled Training days closer to the occurrence of Probes than did distance travelled data

An analysis was done to match the day of training whose data most resembled the data obtained during the Probe. This form of analysis was done separately for Car path data as well as Distance travelled data, and an analysis was conducted to determine if the distributions of matched days differed between these two measures of performance (Figure 31). A kolmogorov-smirnov test conducted between the two distributions found them to be significantly different. This analysis is consistent with the position that kinematic measures of performance would suggest that the skill level of participants was higher than that suggested by the measure of task success.

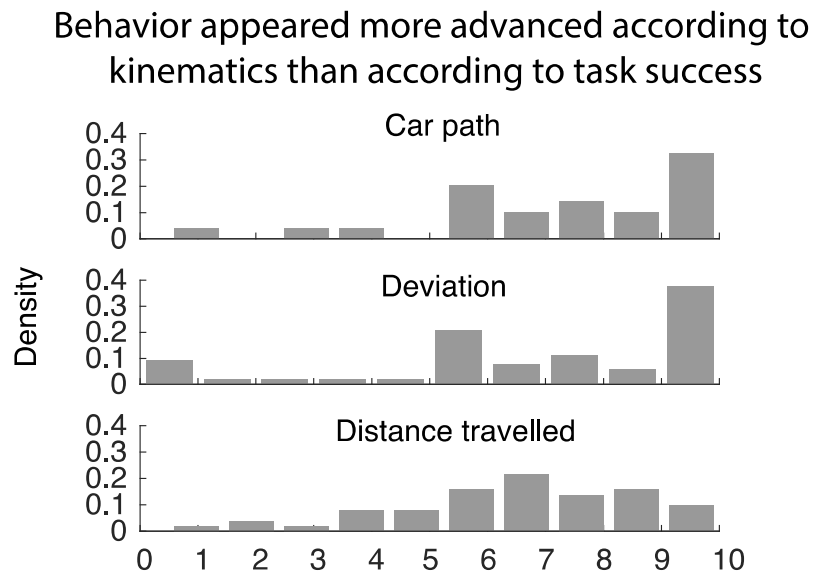


Figure 31: Kinematic measures during Probes more resembled advanced stages of practice, while task success measures more resembled intermediate stages. a, The day of practice that best matched measures of performance during Probes was found by computing the maximum likelihood of the Probe data among the data from each day of practice. The best matched day was more advanced for measures of kinematics (car path and policy deviation) than it was for the distance travelled, a measure of task success.

Discussion

Continuous movement skills – learned behaviors like skiing, or serving in tennis – are of special interest in human behavior and neural sciences. Unlike adapting to perturbations from baseline movements^{65–67}, or learning new sequences of actions already in one’s movement repertoire^{8,18,22,193}, learning novel continuous behaviors appears to be a uniquely human characteristic^{201,202}. It is important to study the mechanisms responsible for such a unique trait in nature. To do so, we created a novel driving-simulator video game, and devised a task that required learning a new continuous-movement skill. This task allowed us to study the process of *de novo* learning of novel continuous behaviors in ways that other tasks do not.

Participants in this experiment practiced the game for up to two weeks, with Probes for generalization assigned at one of four possible times throughout practice, on Day 1, 3, 5, or 10. There were significant changes in performance as measured through the distance travelled, survival, stereotypy, and policy compliance measures over the ten days of practice. During probes, task success (the distance travelled and survival measures) dropped by a constant amount from Day 3 onward. However, kinematic measures (the mean car path, stereotypy among car paths, and compliance with movement policy), did not change significantly during the Probes on any of the day tested. Furthermore, data from kinematic measures were best matched (in a maximum-likelihood sense) to data from the Training track that were more advanced (in days of practice) than was the case for task-success measures.

Thus, the kinematics of movements in the task could not account for the drop in task success that occurred during the Probes after Day 1. Instead, the probability of making an error leading to a fall-off increased. These results mean that, rather than the Probes causing regression in execution ability *per se*, they instead caused an increase in the probability of rare, outlier events that occasionally occurred during Training as well.

One primary question that motivated this study was whether learning *de novo*, continuous-movement skills is done through an action-sequencing mechanism, as is commonly assumed^{8,18,50,196}. These results are not consistent with that theory. The extent to which generalization occurred (90% for task success and 100% for movement kinematics), is not consistent with a sequencing mechanism because the actions required for the Probe track are completely different from those required of the Training track. One possible rebuttal to this conclusion, supported by the chunking theory of sequence learning¹⁸, is that individual movements learned on the Training track could be applied in a different order to achieve superior performance on the Probe track despite not having had specific practice with it. However, this suggestion is unlikely, because the tablet tilt signals required to navigate the Probe track were poorly matched to even the most closely matching signal segments from the Training track (Figure 26). Thus, the sequence learning theory does not appear to be a good model, or to be the appropriate theory, for how *de novo* continuous movement skills are learned.

Finding an interaction between the day that a Probe was given and the amount that task success dropped during that Probe was unexpected, but may reveal more details about the mechanisms of learning in this task. Having observed complete generalization in task success during the Probe on Day 1, but only partial (approximately 90%) generalization during each Probe thereafter, means that some change in representation occurred between Days 1 and 3 that persistent for the duration of practice tested. One possible hypothesis for the nature of such a transformation is that the representation of actions in the task became, at least partially, model-free in nature, and thus became sensitive to changes that would require synthesizing novel actions²⁰³. However, this idea is inconsistent with the fact that the drop in task success during Probes on Days 3, 5, and 10 was constant. Were behavior to have become partially task-specific and partially general, the drop in task success would be expected to increase with more practice, because the additional practice would have acted on both of these components, thereby increasing their separation. This, however, was not the case; the drop remained constant and insensitive to additional practice. For that theory to hold, it would have had to be that the model-free component of learning had a short window of sensitivity to practice that closed some time after Day 1 but before Day 3. This idea is, to our knowledge, without precedent in the literature, and therefore unlikely. A more parsimonious explanation, and one that does have precedent, is that the change in representation that occurred was related to motivation^{22,204-206}. Under this model, the unfamiliarity with the Probe track might have induced a change in motivational state, thus impacting performance. This would simultaneously explain

how there was full generalization on Day 1 and a practice-invariant drop on Days 3, 5, and 10, as the Probe on Day 1 was not particularly unfamiliar, but equally unfamiliar on Days 3, 5, and 10. There may be other possible explanations for the findings, such as an effect of attention^{179,207}, but in any case, the reason is unlikely related to a change in the principle mechanism of learning.

Another clue for the possible mechanism of learning in this task is the incongruence between generalization as measured through movement kinematics versus task success. While generalization as measured through task success suffered a 10% drop on Days 3 and later, kinematic measures registered no apparent change during the Probes. This interaction was confirmed by finding that the measures of kinematics appeared more advanced when compared to the best-matched Training data than did the measures of task success (see Figure 31). The change that occurred during Probes was not a qualitative one; fall-offs occurred in the same way during Probes as they did during Training. Instead, the probability of making an error during the Probes increased. Thus, the learned continuous-movement skill generalized completely under novel conditions, but some factor aside from the ability to execute the correct actions affected the probability of success. This result is also parsimoniously explained by the model suggesting that the Probes caused a change in motivation, or some other factor, like attention, rather than causing a regression in ability.

How are continuous-action skills learned?

The data and findings from this study cannot parsimoniously support a model for learning based on action sequencing or chunking. How are novel continuous-action skills learned, then? One possibility is that a flexible feedback policy is created that effectively maps states to actions^{66,67,197-199}. In the context of this task, such a policy might include, for instance, recognizing one's location on the track and the upcoming segment of track (i.e. together, the "state"), and then generating the appropriate response given that state. A model such as this could be realized with the help of an internal inverse model that is able to generate appropriate responses given present conditions^{66,67,197}. This concept has more commonly been used to describe feedforward control¹⁹⁷, but could readily extend to feedback control as well²⁰⁸⁻²¹⁰.

The concept of learning an optimal and flexible feedback controller is relatively unexplored in human neuroscience, and has the potential to expand understanding of behavior and learning. Much work has been devoted to studying the response to changes in the environment or conditions, assuming the *a priori* existence of an internal inverse model^{66,67,197}, but much less has been devoted to how such a policy is acquired (though see Diedrichsen, et. al.⁴⁹). Future work will be needed to more fully explore the characteristics of learning such a policy, including studying the acquisition over longer periods of practice the two weeks, and investigating its properties of generalization beyond the simple manipulation that we considered. Furthermore, concepts in behavioral neuroscience such as habit formation^{149,211,212}, model-free vs. model based control^{203,213}; and the influence of cognition to learning

and recall^{34,35,72,214} are relatively unexplored in relation to feedback control of continuous behavior. For instance, might there be habitual selection of controllers, rather than just actions? What cognitive or perceptual factors might influence the recall and selection of a controller? Do motivational factors always remain a modulating influence, or does additional training eventually stamp those influences out?

The concept of learning a flexible feedback controller may also have implications beyond the study of neuroscience and behavior. In rehabilitation following injury or a stroke, for example, therapeutics might need to focus on rebuilding lost controllers. From a practical point of view, this may involve focusing rehabilitation exercises on more general use of the affected limbs, rather than task-specific exercises aimed at re-teaching the specific activities of daily living²¹⁵. Similarly, in sports or industrial training, it may be wise to shift emphasis from specific drills and practice routines to more general ones. It may also help to emphasize activities that build confidence or promote motivation, as we have shown here that these appear to be significant modulating factors.

7 General discussion

In this dissertation, I have sought to study the role of cognition and explicit knowledge in the development of motor skills. I conducted several studies that investigated the dual-nature of adaptation learning, and devised a novel experimental model and methods to study continuous-movement behaviors.

Savings for visuomotor adaptation as action-recall

In Chapter 3, I asked how much prior experience with a visuomotor rotation would be necessary to obtain savings. This study found that minimal practice was necessary to obtain savings – as few as 2 trials under the rotation was sufficient to impart a systematic improvement when tested later. The amount of prior practice did not change the amount of savings observed (i.e. groups ROT₁₀ vs. ROT₄₀ had the same strength of savings), and it appeared that the best prior action was rapidly recalled. Furthermore, the prior rotation experience needed to be in the same direction as the next rotation in order for savings to be observed. This pattern of savings is consistent with a model for the recall of actions as supporting savings⁴².

There are several possible mechanisms that could account for how actions are retained and recalled. One possibility is that, in the presence of the visuomotor perturbation, actions that bring reaches closer to asymptote (e.g. reduced their movement error under the rotation) experience a positive reward prediction-error¹³⁰ and are retained through a reinforcement learning mechanism^{42,165}. Another possibility is that the actions are declarative or explicit in nature, and are remembered and recalled as declarative memory^{7,35,44,72,148,216}. There may even be a combination of the two, where both mechanisms contribute to retention and recall.

This model contrasts with a view in which experience with specific errors encountered during adaptation modifies the error-sensitivity of those errors in a principled, cerebellum-dependent way, leading to faster re-learning when the same errors are experienced again later⁷⁰. This view, versus the action-recall model, has subtly different predictions about the pattern of savings expected during adaptation. For instance, the error sensitivity model would expect that the strength of savings in adaptation would scale with the amount of practice with the perturbation, even at asymptote, as random errors and a bias toward baseline continue to drive changes to the errors experienced. This was not evident in the data from this experiment, as the amount of savings observed was the same whether participants had merely reached asymptote or conducted many trials at asymptote. This finding was, however, consistent with an action-recall model, where the memory for actions would be established primarily during the initial period of adaptation where reward prediction error reduced the most, and that period would be the same regardless of

the time spent on asymptote. Explicit recall of actions, were that the mechanism, would also not necessarily expect for there to be different amounts of savings. Furthermore, the way in which savings would manifest would be expected to reflect a change in rate under the error-sensitivity model, but to appear more like an abrupt jump back to previously acquired reach directions in the action-recall model. We observed evidence for the latter in this experiment.

Thus, the evidence from this study point more towards an action recall model than a model for modification of error sensitivity, although additional experiments could help to bring more confidence to this conclusion. For instance, it is possible that the very rapid adaptation seen in this experiment (reaching baseline within 5 to 10 trials), and the limited ceiling for detecting differences in learning through savings might have made differentiating between the predictions of the two alternative models difficult. Another way to test which model appears to be more consistent is to have a condition that repeats the full range of errors experienced adapting to a given rotation from baseline many times. Under such conditions, the error sensitivity model would be expected to undergo even more drastic modification of error sensitivity which should be reflected in an even faster rate of relearning. The action recall model would instead continue to predict recall of the best previously attained reach direction. Another change that might make distinguishing between these two models more robust would be to increase the magnitude of the rotation from 30° to 45° or 60° to increase the dynamic range for detecting differences in the pattern of relearning.

Aside from the new evidence obtained from the experiments described in Chapter 3 and in the paper⁷¹, there is other evidence in support of an action-recall model. For instance, this model fits parsimoniously into the dual-system framework of learning and memory^{7,148}, in at least two ways. First, the memory for actions could be implicit or explicit, and in fact may undergo a transformation from one to the other depending on the amount of practice and prior experience. Secondly, the dual-system framework suggests that other, parallel mechanisms can act simultaneously and independently of the action-recall mechanism. Such a dual-component model is in fact well supported by data from other studies^{16,23,35,72,74,216}. In contrast, the error-sensitivity modification model does not parsimoniously accommodate the findings of process decomposition in adaptation. For instance, how would the error-sensitivity modification process account for the effects of limiting preparation-time or dividing attention during adaptation, i.e. why should it be sensitive to these manipulations? One of the assumptions behind the mechanism is that it is mediated in the cerebellum by a principled (i.e. inflexible) process of synaptic weight changes, so how could manipulations such as those affect it? The model is capable of fitting certain data quite well⁷⁰, but does not necessarily fit nicely into the broader picture of motor skill learning. For instance, another study, presented here in Chapter 4, further contradicts the error-sensitivity model of learning by demonstrating that recalibration in adaptation remains invariant with practice; i.e. that error-sensitivity does not change at all with experience. Furthermore, the study presented in Chapter 5 goes even further to demonstrate that even after providing much more practice

under the rotation, including repeating the initial phase of adaptation from baseline multiple times, still does not alter the error-sensitivity of the recalibration component of adaptation. These results, present in much greater detail below, fit parsimoniously with the action recall model, but much less so with an error-sensitivity-modification model.

The multiple components to adaptation learning

It appears that adaptation in visuomotor perturbation tasks is accomplished by at least two independent components. One component is implicit and sensitive to sensory prediction errors, while the other is deliberate and more sensitive to reward and failure^{16,23,44,71,74,216,217}. In Chapter 4, we asked which component of adaptation is responsible for savings. To do this, we first confirmed that manipulating the reaction time limits the expression of adaptation^{16,72,74}. The most parsimonious explanation for this finding is that a deliberate component, most likely explicit in nature, was prevented from influencing the reach direction on those trials that had limited preparation time, thereby limiting the full expression of adaptation that was demonstrated when the preparation time was longer. When we tested for savings using the same timed-response paradigm, adaptation was no different than the initial exposure when the preparation time was limited. Despite this lack of savings during Short-PT trials, there was significant savings when there were no restriction on the preparation time.

We concluded that savings for adaptation is supported by deliberate, explicit processing, because only when sufficient PT was made available was adaptation more complete and sensitive to prior experience, expressed as savings. The expression of cognitive, deliberative reasoning is thought to depend on the availability of sufficient preparation time^{169,218,219}. The distinction between a slow, deliberative component that takes into account more information, and a rapid, reflexive component that may be subject to more cognitive biases has been identified in many domains of human behavior²¹⁹. The two modes of operation have been called “System 1”, for the rapid but error-prone component, and “System 2”, for the slower, deliberative component²²⁰. These systems may account for the behavioral differences observed in adaptation learning from the modulation of preparation time; when PT is limited, System 1 is dominant and participants aim their reach directly towards the provided target. Any deviation from the target in these cases is attributable to implicit recalibration learning, which is driven by sensory-prediction error through a cerebellar-mediated mechanism^{125,133,176}. When there is sufficient PT, and no other sources of interference that may prevent the expression of System 2-like reasoning, adaptation is superior, taking into account the more optimal solution of reaching in a direction other than directly towards the displayed target and toward a goal that better cancels the rotation. Similar effects have previously been obtained either by manipulating the available PT in other ways^{16,72}, or in interrupting System 2 processing through dual tasking²²¹, or through startle^{222,223}.

I would speculate that the nature of the memory that is retained for adaptation is explicit, but the study presented in Chapter 4 and in Haith, et. al.⁷² did not directly test for this. It is, however, a parsimonious explanation, and would be consistent with the conclusions from other similar studies that do directly test the nature of the System 2-like component^{35,44}. If this were the case, it would also suggest that the nature of the memory recalled from the previous study, in Chapter 3, was also explicit. This conclusion calls into question the extent to which adaptation is a suitable model for motor skill learning, as many studies stake their conclusions and interpretations on the assumption that adaptation learning is a procedural, or motor, phenomenon^{38,59,224}. If, instead, adaptation learning is an implicit recalibration process that is insensitive to prior practice and contaminated by a cognitive recall phenomenon, or vice versa, many conclusions about skill learning may need to be reconsidered.

However, there may still be principles of motor skill learning hidden in adaptation paradigms. The studies presented so far have shown that adaptation is dissociable into automatic and deliberate components, and that savings, the best sign of long-term memory for adaptation, is supported by the deliberate component. However, motor skills usually require prolonged practice for substantive changes in behavior to be observed^{47,58,172,180}, sometimes called consolidation. It is possible that our first two studies did not provide sufficient practice for the mechanisms involved in skill learning to be expressed. We conducted a third study to discover if the memory supporting savings would ever undergo a transformation from being seemingly

explicit in nature to becoming automatic, or expressible under low latency. Another way to phrase this hypothesis is that consolidation through practice may transform responses from being mediated by System 2 to System 1. This is precisely the hypothesis tested in the experiments described in Chapter 5.

Caching of the explicit, but not the recalibration, components of adaptation

In Chapter 5, we detailed an experiment that provided participants with more practice of the visuomotor transformation, while testing for the dissociation of adaptation into its two components in two different ways. We manipulated the preparation time to test the low-latency response to the perturbation^{16,72}, and we used Aftereffect trials, in which participants were instructed to simply omit any aiming or deliberate compensation^{23,44}. We specifically sought to test whether deliberate compensation for the perturbation would undergo a transformation to being cached, rather than cognitively expensive, and thus expressible at low latency. Measuring the response to Aftereffect trials allowed us to further test whether the implicit recalibration component had also changed, and thus whether any savings in the Low-PT measurement could be attributed to a change in recalibration. If the Aftereffect trials did not change with experience, it would suggest that the recalibration component remains insensitive to practice and does not undergo any modification of its properties, at least not from the type and duration of training used in this study. This would also suggest that any savings in the Short-PT measurements were instead attributable to a process that allowed the deliberate component of learning to be expressed automatically, or become cached. We found

the latter; adaptation under Short-PT trials gradually showed savings, but it could not be attributed to modulation of the recalibration component because Aftereffect trials showed no savings.

These findings point to a model of motor learning where actions are initially represented and remembered explicitly, but that through practice, the representation changes to being cached, or automatic. Such a mechanism may be a critical step in the development of skill, because some tasks may require a minimum speed and accuracy of response in order to be successfully done. For instance, in ice-skating or skiing, certain maneuvers may be required within a certain amount of time to maintain balance and an upright posture, simply due to the physics of the task. Thus, if the appropriate actions become automatic and rapidly expressible, it may make certain tasks or behaviors possible that would not have been without that transformation.

There are at least two possible mechanisms to account for the transformation from deliberate to cached. It could be that deliberative processing forms a cognitive scaffold that shapes behavior in accordance with task goals and constraints. Under this model, behaviors may become cached through some implicit learning mechanism that operates on the movements that were directed by the cognitive scaffold. Declarative memory may assist in more rapidly recalling the scaffold, leading to savings even before an implicit memory is formed for it, but under this model a separate consolidation mechanism remains responsible for caching the

behavior. Alternatively, it could be that the processes that formed the cognitive scaffold become cached with practice, rather than the behaviors. A cognitive scaffold might be, for example, an explicit representation of the planned trajectory of movement²²⁵.

One possible way to differentiate between these two hypotheses would be to have participants cheat in a learning task by either being provided the scaffold without the need or ability to form it themselves, or by allowing participants to form the scaffold but then deprive them of practice in performing the full movement.

Whichever of these conditions leads to consolidation of behavior would reveal which of the two alternative processes, forming the scaffold or performing the actions, are necessary for consolidation. It also might be that both steps, forming the scaffold and executing the movements, are subject to becoming cached.

Whatever the case may be, the principle that behaviors are initially explicit in nature, recalled during repeated episodes of practice, and gradually cached through some mechanisms throughout practice appears to be a consistent explanation for both our observations and many others. These findings are, furthermore, not parsimoniously explained by the error-sensitivity-modification theory⁷⁰.

Our model is also broadly consistent with other findings. For instance, amnesic patients are able to learn so-called procedural skills even without explicit memory of the task^{5,6}. This has classically been considered as proof of the independence between memory for facts versus memory for skills⁷. However, those who

conducted the experiments using amnesic patients instructed the patients in what to do for the tasks each time they practiced them, eliminating the need for explicit memory recall and allowing them to practice the task despite their impairments. Under this arrangement, even amnesic patients improve at the tasks, such as mirror drawing⁵ and rotatory pursuit⁶. These findings were taken as proof of the independence of declarative from procedural memory⁷. However, when amnesic patients were trained in the use of arbitrary, novel objects, they were unable to recall how to use the objects without proper instruction²⁹. If, however, they had their hands placed in the correct initial configuration to use the objects, they could correctly execute the tool's intended actions. These results show that learning appropriate actions, for mirror drawing, rotatory pursuit, or arbitrary associations, is possible without functioning declarative memory, but that initiation of that behavior must be triggered somehow. When declarative memory is available, and participants know the goals of the behavior, they can self-initiate that behavior. When that knowledge is not available, such as in the amnesic patients, the initial state must be either provided or, presumably, arrived at coincidentally, in order for the correct behavior to be elicited. These findings give further evidence to the model of learning in which cognitive processing serves to build a scaffold that directs behavior in accordance with explicit task goals and constraints, and that practicing the actions resulting from having that scaffold results in consolidation of the necessary behavior.

As it pertains to our model, the appropriate response to counteract the perturbation is initially represented via declarative memory, being sensitive to the amount of preparation time available, and to other manipulations^{44,74,217}, but that practice gradually caches that response. When the same errors are encountered during subsequent exposures to the perturbation, the appropriate response is recalled rapidly. In this sense, the errors serve as a cue for recall, rather than as inputs to an inflexible recalibration mechanism. Our results demonstrate that error sensitivity of the recalibration component does not change with practice, but that of the deliberate component does, which, in a way, demonstrates a memory for errors, but not necessarily in the way that had been proposed in⁷⁰. I would predict that, were amnesic patients to participate in Experiment 1 from Chapter 5, they would exhibit normal learning behavior. This prediction in part stems from the fact that, while amnesic patients are severely impaired in declarative memory, they are not generally impaired at cognitive processing^{31,181,226,227}, and thus should be unimpaired at discovering the appropriate deliberative actions to counteract the rotation beyond the minimum adaptation provided through error-based recalibration. Practicing with the assistance of this cognitive scaffold should be sufficient to instill the kind of transformation that was observed in unimpaired participants, as previous studies have demonstrated that practice on asymptote can establish a set point for that behavior⁴².

Some additional questions remain regarding this model for learning. For instance, what is recalled during re-learning: an action, such as an absolute reach direction, or

a reach direction relative to the target? And is this representation different before and after it becomes cached? One possible way to investigate these questions would be to repeat Experiment 1 from Chapter 5, while including tests for generalization to different target directions throughout training. This would reveal whether absolute or relative actions are represented initially and after being cached, and whether those two differ, such as being represented relative to the target initially, but as an absolute reach direction after being cached.

Learning novel continuous-action behaviors by creating a feedback control policy

My final study attempted to explore the mechanisms of learning novel continuous action skills. To do this, we used a custom-built driving simulator video game and devised a novel task. Participants had to learn to navigate a virtual car along a narrow and winding path by tilting a tablet computer. At one of four times throughout practice, participants were tested on their ability to generalize their learning to a novel track. The Probe track was carefully selected to be match to the original, Training track for difficulty and other characteristics (such as the total number of sub-movements and the extent of those sub-movements), but also to have no overlapping segments, so that the actions required to navigate the Probe track were different from all sub-movements needed to navigate the Training track. The characteristics of learning and generalization in this experimental design allowed us to assess whether learning was achieved via a task-specific, or model-free, mechanism versus a flexible, model-based one, and whether there was any change in mechanism throughout practice.

We found that performance generalized almost completely to the Probe track, which suggested that a flexible, model-based mechanism must have been responsible for learning. Measuring performance in the game according to task success (the distance travelled along the track and the survival) suggested that performance during the probes dropped by about 10% from Day 3 and onward. The drop appeared to be invariant after Day 1, which suggested that the reason for the apparent drop in performance might be related to factors other than the ability to navigate the track. If the drop in performance were due to the existence of a learning mechanism that was task-specific, such as memorization of the actions to successfully navigate the Training track, the drop in performance should have grown with additional practice, from Days 3 to 10. However, this was not the case; the drop in performance was constant across training from Day 3 onward. Instead, we suggested that the drop in performance may be due to motivational factors, which are known to modulate performance regardless of the ability to actually execute a given action or maneuver^{22,204} (Figure 32). This conclusion was further supported by the finding that the kinematics of movement – variability among movements, the mean movement, and the policy deviation, - did not regress during the Probes. Thus, it appeared that, according to the kinematics, performance was fully generalized during the Probes. Instead of the kinematics regressing to a previous state of learning, the probability of any given trial being a failed trial increased. The way in which those trials failed did not change. This finding is

consistent with the hypothesis that the Probe trials modulated motivation, rather than changing the state of learning.

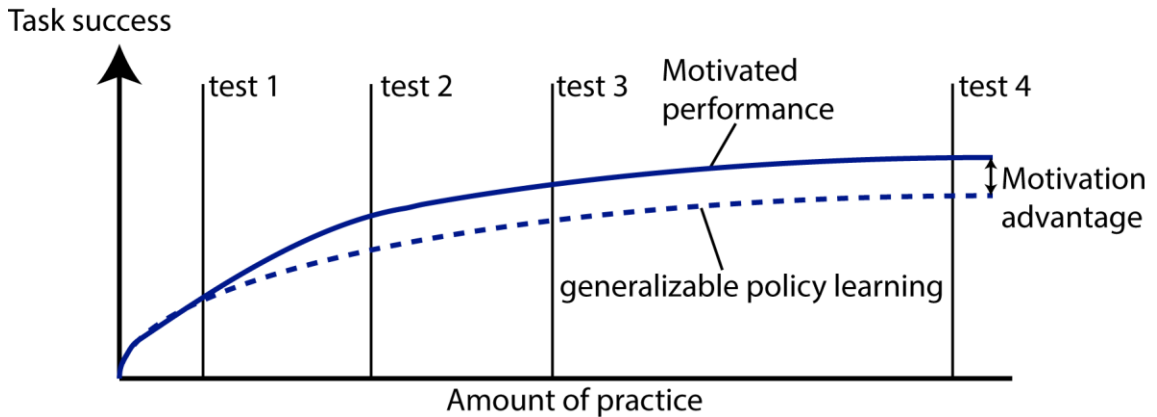


Figure 32: Model of performance with motivation modulation. It is possible that motivation, or possible other, non-skill related factors, can modulate performance when novel conditions are encountered.

These results are inconsistent with the action-sequencing⁵⁰ and chunking^{51,58,228} theories of skill learning, because performance generalized to a track that required different sequences of actions, and novel actions altogether. This finding will be disruptive to popular theories of learning and other concepts in neuroscience, as many studies assume that learning is achieved through action sequencing. Another consequence of this study is that it shows that measures of kinematics, like stereotypy of movements and improved feedback responses, do not imply a sequence learning or model-free mechanism of learning. We observed both increased movement stereotypy and generalization of behavior, two findings that would not necessarily be expected to co-occur.

We suggest that a better model for how novel, continuous-action behaviors, like the one studied here, are learned is through the creation of a flexible feedback control policy that maps states to actions^{66,198,199,224,229}. The idea that a representation of a policy exists for completion of a task is popular for explaining learning of discrete movements via feedforward control²²⁴, but the concept can also be applied to feedback control as well²⁰⁸⁻²¹⁰.

As a proof of concept, even a very simple control rule can reproduce our findings, thus demonstrating how a flexible controller that maps states to actions might be implemented (Figure 33). Assuming that participants can learn to aim the direction of their car toward an arbitrary goal along the track, simply aiming at the center of the track several steps ahead of the car's current location on the track can produce successful trajectories. Such a simple learning rule is consistent with the results from this study, as it would be fully generalizable to any new track, and it might be subject to errors when motivation or attention are modulated. Thus, it appears that learning continuous movement tasks such as the one devised for the study presented in Chapter 6 involve building a flexible feedback control policy rather than rote chunking or sequencing of actions.

It is worth noting that, while we did not directly test, measure, or evaluate the implicit-versus-explicit nature of learning in this task, the study represents a first step toward being able to answer more advanced questions regarding the nature of learning, including assessing the nature of memory for novel behaviors. For

instance, it would be interesting to test whether learning is mediated by a model-based or a model-free mechanism. This study refutes the idea that learning involved the rote memorization of actions, but it does not definitively determine how learning was done, and whether the mechanism or mechanisms involved were model-based vs. model-free. If the mechanism of learning had been model-based, it still may have been implicit, explicit, or a combination of the two, as was the case in adaptation. It is possible that the nature of the policy that was learned may have been initially explicit (e.g. "I shall aim several car-lengths ahead of where I am") and then transformed into being an implicit policy, such as aiming at a particular goal location ahead of the current state of the car without having to explicitly represent it.

This idea introduces additional questions regarding the relationship between explicit and implicit memory, and model-free versus model-based learning. Do there exist mechanisms for each combination of these phenomena, i.e. are there explicit and implicit model-free mechanisms and explicit and implicit model-based ones? It seems likely that each combination of these would exist. Do all such learning mechanisms begin as being explicit and transition, through practice, into being implicit, or could the opposite be true, that some behaviors are initially implicit, but with experience gradually rise to the level of conscious awareness, and thus become explicit? Such a phenomenon, where it to exist, might occur when expert practitioners at a behavior, such as a sport, come to have a detailed and explicit representation of the appropriate behavioral policies for that sport, like that which a

coach might have. It could even be that a behavioral policy is initially represented explicitly, becomes implicit through practice, and then later develops a second explicit representation, which might be different from the first and allow for new modifications of behavior. This may, in fact, be a general principle for how skills can continue to improve for many years, which appears to be the case in many human endeavors like sports, the arts, and trades²³⁰.

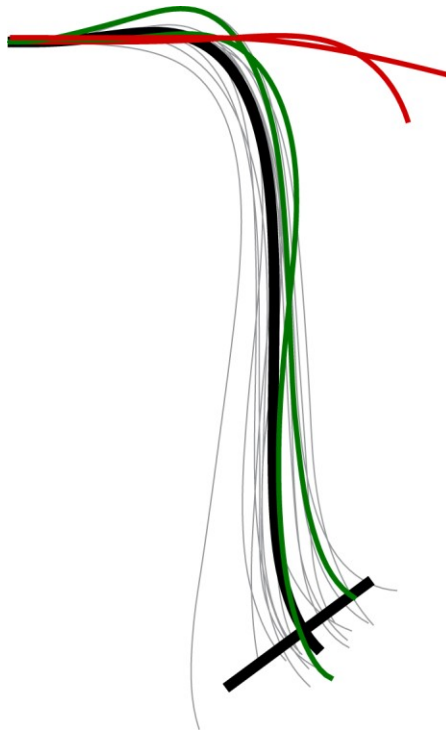


Figure 33: Proof-of-concept control policy. In this simulation, the filter that generates car kinematics from the tablet tilt signal was linearized. Traces in grey show car paths generated from tablet tilt data. The start of the path is at the upper left corner, and the end of the track segment is represented by the black bar that cuts perpendicular to the track's center (the bold black curve). Several synthetic car trajectories were created using a feedback policy that simply directed the tablet tilt direction towards the track's center just ahead of the present location of the car. Lapses in attention were simulated by breaks in policy updating of variable durations. Short breaks were tolerated well (Green traces), while longer breaks led to trajectories that would have fallen off of the track (Red traces). This simulation serves as a proof of concept for what form a feedback policy may take to produce plausible behavior. There was no need for a representation of the actions per se, only a policy for where to aim based on the state of the car.

This study also illustrates the difficulty in assessing behavior in motor skill tasks. For instance, evaluating performance through measures of task success produced one conclusion, while using measures of kinematics produced another. We concluded that the discrepancy between the two measures was accounted for through an effect of motivation^{22,204-206}. On one hand, this illustrates the importance of considering multiple perspectives of the data to draw more robust conclusions about behavior when so many possible outcomes exist. For instance, in a simple two-option forced choice task, there are fewer degrees of freedom to evaluate than in a movement task that generates continuous kinematics (although, as was discussed extensively for Chapters 3 – 5, aspects of behavior such as the reaction time may well be important considerations even for simpler behaviors like forced choice). On the other hand, our observation of the minor incongruence between performance as measured through task success versus kinematics demonstrates the potential folly of drawing concrete conclusions in complex psychophysical experiments when so many possible reasons exist for a particular phenomenon, and it is not always possible to control for each one. Furthermore, this introduces a deeper philosophical issue in the evaluation of complex systems, like human behavior, in general: is it even possible to study a system of interest when controls are applied to it. For instance, controlling factor A while measuring factor B, then control factor B while measuring factor A might produce different relationships between factors A and B because the systems are different when holding one factor constant versus the other. More concretely, and as an example, if we sought to eliminate the effect of motivation in our study, we might inadvertently change the

system sufficiently so as to make the measurements of performance incomparable to those measures taken when motivation was free to change. The resolution of such concerns is unclear, but will likely only be overcome through theoretical work that gradually, through continued failures to falsify, becomes more convincing. On a more practical note, one possible solution to avoiding potential confounds, like motivation, is to assess savings, or measuring differences in the rate of relearning. In that way, it might be possible to draw conclusions about models and mechanisms without altering the properties of the system being studied.

While I believe much has been learned from this study of continuous action learning, many questions and issues remain unresolved. For instance, the tests of generalization were relatively limited, and tested only the most strict interpretation of the action sequencing and chunking theories. How broad is the generalization function of this novel continuous-action skill, and what factors must remain constant for generalization to be robust? For instance, if a track with vastly different states than had been encountered during training were introduced, would performance be more affected? If a different context were tested, such as changing the background or the visual appearance of the character, but maintaining the same relationship between tablet tilt and car dynamics, would performance generalize? How would performance change if a different mapping were introduced, and how different must the mapping be for behavior to resemble truly naïve performance? This study only scratched the surface of studying novel continuous-movement skills, but represents a good first step toward answering these kinds of questions.

Unified theory of motor skill learning

The studies presented in this dissertation have provided evidence against certain assumptions and theories of learning, while demonstrating the plausibility of other hypotheses. With all that has been presented and discussed, it is worth outline a general conceptual model for how motor skills are learned, and to clarify how this model differs from popular models and assumptions that appear in contemporary literature, and what the consequences of this model are. I would like to begin by noting that I view skilled behavior as an emergent phenomenon, in the sense that there does not necessarily have to be a representation for every aspect of behavior. For instance, some characteristics of skilled behavior may be truly stochastic, brought about by random noise, or factors that are uncontrolled, like lapses in attention. Similarly, the generation of certain characteristics of behavior, such as seemingly complex kinematics, might actually have a low-information-content representation, much like the generation of fractals is achieved with very simple mathematical rules. Therefore, a suitably interesting and useful theory or model to “explain” skill learning could be as simple as describing the objects and processes needed to engender the behavior, along with the rules or patterns that describe how these objects and processes behave and interact.

I suggest that some minimum requirements for the ability engage in a skill include having a goal, the anatomy and controlled degrees of freedom to plausibly realize that goal, the impetus to act in order to obtain that goal, and a means of storing and representing a policy that plausibly could lead to attaining that goal. Learning, i.e. modifying in some principled way, any of these processes and objects, further requires the ability to retain the results of those modifications. This is not to say that having these characteristics alone implies that a given system is engaging in skilled behavior or skill learning, but rather than any skilled behavior and skill learning will have these characteristics at a minimum. Behavior is emergent from these minimum objects and processes when policies are executed through the controlled anatomy in pursuit of the given goal. Learning is emergent when any of these things are modified. This might include identifying a new, better goal, finding a policy that results in a better goal, obtaining the goal in a more efficient way, or making the tradeoff between cost and reward in the emergence of behavior overall more net positive.

In human skill and skill learning, it appears that goals can be concrete, such as a visual target, or abstract, such as striking the winning blow in a fencing match. They might be identified and selected in a way that requires cognitive processing, or they may be cached, or automatic, or even seemingly bestowed by nature, such as suckling. They can be subject to learning, with preferences for goals, especially relative to other possible goals in the environment, modifiable through experience or exogenous factors, like satiation.

I will leave considerable latitude in this model as to what may be considered a behavior policy. Something as simple as a decision to turn left, or to aim for a particular location in pursuit of a target may be enough to count as a policy. However, they may also be quite elaborate, including a detailed state-action policy map that includes a representation of an action for every possible state. The policy may be represented in any number of ways, implicitly, explicitly, requiring cognitive planning or being cached, even possibly any combination of these. It might be model-based, model-free, or some elaborate mixture. Without taking a strong stance on the requirements of the policy, there simply must be one that is sufficient to represent and maintain the actions minimally necessary to attain a given goal, and to be able to be modified.

Similarly, the impetus to attain a goal may be represented in any number of ways, and many studies have identified possible ways in which value, reward, effort, and cost are represented²³¹. However, the ability to perceive value in a goal that provides the driving force for acting on that goal must exist. Lastly, having the anatomy and appropriate control to achieve a goal is both necessary and rather obvious. A parrot could hardly be expected to wield an elephant's trunk skillfully, for example. While it may be possible for anatomy to be modifiable through experience, in the way athletes may develop more or different compositions of muscles through training, this type of modification should most likely not be included as necessary for skill learning. Modifiable control, however, may be a critical component of skill

learning, as new modes of control may need to be built in order to learn a novel behavior in a task, such as how children learn control of their limbs, or elephants learn control over their trunks (excluding for developmental reasons).

It is hard to imagine skilled behavior, or skill learning, without these characteristics, objects, and processes. There almost certainly is more that is required for learning to be considered skill learning. Likewise, there may be behaviors and learning mechanisms that have these characteristics which do not count as skilled behavior or skill learning. However, delineating these objects and processes represents a starting point for better defining what skilled behavior is, what it is not, and how it can be learned.

A remaining question is where the divide between learning and skill learning should be drawn. For instance, in the Introduction, Chapter 1, I made the claim that skill learning is uniquely human (or possibly shared only with a few rare mammalian apex predators, such as cetaceans or the great apes). Is this true, and if so, what additional processes or characteristics should be added to the list of minimum components to better describe skill learning? One possibility, to maintain the uniqueness of true skilled behavior from other processes, is that it must initially be represented declaratively. This would exclude behaviors like recalibration in adaptation, which is implicit and automatic²³, and many model-free, or reinforcement learning mechanisms, like developing a bias in a choice task on account of arbitrarily assigned value pairings. However, would such a definition

include developing a cached perturbation compensation strategy, as was shown in Chapter 5? Would it exclude to motor acuity learning²³, since the improvement in performance may have involved the implicit changing of action policies without experiencing any change in goal? These deeper conceptual questions remain to be explored.

Bibliography

1. Descartes, R. *Discourse on Method and the Meditations*. (Penguin UK, 2005).
2. Carter, B. & Charles, N. *Human and Other Animals: Critical Perspectives*. (Springer, 2011).
3. Shields, C. Aristotle's Psychology. in *The Stanford Encyclopedia of Philosophy* (ed. Zalta, E. N.) (Metaphysics Research Lab, Stanford University, 2016).
4. Cohen, N. J. & Squire, L. R. Preserved learning and retention of pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. *Science* **210**, 207–210 (1980).
5. Milner, B. Les troubles de la memoire accompagnant des lesions hippocampiques bilaterales. in *Physiologie de l'hippocampe* 257–272 (Centre National de la Recherche Scientifique, 1962).
6. Corkin, S. Acquisition of motor skill after bilateral medial temporal-lobe excision. *Neuropsychologia* **6**, 255–265 (1968).
7. Milner, B., Squire, L. R. & Kandel, E. R. Cognitive Neuroscience and the Study of Memory. *Neuron* **20**, 445–468 (1998).
8. Knowlton, B. J., Mangels, J. A. & Squire, L. R. A Neostriatal Habit Learning System in Humans. *Science* **273**, 1399–1402 (1996).
9. Scoville, W. B. & Milner, B. Loss of Recent Memory After Bilateral Hippocampal Lesions. *J. Neurol. Neurosurg. Psychiatry* **20**, 11–21 (1957).
10. Warrington, E. K. & Weiskrantz, L. A study of learning and retention in amnesic patients. *Neuropsychologia* **6**, 283–291 (1968).
11. Warrington, E. K. & Weiskrantz, L. Amnesic syndrome: Consolidation or retrieval? *Nature* **228**, 628–630 (1970).

12. Warrington, E. K. & Weiskrantz, L. The effect of prior learning on subsequent retention in amnesic patients. *Neuropsychologia* **12**, 419–428 (1974).
13. Packard, M. G., Hirsh, R. & White, N. M. Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: evidence for multiple memory systems. *J. Neurosci.* **9**, 1465–1472 (1989).
14. Nissen, M. J. & Bullemer, P. Attentional requirements of learning: Evidence from performance measures. *Cognit. Psychol.* **19**, 1–32 (1987).
15. Ap, G. & Jt, M. Cognitive spatial-motor processes. 1. The making of movements at various angles from a stimulus direction. *Exp. Brain Res.* **65**, 361–370 (1987).
16. Fernandez-Ruiz, J., Wong, W., Armstrong, I. T. & Flanagan, J. R. Relation between reaction time and reach errors during visuomotor adaptation. *Behav. Brain Res.* **219**, (2011).
17. Berns, G. S. & Sejnowski, T. J. A computational model of how the basal ganglia produce sequences. *J. Cogn. Neurosci.* **10**, 108–121 (1998).
18. Diedrichsen, J. & Kornysheva, K. Motor skill learning between selection and execution. *Trends Cogn. Sci.* **19**, 227–233 (2015).
19. Povel, D. J. & Collard, R. Structural factors in patterned finger tapping. *Acta Psychol. (Amst.)* **52**, 107–123 (1982).
20. Allen Newell & Rosenbloom, P. Mechanisms of skill acquisition and the law of practice. in *Cognitive Skills and their Acquisition* (ed. Anderson, J.) 1–51 (Lawrence Erlbaum Associates, Inc., 1981).
21. Yamaguchi, M. & Logan, G. D. Pushing typists back on the learning curve: Revealing chunking in skilled typewriting. *J. Exp. Psychol. Hum. Percept. Perform.* **40**, 592–612 (2014).

22. Wong, A. L., Lindquist, M. A., Haith, A. M. & Krakauer, J. W. Explicit knowledge enhances motor vigor and performance: motivation versus practice in sequence tasks. *J. Neurophysiol.* **114**, 219–232 (2015).
23. Mazzoni, P. & Krakauer, J. W. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J. Neurosci.* **26**, 3642–3645 (2006).
24. Schwabe, L. & Wolf, O. T. Stress Modulates the Engagement of Multiple Memory Systems in Classification Learning. *J. Neurosci.* **32**, 11042–11049 (2012).
25. Gordon, A. M., Westling, G., Cole, K. J. & Johansson, R. S. Memory representations underlying motor commands used during manipulation of common and novel objects. *J. Neurophysiol.* **69**, 1789–1796 (1993).
26. Nissen, M. J., Willingham, D. & Hartman, M. Explicit and implicit remembering: When is learning preserved in amnesia? *Neuropsychologia* **27**, 341–352 (1989).
27. Roediger, H. L. Implicit memory: Retention without remembering. *Am. Psychol.* **45**, 1043–1056 (1990).
28. Stanley, J. & Krakauer, J. W. Motor skill depends on knowledge of facts. *Front. Hum. Neurosci.* **7**, (2013).
29. Roy, S. & Park, N. W. Dissociating the memory systems mediating complex tool knowledge and skills. *Neuropsychologia* **48**, 3026–3036 (2010).
30. Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T. & Seidler, R. D. Contributions of spatial working memory to visuomotor learning. *J. Cogn. Neurosci.* **22**, 1917–1930 (2010).
31. Schacter, D. L. & Cooper, L. A. Implicit and explicit memory for novel visual objects: structure and function. *J. Exp. Psychol. Learn. Mem. Cogn.* **19**, 995–1009 (1993).
32. Sun, R., Slusarz, P. & Terry, C. The Interaction of the Explicit and the Implicit in Skill Learning: A Dual-Process Approach. *Psychol. Rev.* **112**, 159–192 (2005).

33. Brown, R. M. & Robertson, E. M. Off-Line Processing: Reciprocal Interactions between Declarative and Procedural Memories. *J. Neurosci.* **27**, 10468–10475 (2007).
34. Keisler, A. & Shadmehr, R. A shared resource between declarative memory and motor memory. *J. Neurosci.* **30**, 14817–14823 (2010).
35. Taylor, J. A., Krakauer, J. W. & Ivry, R. B. Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *J. Neurosci.* **34**, 3023–3032 (2014).
36. Kitago, T., Ryan, S. L., Mazzoni, P., Krakauer, J. W. & Haith, A. M. Unlearning versus savings in visuomotor adaptation: comparing effects of washout, passage of time, and removal of errors on motor memory. *Front. Hum. Neurosci.* **7**, (2013).
37. Lackner, J. R. & Lobovits, D. Adaptation to displaced vision: evidence for prolonged after-effects. *Q. J. Exp. Psychol.* **29**, 65–69 (1977).
38. Brashers-Krug, T., Shadmehr, R. & Bizzi, E. Consolidation in human motor memory. *Nature* **382**, 252–255 (1996).
39. Kojima, Y., Iwamoto, Y. & Yoshida, K. Memory of learning facilitates saccadic adaptation in the monkey. *J. Neurosci. Off. J. Soc. Neurosci.* **24**, 7531–7539 (2004).
40. Krakauer, J. W., Ghez, C. & Ghilardi, M. F. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neurosci. Off. J. Soc. Neurosci.* **25**, 473–478 (2005).
41. Zarah, E., Weston, G. D., Liang, J., Mazzoni, P. & Krakauer, J. W. Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J. Neurophysiol.* **100**, 2537–2548 (2008).
42. Huang, V. S., Haith, A., Mazzoni, P. & Krakauer, J. W. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* **70**, (2011).

43. Villalta, J. I., Landi, S. M., Flo, A. & Della-Maggiore, V. Extinction Interferes with the Retrieval of Visuomotor Memories Through a Mechanism Involving the Sensorimotor Cortex. *Cereb. Cortex N. Y. N 1991* (2013). doi:10.1093/cercor/bht346
44. Morehead, J. R., Qasim, S. E., Crossley, M. J. & Ivry, R. Savings upon Re-Aiming in Visuomotor Adaptation. *J. Neurosci.* **35**, 14386–14396 (2015).
45. Hadjiosif, A. & Smith, M. A. Savings is restricted to the temporally labile component of motor adaptation. (2013).
46. Kleim, J. A. *et al.* Cortical Synaptogenesis and Motor Map Reorganization Occur during Late, But Not Early, Phase of Motor Skill Learning. *J. Neurosci.* **24**, 628–633 (2004).
47. Wymbs, N. F. & Grafton, S. T. The Human Motor System Supports Sequence-Specific Representations over Multiple Training-Dependent Timescales. *Cereb. Cortex* **25**, 4213–4225 (2015).
48. Doyon, J., Penhune, V. & Ungerleider, L. G. Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia* **41**, 252–262 (2003).
49. Telgen, S., Parvin, D. & Diedrichsen, J. Mirror Reversal and Visual Rotation Are Learned and Consolidated via Separate Mechanisms: Recalibrating or Learning De Novo? *J. Neurosci.* **34**, 13768–13779 (2014).
50. Marr, D. A theory of cerebellar cortex. *J. Physiol.* **202**, 437–470.1 (1969).
51. Verwey, W. Concatenating familiar movement sequences: the versatile cognitive processor. *Acta Psychol. (Amst.)* **106**, 69–95 (2001).
52. Grol, M. J., de Lange, F. P., Verstraten, F. A. J., Passingham, R. E. & Toni, I. Cerebral changes during performance of overlearned arbitrary visuomotor associations. *J. Neurosci. Off. J. Soc. Neurosci.* **26**, 117–125 (2006).

53. Murray, E. A. & Wise, S. P. Role of the hippocampus plus subjacent cortex but not amygdala in visuomotor conditional learning in Rhesus monkeys. *Behav. Neurosci.* **110**, 1261–1270 (1996).
54. Shmuelof, L., Krakauer, J. W. & Mazzoni, P. How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *J. Neurophysiol.* **108**, 578–594 (2012).
55. Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P. & Smith, M. A. Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nat. Neurosci.* **17**, 312–321 (2014).
56. Cohen, R. G. & Sternad, D. Variability In Motor Learning: Relocating, Channeling and Reducing Noise. *Exp. Brain Res. Exp. Hirnforsch. Exp. Cerebrale* **193**, 69–83 (2009).
57. Manley, H., Dayan, P. & Diedrichsen, J. When money is not enough: awareness, success, and variability in motor learning. *PLoS One* **9**, (2014).
58. Kawai, R. *et al.* Motor Cortex Is Required for Learning but Not for Executing a Motor Skill. *Neuron* **86**, 800–812 (2015).
59. Shadmehr, R. Generalization as a Behavioral Window to the Neural Mechanisms of Learning Internal Models. *Hum. Mov. Sci.* **23**, 543–568 (2004).
60. Braun, D. A., Aertsen, A., Wolpert, D. M. & Mehring, C. Motor task variation induces structural learning. *Curr. Biol. CB* **19**, 352–357 (2009).
61. Goodbody, S. J. & Wolpert, D. M. Temporal and Amplitude Generalization in Motor Learning. *J. Neurophysiol.* **79**, 1825–1838 (1998).
62. Berniker, M., Mirzaei, H. & Kording, K. P. The effects of training breadth on motor generalization. *J. Neurophysiol.* **112**, 2791–2798 (2014).

63. Daw, N. D., Niv, Y. & Dayan, P. Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nat. Neurosci.* **8**, 1704–1711 (2005).
64. Schwitzgebel, E. Introspection. in *The Stanford Encyclopedia of Philosophy* (ed. Zalta, E. N.) (Metaphysics Research Lab, Stanford University, 2016).
65. Snoddy, G. s. Learning and stability: a psychophysiological analysis of a case of motor learning with clinical applications. *J. Appl. Psychol.* **10**, 1–36 (1926).
66. Shadmehr, R. & Mussa-Ivaldi, F. A. Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* **14**, 3208–3224 (1994).
67. Krakauer, J. W., Ghilardi, M.-F. & Ghez, C. Independent learning of internal models for kinematic and dynamic control of reaching. *Nat. Neurosci.* **2**, 1026–1031 (1999).
68. Criscimagna-Hemminger, S. E. & Shadmehr, R. Consolidation Patterns of Human Motor Memory. *J. Neurosci.* **28**, 9610–9618 (2008).
69. Krakauer, J. W. & Shadmehr, R. Consolidation of motor memory. *Trends Neurosci.* **29**, (2006).
70. Herzfeld, D. J., Vaswani, P. A., Marko, M. K. & Shadmehr, R. A memory of errors in sensorimotor learning. *Science* **345**, 1349–1353 (2014).
71. Huberdeau, D. M., Haith, A. M. & Krakauer, J. W. Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *J. Neurophysiol.* **114**, 969–977 (2015).
72. Haith, A. M., Huberdeau, D. M. & Krakauer, J. W. The Influence of Movement Preparation Time on the Expression of Visuomotor Learning and Savings. *J. Neurosci.* **35**, 5109–5117 (2015).
73. Taylor, J. A. & Thoroughman, K. A. Motor Adaptation Scaled by the Difficulty of a Secondary Cognitive Task. *PLoS ONE* **3**, e2485 (2008).

74. Benson, B. L., Anguera, J. A. & Seidler, R. D. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J. Neurophysiol.* **105**, 2843–2851 (2011).
75. Decker, J. H., Otto, A. R., Daw, N. D. & Hartley, C. A. From Creatures of Habit to Goal-Directed Learners: Tracking the Developmental Emergence of Model-Based Reinforcement Learning. *Psychol. Sci.* **27**, 848–858 (2016).
76. Franklin, D. W. & Wolpert, D. M. Specificity of reflex adaptation for task-relevant variability. *J. Neurosci. Off. J. Soc. Neurosci.* **28**, 14165–14175 (2008).
77. Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F. & Ghez, C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J. Neurosci.* **20**, 8916–8924 (2000).
78. Kording, K. P., Tenenbaum, J. B. & Shadmehr, R. The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nat. Neurosci.* **10**, 779–786 (2007).
79. van Beers, R. J. Motor learning is optimally tuned to the properties of motor noise. *Neuron* **63**, 406–417 (2009).
80. Redding, G. M. & Wallace, B. First-trial adaptation to prism exposure. *J. Mot. Behav.* **35**, 229–245 (2003).
81. Keisler, A. & Shadmehr, R. A shared resource between declarative memory and motor memory. *J. Neurosci. Off. J. Soc. Neurosci.* **30**, 14817–14823 (2010).
82. Taylor, J. A. & Ivry, R. B. Flexible cognitive strategies during motor learning. *PLoS Comput. Biol.* **7**, e1001096 (2011).
83. Taylor, J. A., Krakauer, J. W. & Ivry, R. B. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J. Neurosci.* **34**, 3023–3032 (2014).

84. Krakauer, J. W., Ghez, C. & Ghilardi, M. F. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neurosci. Off. J. Soc. Neurosci.* **25**, 473–478 (2005).
85. Xivry, J.-J. O. de & Lefèvre, P. Formation of model-free motor memories during motor adaptation depends on perturbation schedule. *J. Neurophysiol.* jn.00673.2014 (2015). doi:10.1152/jn.00673.2014
86. Kobak, D. & Mehring, C. Adaptation paths to novel motor tasks are shaped by prior structure learning. *J. Neurosci. Off. J. Soc. Neurosci.* **32**, 9898–9908 (2012).
87. Yousif, N. & Diedrichsen, J. Structural learning in feedforward and feedback control. *J. Neurophysiol.* **108**, 2373–2382 (2012).
88. Gonzalez Castro, L. N., Hadjiosif, A. M., Hemphill, M. A. & Smith, M. A. Environmental consistency determines the rate of motor adaptation. *Curr. Biol. CB* **24**, 1050–1061 (2014).
89. Medina, J. F., Garcia, K. S. & Mauk, M. D. A Mechanism for Savings in the Cerebellum. *J. Neurosci.* **21**, 4081–4089 (2001).
90. Smith, M. A., Ghazizadeh, A. & Shadmehr, R. Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol.* **4**, (2006).
91. Berniker, M. & Kording, K. Estimating the sources of motor errors for adaptation and generalization. *Nat. Neurosci.* **11**, 1454–1461 (2008).
92. Ajemian, R., D’Ausilio, A., Moorman, H. & Bizzi, E. Why professional athletes need a prolonged period of warm-up and other peculiarities of human motor learning. *J. Mot. Behav.* **42**, 381–388 (2010).
93. Haith, A. M., Huberdeau, D. M. & Krakauer, J. W. The influence of movement preparation time on the expression of visuomotor learning and savings. *J. Neurosci.* **In Press**, (2015).

94. Huberdeau, D. M., Krakauer, J. W. & Haith, A. M. Dual-process decomposition in human sensorimotor adaptation. *Curr. Opin. Neurobiol.* **33**, (2015).
95. Morehead, R., Crossley, M. & Ivry. Savings upon re-aiming in visuomotor adaptation. *Proc Transl. Comput. Mot. Control San Diego, CA*, (2013).
96. Joiner, W. M. & Smith, M. A. Long-term retention explained by a model of short-term learning in the adaptive control of reaching. *J. Neurophysiol.* **100**, 2948–2955 (2008).
97. Criscimagna-Hemminger, S. E. & Shadmehr, R. Consolidation patterns of human motor memory. *J. Neurosci. Off. J. Soc. Neurosci.* **28**, 9610–9618 (2008).
98. Marko, M. K., Haith, A. M., Harran, M. D. & Shadmehr, R. Sensitivity to prediction error in reach adaptation. *J. Neurophysiol.* **108**, 1752–1763 (2012).
99. Semrau, J. A., Daitch, A. L. & Thoroughman, K. A. Environmental experience within and across testing days determines the strength of human visuomotor adaptation. *Exp. Brain Res.* **216**, 409–418 (2012).
100. van der Kooij, K., Brenner, E., van Beers, R. J. & Smeets, J. B. J. Visuomotor Adaptation: How Forgetting Keeps Us Conservative. *PLoS ONE* **10**, (2015).
101. Vaswani, P. A. *et al.* Persistent Residual Errors in Motor Adaptation Tasks: Reversion to Baseline and Exploratory Escape. *J. Neurosci.* **35**, 6969–6977 (2015).
102. Wilson, R. C., Nassar, M. R. & Gold, J. I. A Mixture of Delta-Rules Approximation to Bayesian Inference in Change-Point Problems. *PLoS Comput. Biol.* **9**, (2013).
103. Pekny, S. E., Criscimagna-Hemminger, S. E. & Shadmehr, R. Protection and expression of human motor memories. *J. Neurosci. Off. J. Soc. Neurosci.* **31**, 13829–13839 (2011).
104. Stern, Y., Mayeux, R., Hermann, A. & Rosen, J. Prism adaptation in Parkinson's disease. *J. Neurol. Neurosurg. Psychiatry* **51**, 1584–1587 (1988).
105. Gutierrez-Garralda, J. M. *et al.* The effect of Parkinson's disease and Huntington's disease on human visuomotor learning. *Eur. J. Neurosci.* **38**, 2933–2940 (2013).

106. Leow, L.-A., de Ruyg, A., Loftus, A. M. & Hammond, G. Different mechanisms contributing to savings and anterograde interference are impaired in Parkinson's disease. *Front. Hum. Neurosci.* **7**, (2013).
107. Mongeon, D., Blanchet, P. & Messier, J. Impact of Parkinson's disease and dopaminergic medication on adaptation to explicit and implicit visuomotor perturbations. *Brain Cogn.* **81**, 271–282 (2013).
108. Marinelli, L. *et al.* Learning and consolidation of visuo-motor adaptation in Parkinson's disease. *Parkinsonism Relat. Disord.* **15**, 6–11 (2009).
109. Bédard, P. & Sanes, J. N. Basal ganglia-dependent processes in recalling learned visual-motor adaptations. *Exp. Brain Res.* **209**, 385–393 (2011).
110. Chiaravalloti, N. D. *et al.* The source of the memory impairment in Parkinson's disease: Acquisition versus retrieval. *Mov. Disord.* **29**, 765–771 (2014).
111. Costa, A. *et al.* Free and Cued Recall Memory in Parkinson's Disease Associated with Amnesic Mild Cognitive Impairment. *PLoS ONE* **9**, (2014).
112. Eichenbaum, H. A cortical–hippocampal system for declarative memory. *Nat. Rev. Neurosci.* **1**, 41–50 (2000).
113. Shmuelof, L., Krakauer, J. W. & Mazzoni, P. How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *J. Neurophysiol.* **108**, 578–594 (2012).
114. Karni, A. *et al.* The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U. S. A.* **95**, 861–868 (1998).
115. Reis, J. *et al.* Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 1590–1595 (2009).

116. Sampaio-Baptista, C. *et al.* Gray matter volume is associated with rate of subsequent skill learning after a long term training intervention. *NeuroImage* **96**, 158–166 (2014).
117. Fitts, Paul M. Perceptual Motor Skill Learning. in *Categories of Human Learning* (ed. Melton, A. W.) 244–83 (Academic Press Inc., 1964).
118. Anderson, J. Acquisition of cognitive skill. *Psychol. Rev.* **89**, (1982).
119. Flanagan, J. R. & Beltzner, M. A. Independence of perceptual and sensorimotor predictions in the size–weight illusion. *Nat. Neurosci.* **3**, 737–741 (2000).
120. Flanagan, J. R., Bittner, J. P. & Johansson, R. S. Experience Can Change Distinct Size-Weight Priors Engaged in Lifting Objects and Judging their Weights. *Curr. Biol.* **18**, 1742–1747 (2008).
121. Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J. & Thach, W. T. Throwing while looking through prisms. *Brain* **119**, 1199–1211 (1996).
122. Maschke, M., Gomez, C. M., Ebner, T. J. & Konczak, J. Hereditary Cerebellar Ataxia Progressively Impairs Force Adaptation During Goal-Directed Arm Movements. *J. Neurophysiol.* **91**, 230–238 (2004).
123. Smith, M. A. & Shadmehr, R. Intact Ability to Learn Internal Models of Arm Dynamics in Huntington’s Disease But Not Cerebellar Degeneration. *J. Neurophysiol.* **93**, 2809–2821 (2005).
124. Chen, H., Hua, S. E., Smith, M. A., Lenz, F. A. & Shadmehr, R. Effects of Human Cerebellar Thalamus Disruption on Adaptive Control of Reaching. *Cereb. Cortex N. Y. N* **16**, 1462–1473 (2006).
125. Tseng, Y., Diedrichsen, J., Krakauer, J. W., Shadmehr, R. & Bastian, A. J. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J. Neurophysiol.* **98**, 54–62 (2007).

126. Rabe, K. *et al.* Adaptation to Visuomotor Rotation and Force Field Perturbation Is Correlated to Different Brain Areas in Patients With Cerebellar Degeneration. *J. Neurophysiol.* **101**, 1961–1971 (2009).
127. Rabe, K. *et al.* Size–Weight Illusion, Anticipation, and Adaptation of Fingertip Forces in Patients With Cerebellar Degeneration. *J. Neurophysiol.* **101**, 569–579 (2009).
128. Synofzik, Matthis, Lindner, Axel & Thier, P. The cerebellum updates predictions about the visual consequences of one’s behavior. *Curr. Biol.* **18**, 814–8 (2008).
129. Taylor, J. A., Klemfuss, N. M. & Ivry, R. B. An Explicit Strategy Prevails When the Cerebellum Fails to Compute Movement Errors. *Cerebellum Lond. Engl.* **9**, 580–586 (2010).
130. Izawa, J. & Shadmehr, R. Learning from Sensory and Reward Prediction Errors during Motor Adaptation. *PLoS Comput. Biol.* **7**, (2011).
131. Izawa, J., Criscimagna-Hemminger, S. E. & Shadmehr, R. Cerebellar contributions to reach adaptation and learning sensory consequences of action. *J. Neurosci.* **32**, 4230–4239 (2012).
132. Wolpert, D. M. & Miall, R. C. Forward Models for Physiological Motor Control. *Neural Netw. Off. J. Int. Neural Netw. Soc.* **9**, 1265–1279 (1996).
133. Bastian, A. J. Learning to predict the future: the cerebellum adapts feedforward movement control. *Curr. Opin. Neurobiol.* **16**, 645–649 (2006).
134. Haith, A. M. & Krakauer, J. W. Model-Based and Model-Free Mechanisms of Human Motor Learning. *Adv. Exp. Med. Biol.* **782**, 1–21 (2013).
135. Saijo, N. & Gomi, H. Multiple Motor Learning Strategies in Visuomotor Rotation. *PLoS ONE* **5**, (2010).

136. Valls-Solé, J., Valdeoriola, F., Molinuevo, J. L., Cossu, G. & Nobbe, F. Prepulse modulation of the startle reaction and the blink reflex in normal human subjects. *Exp. Brain Res.* **129**, 49–56 (1999).
137. Wright, Z. A., Rogers, M. W., MacKinnon, C. D. & Patton, J. L. Startle stimuli reduce the internal model control in discrete movements. *Conf. Proc. Annu. Int. Conf. IEEE Eng. Med. Biol. Soc. IEEE Eng. Med. Biol. Soc. Annu. Conf.* **2009**, 4590–4594 (2009).
138. Wright, Z., Patton, J. L. & Ravichandran, V. Startle reduces recall of a recently learned internal model. *IEEE Int. Conf. Rehabil. Robot. Proc.* **2011**, 5975376 (2011).
139. Howard, I. S., Franklin, D. W., Ingram, J. N. & Wolpert, D. M. Gone in 0.6 seconds: The encoding of motor memories depends on recent sensorimotor states. *J. Neurosci. Off. J. Soc. Neurosci.* **32**, 12756–12768 (2012).
140. Stafford, T. *et al.* A Novel Task for the Investigation of Action Acquisition. *PLoS ONE* **7**, (2012).
141. Ghez, C. *et al.* Discrete and continuous planning of hand movements and isometric force trajectories. *Exp. Brain Res.* **115**, 217–233 (1997).
142. Pruszynski, J. A., Kurtzer, I. & Scott, S. H. Rapid Motor Responses Are Appropriately Tuned to the Metrics of a Visuospatial Task. *J. Neurophysiol.* **100**, 224–238 (2008).
143. Day, B. L. & Lyon, I. N. Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp. Brain Res.* **130**, 159–168 (2000).
144. van Sonderen, J. F., Denier van der Gon, J. J. & Gielen, C. C. Conditions determining early modification of motor programmes in response to changes in target location. *Exp. Brain Res.* **71**, 320–328 (1988).
145. Prablanc, C., Desmurget, M. & Gréa, H. Neural control of on-line guidance of hand reaching movements. *Prog. Brain Res.* **142**, 155–170 (2003).

146. Perfiliev, S., Isa, T., Johnels, B., Steg, G. & Wessberg, J. Reflexive limb selection and control of reach direction to moving targets in cats, monkeys, and humans. *J. Neurophysiol.* **104**, 2423–2432 (2010).
147. Unsworth, N., Spillers, G. J., Brewer, G. A. & McMillan, B. Attention control and the antisaccade task: a response time distribution analysis. *Acta Psychol. (Amst.)* **137**, 90–100 (2011).
148. Squire, L. R. Declarative and nondeclarative memory: multiple brain systems supporting learning and memory. *J. Cogn. Neurosci.* **4**, 232–243 (1992).
149. Dayan, P. Goal-directed control and its antipodes. *Neural Netw.* **22**, 213–219 (2009).
150. Knopman, D. & Nissen, M. J. Procedural learning is impaired in Huntington's disease: evidence from the serial reaction time task. *Neuropsychologia* **29**, 245–254 (1991).
151. Robertson, E. M. The Serial Reaction Time Task: Implicit Motor Skill Learning? *J. Neurosci.* **27**, 10073–10075 (2007).
152. Jackson, G. M., Jackson, S. R., Harrison, J., Henderson, L. & Kennard, C. Serial reaction time learning and Parkinson's disease: evidence for a procedural learning deficit. *Neuropsychologia* **33**, 577–593 (1995).
153. Yang, Y. & Lisberger, S. G. Role of plasticity at different sites across the time course of cerebellar motor learning. *J. Neurosci. Off. J. Soc. Neurosci.* **34**, 7077–7090 (2014).
154. Hikosaka, O. *et al.* Long-term retention of motor skill in macaque monkeys and humans. *Exp. Brain Res.* **147**, 494–504 (2002).
155. Nguyen-Vu, T. D. B. *et al.* Cerebellar Purkinje cell activity drives motor learning. *Nat. Neurosci.* **16**, 1734–1736 (2013).
156. Huang, V. S., Haith, A., Mazzoni, P. & Krakauer, J. W. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* **70**, (2011).

157. Turnham, E. J. A., Braun, D. A. & Wolpert, D. M. Facilitation of learning induced by both random and gradual visuomotor task variation. *J. Neurophysiol.* **107**, 1111–1122 (2012).
158. Leow, L.-A., de Rugy, A., Marinovic, W., Riek, S. & Carroll, T. J. Savings for visuomotor adaptation require prior history of error, not prior repetition of successful actions. *J. Neurophysiol.* **116**, 1603–1614 (2016).
159. McDougle, S. D., Ivry, R. B. & Taylor, J. A. Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends Cogn. Sci.* **20**, 535–544 (2016).
160. Anguera, J. A. *et al.* The effects of working memory resource depletion and training on sensorimotor adaptation. *Behav. Brain Res.* **228**, 107–115 (2012).
161. H, R. & SINGER, G. SENSORY ADAPTATION AND BEHAVIORAL COMPENSATION WITH SPATIALLY TRANSFORMED VISION AND HEARING. *Psychol. Bull.* **67**, 307–322 (1967).
162. Plihal, W. & Born, J. Effects of Early and Late Nocturnal Sleep on Declarative and Procedural Memory. *J. Cogn. Neurosci.* **9**, 534–547 (1997).
163. Karpicke, J. D. & Roediger, H. L. The Critical Importance of Retrieval for Learning. *Science* **319**, 966–968 (2008).
164. James, W. *Habit*. (H. Holt, 1890).
165. Sutton, R. S. & Barto, A. G. *Introduction to reinforcement learning*. (MIT Press, 1998).
166. Fitts, Paul M. Perceptual-Motor Skill Learning. *Categ. Hum. Learn.* 243–85 (1964).
167. Eldridge, L. L., Masterman, D. & Knowlton, B. J. Intact implicit habit learning in Alzheimer’s disease. *Behav. Neurosci.* **116**, 722–726 (2002).
168. Stanley, J. & Krakauer, J. W. Motor skill depends on knowledge of facts. *Front. Hum. Neurosci.* **7**, 503 (2013).

169. Frederick, S. Automated choice heuristics. in *Heuristics and biases: The psychology of intuitive judgment* (eds. Gilovich, T., Griffin, D. & Kahneman, D.) 548–558 (Cambridge University Press, 2002).
170. Bryan, W. L. & Harter, N. Studies in the physiology and psychology of the telegraphic language. *Psychol. Rev.* **4**, 27–53 (1897).
171. Kimble, G. A. & Perlmutter, L. C. The problem of volition. *Psychol. Rev.* **77**, 361–384 (1970).
172. Martel, G. *et al.* Dynamic interplays between memory systems depend on practice: the hippocampus is not always the first to provide solution. *Neuroscience* **150**, 743–753 (2007).
173. Bourne, L. E. *Human conceptual behavior*. (Allyn an Bacon, 1966).
174. Li, J. X., Medina, J. F., Frank, L. M. & Lisberger, S. G. Acquisition of neural learning in cerebellum and cerebral cortex for smooth pursuit eye movements. *J. Neurosci. Off. J. Soc. Neurosci.* **31**, 12716–12726 (2011).
175. Diedrichsen, J., Verstynen, T., Lehman, S. L. & Ivry, R. B. Cerebellar Involvement in Anticipating the Consequences of Self-Produced Actions During Bimanual Movements. *J. Neurophysiol.* **93**, 801–812 (2005).
176. Butcher, P. *et al.* Cerebellar degeneration disrupts adaptation and strategy use in sensorimotor learning. *Proc Transl. Comput. Mot. Control* **San Diego, CA**, (2014).
177. Xu-Wilson, M., Chen-Harris, H., Zee, D. S. & Shadmehr, R. Cerebellar contributions to adaptive control of saccades in humans. *J. Neurosci. Off. J. Soc. Neurosci.* **29**, 12930–12939 (2009).
178. Ito, M. Control of mental activities by internal models in the cerebellum. *Nat. Rev. Neurosci.* **9**, 304–313 (2008).

179. Berry, D. C. & Broadbent, D. E. Interactive tasks and the implicit-explicit distinction. *Br. J. Psychol.* **79**, 251–272 (1988).
180. Fitts, P. & Posner, M. *Human performance*.
181. Schacter, D. L., Wang, P. L., Tulving, E. & Freedman, M. Functional retrograde amnesia: A quantitative case study. *Neuropsychologia* **20**, 523–532 (1982).
182. Squire, L. R. & Zola, S. M. Episodic memory, semantic memory, and amnesia. *Hippocampus* **8**, 205–211 (1998).
183. Tulving, E. Memory and consciousness. *Can. Psychol. Can.* **26**, 1–12 (1985).
184. Spencer, R. M. C., Zelaznik, H. N., Diedrichsen, J. & Ivry, R. B. Disrupted Timing of Discontinuous But Not Continuous Movements by Cerebellar Lesions. *Science* **300**, 1437–1439 (2003).
185. Morasso, P., Ivaldi, F. A. M. & Ruggiero, C. How a discontinuous mechanism can produce continuous patterns in trajectory formation and handwriting. *Acta Psychol. (Amst.)* **54**, 83–98 (1983).
186. Bottaro, A., Yasutake, Y., Nomura, T., Casadio, M. & Morasso, P. Bounded stability of the quiet standing posture: An intermittent control model. *Hum. Mov. Sci.* **27**, 473–495 (2008).
187. Mueller, H. & Sternard, D. Decomposition of Variability in the Execution of Goal-Oriented Tasks: Three Components of Skill Improvement. (2004). Available at: <http://psycnet.apa.org/?&fa=main.doiLanding&doi=10.1037/0096-1523.30.1.212>. (Accessed: 18th June 2016)
188. Guo, J.-Z. *et al.* Cortex commands the performance of skilled movement. *eLife* **4**, e10774 (2015).

189. Ranganathan, R., Wieser, J., Mosier, K. M., Mussa-Ivaldi, F. A. & Scheidt, R. A. Learning redundant motor tasks with and without overlapping dimensions: facilitation and interference effects. *J. Neurosci. Off. J. Soc. Neurosci.* **34**, 8289–8299 (2014).
190. Davids, K., Bennett, S. & Newell, K. M. *Movement System Variability*. (Human Kinetics, 2006).
191. Eliassen, J. C., Souza, T. & Sanes, J. N. Experience-Dependent Activation Patterns in Human Brain during Visual-Motor Associative Learning. *J. Neurosci.* **23**, 10540–10547 (2003).
192. Willingham, D. B., Salidis, J. & Gabrieli, J. D. E. Direct Comparison of Neural Systems Mediating Conscious and Unconscious Skill Learning. *J. Neurophysiol.* **88**, 1451–1460 (2002).
193. Karni, A. *et al.* The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U. S. A.* **95**, 861–868 (1998).
194. Ramkumar, P. *et al.* Chunking as the result of an efficiency computation trade-off. *Nat. Commun.* **7**, 12176 (2016).
195. David A. Rosenbaum, Richard A. Carlson & Gilmore, and R. O. Acquisition of Intellectual and Perceptual-Motor Skills. *Annu. Rev. Psychol.* **52**, 453–470 (2001).
196. Korman, M., Raz, N., Flash, T. & Karni, A. Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 12492–12497 (2003).
197. Kawato, M. Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* **9**, 718–727 (1999).
198. Kobak, D. & Mehring, C. Adaptation Paths to Novel Motor Tasks Are Shaped by Prior Structure Learning. *J. Neurosci.* **32**, 9898–9908 (2012).

199. Thoroughman, Kurt A. & Shadmehr, R. Learning of action through adaptive combinations of motor primitives. *Nature* **407**, 742–7 (2000).
200. Holm, S. A Simple Sequentially Rejective Multiple Test Procedure. *Scand. J. Stat.* **6**, 65–70 (1979).
201. Csibra, G. Teachers in the wild. *Trends Cogn. Sci.* **11**, 95–96 (2007).
202. Caro, T. M. & Hauser, M. D. Is there teaching in nonhuman animals? *Q. Rev. Biol.* **67**, 151–174 (1992).
203. Daw, N. D., Niv, Y. & Dayan, P. Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nat. Neurosci.* **8**, 1704–1711 (2005).
204. Mazzoni, P., Hristova, A. & Krakauer, J. W. Why Don't We Move Faster? Parkinson's Disease, Movement Vigor, and Implicit Motivation. *J. Neurosci.* **27**, 7105–7116 (2007).
205. Tanaka, H., Krakauer, J. W. & Qian, N. An Optimization Principle for Determining Movement Duration. *J. Neurophysiol.* **95**, 3875–3886 (2006).
206. Niv, Y., Joel, D. & Dayan, P. A normative perspective on motivation. *Trends Cogn. Sci.* **10**, 375–381 (2006).
207. Treisman, A. & Geffen, G. Selective attention: Perception or response? *Q. J. Exp. Psychol.* **19**, 1–17 (1967).
208. Nashed, J. Y., Crevecoeur, F. & Scott, S. H. Rapid Online Selection between Multiple Motor Plans. *J. Neurosci.* **34**, 1769–1780 (2014).
209. Todorov, E. & Jordan, M. I. Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* **5**, 1226–1235 (2002).
210. Hadjiosif, A. M. & Smith, M. A. Flexible Control of Safety Margins for Action Based on Environmental Variability. *J. Neurosci. Off. J. Soc. Neurosci.* **35**, 9106–9121 (2015).

211. Dickinson, A. Actions and Habits: The Development of Behavioural Autonomy. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **308**, 67–78 (1985).
212. Dolan, R. J. & Dayan, P. Goals and Habits in the Brain. *Neuron* **80**, 312–325 (2013).
213. Cushman, F. & Morris, A. Habitual control of goal selection in humans. *Proc. Natl. Acad. Sci.* 201506367 (2015). doi:10.1073/pnas.1506367112
214. Taylor, J. A. & Ivry, R. B. The role of strategies in motor learning. *Ann. N. Y. Acad. Sci.* **1251**, 1–12 (2012).
215. Krakauer, J. W., Carmichael, S. T., Corbett, D. & Wittenberg, G. F. Getting Neurorehabilitation Right: What Can Be Learned From Animal Models? *Neurorehabil. Neural Repair* **26**, 923–931 (2012).
216. Huberdeau, D. M., Krakauer, J. W. & Haith, A. M. Dual-process decomposition in human sensorimotor adaptation. *Curr. Opin. Neurobiol.* **33**, 71–77 (2015).
217. Hadjiosif, A. M. & Smith, M. A. Savings is restricted to the temporally labile component of motor adaptation. *Proc. Transl. Comput. Mot. Control San Diego, CA*, (2013).
218. Kahneman, D. *Thinking, fast and slow*. (Macmillan, 2011).
219. Frederick, S. Cognitive Reflection and Decision Making. *J. Econ. Perspect.* **19**, 25–42 (2005).
220. Stanovich, K. E. & West, R. F. Individual differences in reasoning: implications for the rationality debate? *Behav. Brain Sci.* **23**, 645-665-726 (2000).
221. Taylor, J. A. & Thoroughman, K. A. Divided attention impairs human motor adaptation but not feedback control. *J. Neurophysiol.* **98**, 317–326 (2007).
222. Hackley, S. A. The speeding of voluntary reaction by a warning signal. *Psychophysiology* **46**, 225–233 (2009).
223. Hackley, S. A. & Valle-Inclán, F. Which stages of processing are speeded by a warning signal? *Biol. Psychol.* **64**, 27–45 (2003).

224. Imamizu, H. *et al.* Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* **403**, 192–195 (2000).
225. Wong, A. L., Haith, A. M. & Krakauer, J. W. Motor Planning. *Neurosci. Rev. J. Bringing Neurobiol. Neurol. Psychiatry* **21**, 385–398 (2015).
226. Squire, L. R. & Zola, S. M. Structure and function of declarative and nondeclarative memory systems. *Proc. Natl. Acad. Sci.* **93**, 13515–13522 (1996).
227. Tulving, E. How many memory systems are there? *Am. Psychol.* **40**, 385–398 (1985).
228. Diedrichsen, Jorn. Motor skill learning between selection and execution. *Trends Cogn. Sci.* **19**, (2015).
229. Shadmehr, R., Smith, M. A. & Krakauer, J. W. Error correction, sensory prediction, and adaptation in motor control. *Annu. Rev. Neurosci.* **33**, (2010).
230. Ericsson, A. & Pool, R. *Peak: Secrets from the New Science of Expertise*. (MARINER BOOKS, 2016).
231. Shadmehr, R., Huang, H. J. & Ahmed, A. A. A Representation of Effort in Decision-Making and Motor Control. *Curr. Biol.* **26**, 1929–1934 (2016).

Curriculum Vitae

Education

Ph.D. Candidate, Biomedical Engineering
The Johns Hopkins University
Baltimore, MD
Aug. 2010 – Present

B.S., Biomedical Engineering
The Johns Hopkins University
Baltimore, MD
Sept. 2006 – May, 2010

Work Experience

- Johns Hopkins Applied Physics Lab 06/2009 – 08/2009
Columbia, MD
National Security Technology Department, Biomedicine
Intern
I implemented a real-time signal-processing algorithm for a robotic upper- limb prosthesis that was developed for the DARPA Revolutionizing Prosthetics program.

- Johns Hopkins Applied Physics Lab 06/2008 – 08/2008
Columbia, MD
National Security Technology Department, Biomedicine
Intern
I implemented data logging and experiment-control software for a model-based design tool that allowed real-time simulation of a robotic arm.

- American Red Cross 06/2007 – 08/2007
Washington, DC
Biomedical Services Division, Presidential Intern
I presented findings and recommendations from a Six-Sigma study of internal document control processes.

- National Institutes of Health
Bethesda, MD
PET Radiopharmaceutical Sciences, Intramural Research
Intern
I tested micro-reactor designs and compared their synthesis yields
to conventional protocols.

06/2006 – 08/2006

Refereed Publications

- **Huberdeau D. M.**, Haith A.M., Krakauer J.W. Formation of a long-term motor memory after only a few trials of practice. *J. Neurophysiol.* 114(2):969-77, 2015.
- Haith, A. M., **Huberdeau, D. M.**, Krakauer, J. W. The influence of movement preparation time on the expression of visuomotor learning and savings. *J. Neurosci.* 35(13):5109-5117, 2015.
- Haith A.M., **Huberdeau D.M.**, Krakauer J.W. Hedging your bets: Intermediate movements as optimal behavior in the context of an incomplete decision. *PLoS Comput. Biol.* 11(3): e1004171, 2015.
- **Huberdeau D.M.**, Walker H., Huang H., Montgomery E., Sarma SV. Analysis of local field potential signals: a systems approach. *Conf Proc IEEE Eng Med Biol Soc.* 2011:814-7, 2011.
- Smith R.J., **Huberdeau D.M.**, Tenore F., Thakor N.V. Real-Time Myoelectric Decoding of Individual Finger Movements for a Virtual Target Task. *Conf Proc IEEE Eng Med Biol Soc.* 2009:2376-79, 2009.
- Smith R.J., Tenore F., **Huberdeau D.M.**, Thakor N.V. Continuous Decoding of Finger Position from Surface EMG Signals for Control of Powered Prostheses. *Conf Proc IEEE Eng Med Biol Soc.* 2008:197-200, 2008.

Submitted or In-preparation

- **Huberdeau D.M.**, Haith A.M., Krakauer J.W. Dissecting learning and generalization of a continuous motor skill with a novel video game. *In preparation.*

- **Huberdeau D.M.**, Krakauer J.W., Haith A.M. Practice induces a qualitative change in the memory supporting savings for visuomotor learning. *In preparation*.

Reviews

- **Huberdeau D.M.**, Krakauer J.W., Haith A.M. Dual processes and decomposition in human sensorimotor adaptation. *Curr Opin in Neurobiol.* 33:71-77, 2015.

Patent Submissions

- Hoi, Jennifer; Luong, Eli; Rupperecht, Laura; Medina, Christine; **Huberdeau, David**; Chao, Joe; Harran, Michelle; Acharya, Soumyadipta. 2008. Surgical Metal Detection Apparatus and Methods. Patent Application 20080294036, filed Nov. 27, 2008. *Patent Pending*.

Conferences & Presentations

- Society for Neuroscience Annual Meeting. Chicago, IL. October 2015: *Proceduralization of declarative knowledge in a motor adaptation task following prolonged training*. Poster presentation.
- Neural Control of Movement Conference. Charleston, SC. April 2015: *The relationship between task specificity and training duration for a novel video gaming skill*. Poster presentation.
- Johns Hopkins University Sensory Motor Research Day. Baltimore, MD. December 2014: *The curse of task-specificity in motor skill learning*. Podium presentation.
- Society for Neuroscience Annual Meeting. Washington, DC. November 2014: *Long-term learning in adaptation paradigms: Cognitive versus motor memory*. Poster presentation.

- Society for Neuroscience Annual Meeting. Washington, DC. November 2014: *The curse of task specificity: Skill becomes more task specific with practice*. Poster presentation.
- Motor Control and Rehabilitation: A Collaborative Johns Hopkins University - University College London Meeting. Baltimore, MD. September 2014: *Procedural Versus Declarative Motor Memory*. Podium presentation.
- Society for Neuroscience Annual Meeting. San Diego, CA. November 2013: *Model-free reinforcement of learned movements is invariant to exposure duration*. Poster presentation.
- Society for Neuroscience Annual Meeting. New Orleans, LA. October 2012: *Continuous and discrete re-planning of reaching movements following abrupt changes to task goals*. Poster presentation.
- Neural Control of Movement Conference. Venice, Italy. April 2012: *Behavioral insights into neural mechanisms of movement planning: Continuous and abrupt updating of a motor plan following changes in task goals*. Poster presentation.
- Engineering in Medicine and Biology Society Annual Conference (EMBC). Boston, MA. August 2011: *Analysis of Local Field Potential Signals: A Systems Approach*. Podium presentation.
- Biomedical Engineering Society Annual Meeting. Pittsburgh, PA. October 2009: *Independent Linear Classification of Forearm Myoelectric Signals for the Control of a Multi-Fingered Prosthetic Hand with Reduced System Training Requirements*. Poster presentation.
- Decisions and Controls Conference. Cancun, Mexico. December 2008: *Real-time Myoelectric Signal Processing for Control of Dexterous Virtual Prostheses*. Workshop presentation.
- Engineering in Medicine and Biology Society Annual Conference (EMBC). Vancouver, BC. August 2008: *Continuous Decoding of Finger Positions from Surface EMG Signals for the Control of Powered Prostheses*. Workshop presentation.

- Northeast Bioengineering Conference. Providence, RI. April 2008: *Real-time Finger Tracking to Improve Upper-Limb Prosthetics Control*. Podium presentation.

Research Experience

- Brain, Learning, Animation, and Movement (BLAM) Lab 08/2011 – 05/2017
(expected)
 PI: John W. Krakauer
 Johns Hopkins University, Baltimore, MD
 I studied human cognition, movement, and learning. I designed custom-built video games to study computational mechanisms of longitudinal motor learning. I performed psychophysical studies and analyzed movement kinematics. I published three journal articles, one review article, and have two journal articles in preparation.
- Neuromedical Control Systems Lab 11/2010 – 4/2011
 PI: Sridevi Sarma
 Johns Hopkins University, Baltimore, MD
 I developed a computational model as a tool to detect differences in neural firing patterns between affected and unaffected regions of the globus pallidus in human dystonia patients.
- Vestibular Neuroengineering Laboratory 07/2010 – 11/2010
 PI: Charles Della Santina
 Johns Hopkins University, Baltimore, MD
 I conducted experiments to test methods of stimulating the vestibulocochlear nerve with an infrared laser in chinchillas.
- JHU Neuroengineering and Biomedical Instrumentation Lab 09/2007 – 10/2009
 PI: Nitish Thakor
 Johns Hopkins University, Baltimore, MD
 I built software for a sensor-laden glove that measured finger joint angles in real time. I developed signal-processing algorithms for control of a dexterous upper-limb prosthetic device. I published two refereed articles.

Design Experience

- Biomedical Engineering Design Team, Team Leader 09/2009 – 05/2010
Mentor: Dr. Harikrishna Tandri

Johns Hopkins University, Baltimore, MD

I led a team of ten students to design the Rapid Hypothermia Induction Device, a device intended to induce hypothermia in cardiac arrest patients to mitigate hypoxic brain damage. I served as project manager, led the conceptual design of the device, led proof of concept testing, served as spokesman, and applied for funding grants. My team won a \$500 funding grant, a \$10,000 national prize, and two prizes at the Johns Hopkins Design Day competition.

- Biomedical Engineering Design Team, Team Member 01/2007 – 05/2007
Mentor: Dr. Lew Schon

Johns Hopkins University, Baltimore, MD

The team designed a surgical metal detector instrument to assist removing orthopedic screws. I designed, prototyped, and tested the metal detecting circuit, managed the fabrication of the hardware, and delivered team presentations to judging panels. The team won a prize at the Johns Hopkins Design Day competition and applied for a patent for the device.

Teaching Experience

- Teaching assistant for the Center for Biomedical Innovation and Design (CBID) 06/2013 – 05/2014

Review Services

- Served as reviewer for Experimental Brain Research. 08/2012

Affiliations/Memberships

- Member, Society of Neuroscience 2012 - Present

Honors and Awards

- National Collegiate Inventors and Innovators Alliance \$500 stipend 2010
- Johns Hopkins University Design Day Audience Choice Award 2010
- Johns Hopkins University Design Day Second Place Prize 2010
- National Collegiate Inventors and Innovators Alliance \$10,000 BMEidea prize 2010
- Johns Hopkins University Provost Undergraduate Research Award 2008
- Fort Detrick Society of American Military Engineers Scholarship 2007

Skills

- Experiment design
- Motion capture and movement analysis
- Human behavior modeling
- Statistics
- Matlab and Simulink
- Written and oral communications