

Factors impacting the time course of visuomotor reach adaptation

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Abstract

Reaching with altered visual feedback leads to adaptation of internal motor plans, which result in aftereffects, deviated reaching without visual feedback, and proprioceptive recalibration, a shift in perceived hand location (Cressman & Henriques, 2010). However, the rate or speed by which these implicit motor and sensory changes emerge and how this timecourse may be affected by the quality of the feedback during training has yet to be investigated. In a series of experiments, I looked at the speed and size of implicit changes, specifically reach aftereffects and shifts in felt hand position, how fast they emerge and how they vary as a function of the quality of error signals and certainty of the rotation during training. In the first experiment, participants had full access to error signals during training with altered visual feedback of their hand, and during this training, reach aftereffects, and active and passive hand localizations were measured after every single reach-training trial. This gave us a baseline of how fast these implicit components shifted during 'classic' training. Shifts in felt hand position reached saturation within one trial and reach aftereffects also reached saturation within three trials of visuomotor rotation training which is much faster than previously believed. In the second experiment we reduced error signal information during training by removing the hand cursor until the reach movement was complete or by constraining hand movements along a channel, so the cursor always went straight to the target. The goal was to investigate if and to what extent these error signals affected the timecourse of proprioceptive recalibration. Despite this reduction, we could not detect a decrease in the rate or

size of shifts in felt hand position, indicating the robustness and invariance of these visually-induced changes in proprioceptive estimates. In the third and final experiment, we reduced certainty in the rotation by changing it every 12 trials and still measured estimates of felt hand position on a trial-by-trial basis. We once again found shifts in felt hand position in the expected size and direction that peaked just as fast as the previous experiments, indicating that proprioceptive recalibration is a consistent aspect of reach adaptation to altered visual feedback. The rapid speed by which saturation is attained may also suggest that shifts in proprioceptive recalibration may be a driving factor in reach adaptation, as it saturates far earlier than adaptation does.

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Chapter 1: General Introduction

Humans are mobile beings that have evolved the ability to make specialized hand movements that are precise and varied. With the variety of ways we can move, reaching movements have received a lot of research attention as they are similar across individuals. In order to accurately move our hands to an object, we must integrate sensory signals concerning target location and proprioceptive information regarding the arm and hands relative positions, as illustrated in Fig 1.1 (Van Beers et al., 2002).

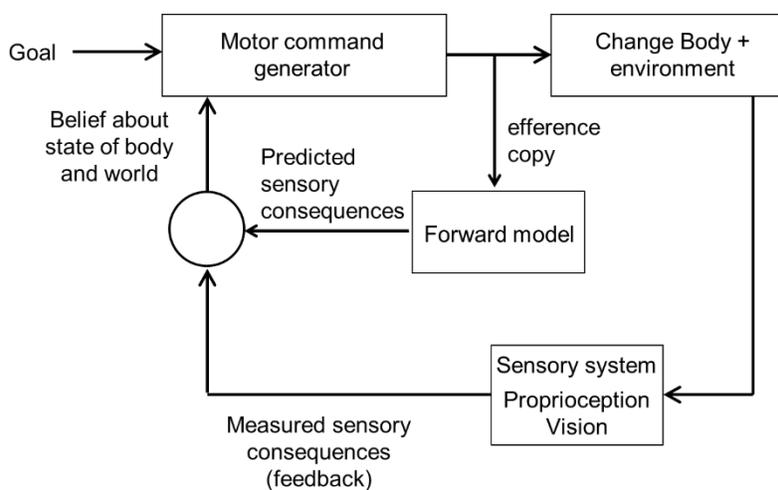


Figure 1.1 Connection between motor commands and sensory consequences of arm movements. When visual and proprioceptive information correspond our actual and predicted sensory consequences match and the motor command is not adjusted. When there is discrepancy between the efference copy and actual sensory consequences of the movement then the motor command is updated.

Visual and proprioceptive information ordinarily correspond with each other, but there are times when our senses do not match. When this is the case, we typically rely more on vision than proprioception (Van Beers et al., 2002). Creating a mismatch between visual and proprioceptive sensory information allows us to investigate how humans account for these discrepancies.

When reaching to a visual target, these movements show consistently straight trajectories with a bell-shaped velocity curve (Kalaska et al., 1997; Shadmehr &

Krakauer, 2008). Even when the hand is perturbed during reaches, participants will still try to achieve this straight trajectory by adapting their reaching movements. In a lab setting, this misalignment between the direction of movement of the hand and cursor during reach movement is called visuomotor rotation, as illustrated in Fig 2.1B. This misalignment not only introduces a discrepancy between vision and proprioception, but also a discrepancy between the actual and predicted sensory consequences of their movement (Fig 1.1), which both in turn drive reach adaptation. People consistently respond to visuomotor rotation by learning to steer their unseen hand in a new direction in order to compensate for the perturbation (Barkley et al., 2014; Neva & Henriques, 2013; Salomonczyk et al., 2011; Smith et al., 2006; Wigmore et al., 2002).

Speed of Reach Adaptation

When first moving a misaligned cursor to a target, the cursor initially misses the target, but with training, people reduce the errors to compensate for most, if not all of the misalignment, and this is known as adaptation. Adaptation can take as few as 20 trials for a single target (Krakauer et al., 2000). The required number of trials increases as the number of targets increase, especially if the targets are spread out as there is little generalization of learning to the targets in completely opposite directions (Krakauer et al., 2000).

Removing visual feedback of the hand cursor during the outward movement so that the cursor only appears at the end of the movement, can slow down the speed of adaptation (Barkley et al., 2014; Brudner et al., 2016; Heuer & Hegele, 2008; Hinder et al., 2008, 2010; Rand & Rentsch, 2016; Schween et al., 2014; Taylor et al., 2014;

Wijeyaratnam et al., 2019). This is called terminal or endpoint feedback and still produces robust cursor adaptation (Barkley et al., 2014; Taylor et al., 2014; Wijeyaratnam et al., 2019). Reach adaptation studies often quantify the change in speed of adaptation by measuring the average of multiple trials at the beginning of training or looking at the overall extent of adaptation. This has left a gap in knowledge regarding the time course of both reach adaptation, and other related changes, which we try to fill in this dissertation.

Reach Aftereffects

Once people adapt to a misaligned cursor, they continue to deviate their reaches when both the visual perturbation and any visual feedback of performance is removed, as illustrated in Fig 2.3B. This is even the case when participants are told to move their hand directly to the target, and even when they are aware of the cursor misalignment and have been told it has been removed (Gastrock et al., 2020; Shadmehr et al., 2010; Shadmehr & Mussa-Ivaldi, 1994). These reach aftereffects are thought to reflect the unconscious or implicit component of adaptation, which is separate from reach adjustments due to explicit cognitive strategies (Heirani Moghaddam et al., 2021; Taylor et al., 2014). The inability to suppress these reach deviations in the absence of the misaligned cursor suggests that reach aftereffects are predominantly implicit. Reach aftereffects, usually 15° - 20° , are smaller than reaches produced when compensating for a cursor (Barkley et al., 2014; Gastrock et al., 2020; Modchalingam et al., 2019; Ruttle et al., 2016; Wong & Henriques, 2009). The magnitude of these reach aftereffects appears to be independent of the size of visuomotor rotation during training, staying 15° (Bond & Taylor, 2015; Brudner et al., 2016; Heirani Moghaddam et al., 2021; Hutter &

Taylor, 2018; Leow et al., 2017, 2018; Neville & Cressman, 2018; Taylor et al., 2014; Wilterson & Taylor, 2021). Yet this implicit reach adaptation can be as large as 25° for large rotations when they are introduced in smaller steps (Modchalingam et al., 2023; Salomonczyk et al., 2011). Yet it is unknown how quickly reach aftereffects emerge, nor the timecourse of these implicit motor changes. Nearly all studies that measure reach aftereffects do so only after hundreds of training trials with a misaligned cursor. This follows from the assumption that unconscious learning that contributes to reach aftereffects are slow to emerge. My earlier studies (Ruttle et al., 2016, 2018) were the first to reveal that reach aftereffects could emerge after just six rotated training trials. Thus, one of the main goals of this dissertation is to more rigorously quantify the timecourse of these implicit motor changes.

State Estimation

The brain needs to know where the limbs are with respect to the body to make accurate reaches. State estimation uses sensory signals from vision and proprioception to identify the location of the hand (Sober & Sabes, 2003, 2005; Van Beers, Sittig, & Denier Van Der Gon, 1999). Proprioception provides information regarding where an individual's limbs are with respect to other limbs and the trunk of the body (Yousif et al., 2015). Proprioception has been divided into at least two subtypes: static and dynamic (Fuentes & Bastian, 2010). Static proprioception involves sensing the limb's position while it is stationary (Yousif et al., 2015). Dynamic proprioception involves estimations of limb position and velocity during an active reach or during passive placement. The proprioceptive signals arise from four main mechanoreceptors: muscle spindles, Golgi tendon organs, receptors in the joint capsules, and stretch-sensitive receptors in the

skin (Yousif et al., 2015). Muscle spindles, which are innervated by large myelinated primary afferent fibres (Aa), signal the length and rate of change in the muscle (Edin & Vallbo, 1990; Gilman, 2002). The Golgi tendon organs respond to muscle tension and are innervated by large myelinated 1b and Aa fibres (Prochazka & Wand, 1980). The final two signals play a much more minor role and are innervated by small and large myelinated fibres (Aimonetti et al., 2007). These peripheral signals are sent to the somatosensory cortex within the parietal lobe where they are integrated to provide tactile and proprioceptive information.

When available, vision also contributes to our estimate of hand position, and in some cases, its contribution outweighs that of proprioception, like when moving a visible hand toward a visual target. However, both sensory modalities suffer from delays associated with sensory processing and transmission. To overcome some of these delays and provide more information, the brain also uses a copy of the motor command, known as an efference copy, to predict ongoing movements, as illustrated in Fig 1.1 (Desouza et al., 2000; Miall et al., 2007). These predictions are incredibly important for making quick movements and reacting to unexpected perturbations. With state estimation being an iterative process, the brain continually updates the estimate of location. Thus, prediction and sensory feedback together contribute to state estimation, and most theories of motor learning suggest that discrepancies between prediction and sensory feedback drive motor adaptation (Shadmehr et al., 2010; Taylor & Ivry, 2011; Tseng et al., 2007).

To rigorously measure how well people can localize their unseen hand, we use a robot that can move or constrain hand movement to land on certain locations in the

workspace. Once the unseen hand is in place, there are a couple ways to measure where people perceive their hand. One method involves a perceptual task where the participants report the felt location of the trained hand with respect to a visual or proprioceptive reference marker (Jones et al., 2012; Mattar et al., 2013; Mostafa et al., 2014; Nourouzpour et al., 2014; Ostry et al., 2010; Salomonczyk et al., 2011). Based on many trials of the perceptual reports, a psychometric function is fit to the data to derive a perceived estimate of hand direction. Thus, this method requires many trials to measure one perceived hand location. The method used in this dissertation is different in that it requires participants to directly indicate the location they perceived their adapted hand to be, using their other untrained hand. Instead of reporting left or right, the participant uses a touchscreen, located in the axial plane, to indicate their felt hand position, as illustrated in Fig 2.1A ('t Hart & Henriques, 2016; Clayton et al., 2014; Gastrock et al., 2020; Izawa et al., 2012; Modchalingam et al., 2019; Mostafa et al., 2019; Ruttle et al., 2016; Yousif et al., 2015). This method requires far fewer trials to measure the felt hand position at one location with the same precision as the perceptual method (Clayton et al., 2014). Moreover, it allows us to measure the timecourse of visual-induced proprioceptive recalibration on a much finer scale.

We are also able to roughly measure efferent-based estimates of hand position by having the participant actively move their hidden hand out to a self-directed location. By having the participant actively move their unseen hand, instead of having their hand passively moved by the robot, we can probe proprioception at the end of the movement and the predicted sensory consequences of the movement. Thus, we are then able to subtract the estimates of passive hand location from estimates of active hand location to

extract the changes attributed solely to predicted sensory consequences and not proprioception ('t Hart & Henriques, 2016).

These methods of measuring estimates of hand location have shown that participants are very good at localizing their hand prior to a visual-proprioceptive mismatch being applied, generally localizing their felt hand within a few degrees of their actual hand (Clayton et al., 2014; Gastrock et al., 2020; Jones et al., 2012; Ruttle et al., 2016, 2018). Indicating both passive and active estimates of hand location provide a reliable measure of perceived hand location that can be used to explore the effect of visuomotor training on both proprioceptive and predictive estimates of hand motion.

Proprioceptive Recalibration

During rotated cursor training, participants experience a visual-proprioceptive mismatch in their seen and felt hand location. This contradiction in sensory information leads to shifts in estimates of hand location and in the direction of the visible hand cursor (Cameron et al., 2012; Cressman & Henriques, 2010; Salomonczyk et al., 2011). This is sometimes called proprioceptive recalibration and has been found to be entirely implicit, this is evidenced when obvious misalignment of the visual feedback does not reduce the size or reliability of recalibration (Gastrock et al., 2020). The robust recalibration is smaller than the accompanying changes in movements; usually only 6° ('t Hart & Henriques, 2016; Gastrock et al., 2020). This amount of change in felt estimate of hand location appears to be the same whether people train with a small, largely unnoticeable, visuomotor rotation like 30°, as well as a large, very salient rotation like 60° (Modchalingam et al., 2019). This “cap” on the size of the

proprioceptive recalibration is like the cap found for reach aftereffects as discussed above. That is, training with visuomotor rotations ranging from 30° to 60° leads to changes in hand estimate of 6° and reach aftereffects of roughly 15° . Thus, the effect that visual perturbation has on realigning our motor and proprioceptive signals may be limited to some small amount which may be more ecologically based and fall below conscious awareness.

Also, like reach aftereffects, it was originally assumed that proprioceptive recalibration would require many training trials before emerging. Yet, in my previous papers, we were surprised to find that people misestimate their unseen hand by the usual 6° after experiencing misaligned feedback of the hand for only six trials (Ruttle et al., 2016, 2018). Consistent with these two studies, these unconscious or implicit sensory and motor changes that occur during training with visual perturbation can emerge quite quickly. This observation motivated the current dissertation, where we more rigorously measure the timecourse of these changes.

As described above, during volitional movement, a copy of the motor command is used by the brain to also predict the sensory consequences of movements, as illustrated in Fig 1.1, which in turn is assumed to drive adaptation. (Haith & Krakauer, 2013). Yet given that predicted estimates are always accompanied by proprioception, it is difficult to measure predicted estimates, as well as changes in prediction during adaptation. We have attempted to do so by measuring estimates of hand location after people actively generate and direct their own unseen hand movement as described earlier. This can be compared with estimates of hand location produced when the hand is passively moved to the same place later. By taking the difference in the estimates of

hand location after self-generated and passive hand displacement, we can try to isolate efferent-based changes in hand localization. The extent by which updates in predicted consequences affect our estimates of hand position has only recently been investigated ('t Hart & Henriques, 2016; Cameron et al., 2012; Gastrock et al., 2020; Modchalingam et al., 2019; Mostafa et al., 2019). Training with altered visual feedback of the hand leads to changes in efferent-based estimates of hand location, beyond those associated with proprioception (i.e., proprioceptive recalibration). Moreover, these shifts in estimates of hand position when participants generate their own hand movement for localization are slightly larger than those when the hand is passively moved by a robot to the same locations ('t Hart & Henriques, 2016; Gastrock et al., 2020; Modchalingam et al., 2019; Mostafa et al., 2019); and this difference can be attributed to changes in efferent-based contribution to hand location. Again, this shift in estimate of hand position is unconscious, and even being aware of the visual misalignment does not reduce these shifts in both predicted or felt hand position (Gastrock et al., 2020). By measuring active shifts in felt hand position, we can isolate the proprioceptive and efferent based contributions to proprioceptive recalibration. Consequently, within this dissertation we try to identify changes to the speed or extent these shifts develop.

Reach Adaptation Error Signals

Reach adaptation is thought to be driven by multiple different error signals. I will briefly describe three such error signals: task error, sensory prediction errors (Krakauer et al., 2019) and the visual-proprioceptive mismatch (Salomonczyk et al., 2013). Task errors reflect the discrepancy between the cursor and unseen hand (Leow et al., 2018). This error signal is most salient, especially at the end of the reach when the cursor

misses the visual target. This error information can then be used on the next trial to update the movement, and indeed task errors are reduced across training. While task error appears to be useful for helping people direct the cursor toward the target, i.e., to compensate for the cursor rotation, it does not seem to be necessary for producing implicit reach aftereffects or proprioceptive recalibration. Training tasks where the task error is constantly zero, for instance, by constraining hand movements so the misaligned cursor always moves straight to the target, still leads to proprioceptive recalibration of about 6° and slightly smaller reach aftereffects (Mostafa et al., 2019; Ruttle et al., 2018; Salomonczyk et al., 2013). This simple method for removing task errors shows that implicit adaptation occurs even without experiencing the visual difference between endpoint and cursor.

The second error signal of interest is sensory prediction error. As described above, sensory prediction error is the difference between your predicted movement location and actual location, based on sensory information about the start position and a copy of motor command (Shadmehr et al., 2010; Taylor & Ivry, 2011; Tseng et al., 2007), as shown in Fig 1.1. This sensory prediction is present in every adaptation paradigm when the perturbed hand moves in a way that is different than expected. This is thought to be the main signal that drives implicit adaptation, specifically reach aftereffects, as well as deviated reaches to untrained targets (Izawa & Shadmehr, 2011).

A third, less studied error reflects the mismatch between visual and proprioceptive feedback of the hand. The visual-proprioceptive mismatch is used during the reaching movement to compare the actual and seen hand location. (Salomonczyk et

al., 2013). The fact that reach aftereffects deviated much less than the reaches with the misaligned cursor may be partly due to the absence of this sensory mismatch when altered visual feedback is removed after sufficient training. In tasks where sensory prediction error and task error are removed due to constraining hand movements and thus eliminating cursor errors and volitional movements, reach aftereffects and proprioceptive recalibration still occur. This consistent appearance of implicit adaptation, despite the decreased or removed access to the other error signals, shows that the visual-proprioceptive mismatch is a vital source of sensory information used during reach adaptation.

Models of Reach Adaptation

Reach aftereffects and estimates of hand location are generally considered to be implicit components of motor learning. But implicit adaptation has been assumed by the field to develop slowly, emerging well after an initial stage of learning which is more declarative or explicitly based. Some laboratories have suggested that the implicit and explicit processes that contribute to adaptation can be mapped onto the slow and fast processes that make-up a two-rate state space model (McDougle et al., 2015; Smith et al., 2006). This model is comprised of two processes, a fast process that learns quickly but also forgets quickly, and a slow process that learns slowly but also forgets slowly. The combination of these two processes creates the behaviour we see participants exhibit during adaptation training. Recently, one group has found that the explicit component of adaptation measured when people are asked to indicate their strategy for overcoming the perturbation resembles the fast process (McDougle et al., 2015). These findings suggest that the remaining reach deviations are due to the implicit portion of

learning which would map onto the slow process. However, no one has directly measured implicit components of learning, such as reach aftereffects and changes in hand location to determine the actual rate by which these implicit measures emerge. Likewise, the assumption that implicit and explicit components of learning are additive, and that one precedes the other has never been tested. This knowledge gap will be addressed in the present set of experiments, which are designed to explore these unanswered motor learning questions within the mechanistic framework of the two-rate state space model.

Overview of Projects

My research will focus on understanding how early implicit components of motor learning, specifically reach aftereffects and efferent-based and proprioceptive changes in hand estimates, appear, and reach asymptote under varying motor learning conditions. My master's research showed that proprioceptive estimates of hand location and reach aftereffects appear in as few as six rotated training trials (Ruttle et al., 2016, 2018). However, it is still unclear if reach aftereffects or estimates of hand location, both efferent and afferent, emerge even earlier and how quickly they reach asymptote. Here we measured implicit components of motor learning after every single training trial to directly measure the rate of change and asymptote. We hypothesized that the human motor learning system is capable of adapting to new situations using implicit learning strategies. An exploratory aspect of this research was which situations affected the speed of this implicit learning. We believed that our direct measures of implicit learning would appear quicker and have different asymptotes than that of the slow process mentioned in the two-rate state space model, regardless of the training conditions. We

also pushed the limits of changes in estimates of hand location by periodically altering the magnitude and direction of the rotation to see if the rate and extent of the change would be reduced in the face of uncertainty.

To test the mechanistic framework described above; we conducted three experiments to measure the timecourse of these implicit changes. The rotation schedule used in Chapter 2 and Chapter 3 allowed us to estimate the earliest appearance of our measures of implicit learning as well as fit the two-rate model to our data to compare measures of implicit learning to the slow process predicted by the model. Chapter 2 involved classic visuomotor rotation training to replicate and extend previous findings (Ruttle et al., 2016, 2018), while in Chapter 3, we changed feedback during training to quantify how this affects the timecourse of proprioceptive recalibration. Participants either saw the misaligned cursor at the end of each reach movement (known as terminal feedback) or saw the cursor the entire movement, but the robot constrained their hand movement during training (thereby removing volitional control), which we call cross-sensory exposure training. We expected to see a slower rate of change in estimates of hand position during terminal feedback compared to classic or exposure training. Chapter 4 tested whether visual recalibration of hand proprioception continued to recalibrate rapidly in the face of uncertainty or variation in the visual feedback across training. We predicted that the speed and extent by which proprioception changes may decrease when training with a random visual distortion, as uncertainty rises.

Chapter 2: Implicit motor learning within three trials

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Abstract

In motor learning, the slow development of implicit learning is traditionally taken for granted. While much is known about training performance during adaptation to a perturbation in reaches, saccades and locomotion, little is known about the time course of the underlying implicit processes during normal motor adaptation. Implicit learning is characterized by both changes in internal models and state estimates of limb position. Here, we measure both as reach aftereffects and shifts in hand localization in our participants, after every training trial. The observed implicit changes were near asymptote after only one to three perturbed training trials and were not predicted by a two-rate model's slow process that is supposed to capture implicit learning. Hence, we show that implicit learning is much faster than conventionally believed, which has implications for rehabilitation and skills training.

Introduction

An established convention of motor learning asserts that automatic or implicit components of learning emerge later in training following an initial more explicit or declarative stage, even for skill-maintenance tasks, like adaptation (Benson et al., 2011; Bond & Taylor, 2015; Mazzoni & Krakauer, 2006; Miyamoto et al., 2020; Taylor et al.,

2014; Van Es & Knapen, 2019). Perturbations in reach, saccade and locomotion adaptation evoke relatively quick adjustments to behaviour (Kim et al., 2018; Krakauer et al., 2000; Long et al., 2016; Malone & Bastian, 2010; Miyamoto et al., 2020; Morehead et al., 2017; Van Es & Knapen, 2019; Werner & Bock, 2007), and some work has attempted to either infer implicit learning based on the assumption that implicit and explicit adaptation simply add to produce behavior (McDougle et al., 2015) or measure it in paradigms that require explicitly suppressing natural responses to visual feedback (Kim et al., 2018; Morehead et al., 2017). However, it has not been directly measured how quickly implicit changes emerge. Two main implicit changes involved in error-based learning are updates in internal models as well as the resulting changes in our state estimates (Krakauer et al., 2019; Leow et al., 2018; Salomonczyk et al., 2013). Here, we show that implicit changes during visuomotor adaptation occur immediately and do not require prolonged training at all.

One hallmark of implicit learning: reach aftereffects, is the persistence of motor changes even when the perturbation is removed, which is thought to reflect a change in internal models during adaptation (Krakauer et al., 2019; Wolpert et al., 1995). Yet reach aftereffects are almost always measured after hundreds of training trials, so its time course is largely unknown.

Another implicit change is a shift in our perceived hand location or state estimate that occurs in both visuomotor and force field adaptation (Cameron et al., 2012; Cressman & Henriques, 2009; Izawa et al., 2012; Izawa & Shadmehr, 2011; Salomonczyk et al., 2013; Synofzik et al., 2008). A further shift in estimates of hand position can be attributed to efferent-based updates of the internal model ('t Hart &

Henriques, 2016; Izawa et al., 2012). These two sources of hand location estimates have been shown to be unaffected by cognitive strategy and are largely independent (Modchalingam et al., 2019; Vachon et al., 2020). Work from our lab has shown that the changes in hand proprioception following passive exposure to a visual discrepancy, without self-generated movements, can partly account for the resulting changes in reach aftereffects as well (Cressman & Henriques, 2010; Mostafa et al., 2019; Salomonczyk et al., 2013). Thus, while afferent- and efferent- based estimates of hand position are small, they are robust and contribute to movement planning and reach aftereffects.

It is thought that implicit learning arises slowly with exposure to a perturbation along with explicit components of learning (Mazzoni & Krakauer, 2006; McDougale et al., 2015; Miyamoto et al., 2020; Taylor et al., 2014). Our lab has shown that reach aftereffects and proprioceptive recalibration emerge within 6 trials (Ruttle et al., 2016, 2018). In the current study, we push this further by having participants alternate between training and testing trials, while adapting to a 30° rotation, its reversal and then error-clamped trials. Each group of participants performed one type of testing trial that could assess either changes in state estimates or internal models. By probing implicit changes after each training trial, we increase the resolution of measuring implicit changes greatly, and can quantify their rate of change throughout learning.

The time course of adaptation has been described by a state-space model that includes two processes, a process with slow learning and forgetting and a process with fast learning and forgetting (Smith et al., 2006). The model's fast and slow processes have been suggested to map onto explicit and implicit components of learning

respectively (McDougle et al., 2015). While not the main focus of this study, here we compare the rate of change of the models' slow process with that of actual measures of implicit learning.

We find changes in reach aftereffects and state estimates to occur much faster than expected. State estimates asymptote after a single trial and are well described as a proportion of the perturbation. Our results challenge the convention that implicit learning is slow, and show that some implicit changes emerge before, and likely independently and not inferable from, explicit changes in motor control.

Methods

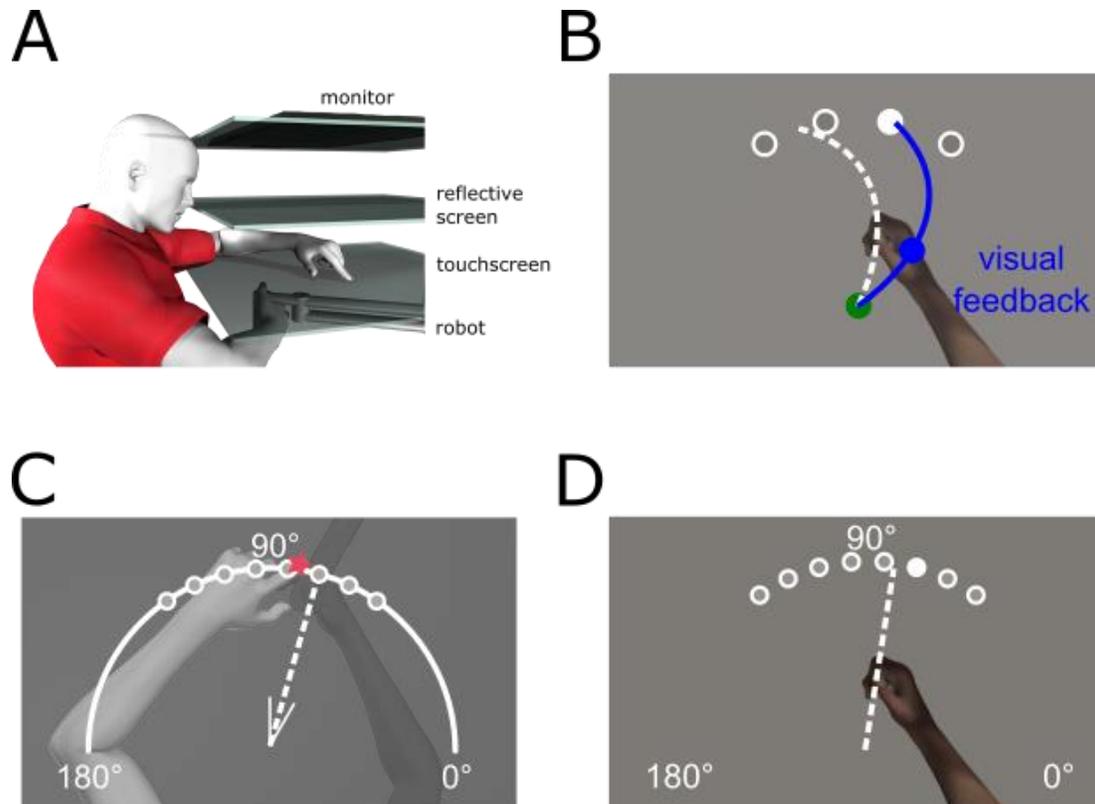
Participants

143 (mean age=20.31, range=17-46, females=101) right-handed, healthy adults participated in this study. All participants gave written informed consent prior to participating. All procedures were in accordance with institutional and international guidelines. All procedures were approved by the York Human Participants Review Subcommittee.

Apparatus

The experimental set-up is illustrated in Fig 2.1. While seated, participants held a vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand such that their thumb rested on top of the handle. A reflective screen was mounted horizontally, 14 cm above the robotic arm. A monitor (Samsung 510 N, 60 Hz) 28 cm above the robotic arm presented visual stimuli

via the reflective screen to appear in the same horizontal plane as the robotic arm. A Keytec touchscreen 2 cm above the robotic arm recorded reach endpoints of the left



hand, to unseen, right hand targets (see (Cressman & Henriques, 2009) for more details). Subject's view of their training (right) arm was blocked by the reflective surface and a black cloth, draped over their right shoulder. The untrained, left hand was illuminated, so that any errors in reaching to the unseen, right target hand could not be attributed to errors in localizing the left, reaching hand.

Figure 2.1. Experimental setup and design. (a) Side view of the experimental set-up. The top layer is the monitor, middle layer is the reflective screen, and the bottom opaque layer is the touchscreen. The robot is depicted beneath with the participants' right hand grasping it. (b–d) Top views of task specific set-ups. (b) Training (and Clamp) trial. The home position is represented by a green circle with a 1 cm diameter; located approximately 20 cm in front of the subject. Targets are represented by white circles with a 1 cm diameter located 12 cm radially from the home position at 60°, 80°, 100° and 120°. Participants hand cursor was also a 1 cm diameter blue circle. (c) Localization test trial. Participants were either passively moved to one of the eight target locations, or actively moved their hand in the direction suggested by the white wedge, consisting of two short straight lines (V-shaped) at the home position, these real and suggested locations are 55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°. Subsequently, participants used a touch screen to indicate on a white arc spanning 180° where their unseen right hand was. (d) No-cursor test trial. Participants made ballistic reaches to one of the 8 target locations also used in localization without

any visual feedback of their movement. Figures were made using Poser Rendering Software version 11, <https://www.posersoftware.com/>.

Trial Types

Reach-training trials

Participants, regardless of group, reached as accurately as possible with their right hand to one of four possible target locations, 60°, 80°, 100° and 120°, which were shown once in a cycle of four trials before being repeated (see Fig 2.1B). In all reaching trials, i.e., with cursor, with clamped cursor and with no cursor, participants had to reach out 12 cm from the home position to a force cushion within 800 ms. Participants received auditory feedback throughout training indicating if they met the distance-time criteria or not. The target would then disappear, and the robot manipulandum returned the right hand to the home position where they waited 250 ms for the next trial. The hand cursor was aligned with the hand for the first 64 training trials, then rotated 30° CW for 160 training trials and then rotated 30° CCW for 16 training trials. This was followed by 48 error-clamped trials, dashed lines in Fig 2.2, which were identical to the reach training trials except that the cursor always moved on a straight line to the target. The distance of the error-clamped cursor from the home position was identical to the distance of the hand from the home position.



Figure 2.2. Experimental Schedule. Participants reached to visual targets with a perturbation denoted by the black line. The dotted line at the end of the paradigm signifies clamp trials where there was no visual error as the cursor always moved to the target regardless of the participants movement direction. Trials included in analysis are as follows: R1 = trials 65–68; R1_Late = trials 221–224; R2 = trials 237–240; EC = 273–288.

Test trials

Participants alternated between one training trial, as described above, and one of four possible test trials. That is, test trials are interleaved with training. Each type of test trial was performed exclusively by participants in one group. These test trials were: (1) a no-cursor reach to a target, “No-cursor”, N=47, (2) a short pause phase with no hand movement, “Pause”, N=32, serving as a control group, (3) localization of the unseen hand position when the hand was passively moved by the robot, “Passive localization”, N=32, or (4) localization of the unseen hand after it was actively moved by the participant, “Active localization”, N=32. After each test trial, the robot returned the participants’ hand back to the home position. Test trials were always executed to one of two targets, 5° on either side of the training target, to reduce distance between test and training targets. All eight targets (55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°; one on each side of each of the training targets) were cycled through before being repeated.

Reaching without a cursor: For the no-cursor group, their test trial required reaching out, again 12 cm, to one of the eight test targets (Fig 2.1D) without a cursor representing their hand. The same distance-time criteria as in reach-training applied but without

reinforcing sounds. This group originally had 32 participants who were simply told that there would be no cursor for these trials. We later add 15 more participants who were specifically told not to include any learned strategy, similar to a previous study in our lab that used a PDP technique and showed no explicit component for a 30° rotation (Modchalingam et al., 2019; Vachon et al., 2020). Since the results did not differ between these two sub-groups, (see OSF for details: <https://osf.io/9db8v/>), the results were collapsed for analyses. Our results are consistent with the current idea that implicit learning caps around 15° (Morehead et al., 2017) and previous studies which found no difference in the size of reach aftereffects when participants are not told about the rotation, then during a set of no-cursor trials, either include or exclude any strategy developed in the training trials (Modchalingam et al., 2019; Vachon et al., 2020; Werner et al., 2015).

Hand localization: The two hand localization groups did test trials measuring estimates of unseen hand location in order to assess different components of state-estimation, after every training trial. For both localization trials (Fig 2.1C), a white arc would appear on the screen, spanning from 0° to 180°, the arc was 12 cm away from the home position. Then the hand was either passively displaced by the robot to one of the eight target locations (passive localization) or the hand movement was self-generated by the participant (active localization). Passive movement of the hand took 650 ms to cover the 12 cm distance. In active localization trials, participants chose their own hand-target location. They were guided with a small V-shaped, 30° wedge that appeared at the home position, the middle of the V-shaped wedge was oriented to the passive localization targets. This active, self-generated movement was stopped by a force

cushion at the 12 cm mark. Regardless of localization trial type once their right, unseen target hand was locked in place, participants used their visible, left index finger, to indicate on the touchscreen, along a 180° arc, where they believed their right, stationary, unseen hand was. The arc was continuously visible until the touchscreen registered the participants estimate.

Data Analysis

We analyzed the reach-training for the no-cursor group and the two hand localization groups separately using the pause group as a control. The reach training trials, hand localization trials and no-cursor trials were analyzed separately from each other, but their rates of change (see below) can be compared.

Reaching with a cursor and clamp trials: To quantify reach performance during training, the angular difference between a straight line from the home position to the target and a straight line from the home position and the point of maximum velocity is computed.

Hand Localization: Estimates of hand location in both the passive and active localization groups were based on the angular endpoint error between the movement endpoint of the right unseen hand and the left hands responses on the touchscreen.

Reaching without a cursor: To determine if participants exhibit reach aftereffects as a result of training, we measured reach endpoint errors during no-cursor trials. The reach error is calculated based on the angular deviation between the reach endpoint and the target location, relative to the home position. We used the endpoint error, instead of

maximum velocity to be able to compare no-cursor trials to hand localization trials. However, a comparison between no-cursor reach deviations at endpoint and at maximum velocity is included in the R notebook.

Analyses

All data was visually screened for incorrect trials. Subsequently, outliers of more than three standard deviations across participants within each trial were also deleted. In all, 2.2% of the data was removed. One participant had to be removed from the no-cursor instructed group as they did not complete the task appropriately. All measures were normalized, by subtracting out each subjects' average performance during the second half of the aligned session (e.g. trials 33-64). To see if there were changes in training and test trials, we conducted ANOVAs consisting of a within-subjects factor of trial set and a between-subjects factor of group. The trial-set factor consisted of four levels: the first 4 rotated trials (R1), the final 4 trials from the first rotation (R1_Late), the final 4 trials from the second rotation (R2) and the last 16 trials, to allow for a less noisy estimate, from the clamp phase (EC). All analyses ignored target location, but each bin of four trials contains a trial to each of the four training targets (effects at different target angles are not distinguishable, see the R notebook). Significant main effects and interactions were followed-up by pairwise comparisons. All results are reported with a Welch t-test and an alpha of .05, where necessary with an fdr correction applied using the p.adjust function in R.

Two-Rate Model

We fitted the two-rate model (Smith et al., 2006) to our data. This two-rate model is composed of a slow process that slowly increases over time until it is the driving force of performance, and a fast process that rises quickly but eventually decays back to zero. The sum of these two processes determines the overt behaviour and can explain the rebound seen in the error-clamp phase. During error-clamps, neither process learns, but the fast process will forget how it adapted to the counter rotation, while the slow process still exhibits part of its adaptation from the long initial training, resulting in a rebound.

This model postulates the reaching behavior exhibited on trial t (X_{t1}), is the sum of the output of the slow ($X_{s,t1}$) and fast process ($X_{f,t1}$) on the same trial:

$$X_{t1} = X_{s,t1} + X_{f,t1}$$

Both processes learn from errors on the previous trial (e_{t0}) by means of a learning rate (L_s and L_f), and they each retain some of their previous state ($X_{s,t0}$ and $X_{f,t0}$) by means of their retention rates (R_s and R_f):

$$X_{s,t1} = L_s * e_{t0} + R_s * X_{s,t0}$$

$$X_{f,t1} = L_f * e_{t0} + R_f * X_{f,t0}$$

The model is further constrained by making sure the learning rate of the slow process is lower than that of the fast process: $L_s < L_f$, and by having the retention rate of the slow process be larger than that of the fast process: $R_s > R_f$. We constrained the parameters to the range $[0,1]$.

All model fitting was done on the mean angular reach deviation at peak velocity during all training reaches, regardless of target angle. The error term was set to zero

during the final error clamp phase of the experiment, as the participant did not experience any performance error. The model was fit in R 3.6.1 (R Core Team, 2020) using a least mean-squared error criterion on the six best fits resulting from a grid-search. The parameter values corresponding to the lowest MSE between data and model was picked as the best fit, and this was repeated for all groups.

Rate of Change

We used an exponential decay function with an asymptote to estimate the rate of change for each of the three trial types. The value of each process on the next trial (P_{t1}) is the current process' value (P_{t0}) minus the product of the rate of change (L) multiplied by the error on the current trial, which is the difference between the asymptote (A) and the process' value on the current trial (P_{t0}).

$$P_{t1} = P_{t0} - L * (A - P_{t0})$$

The parameter L was constrained to the range $[0,1]$, and the parameter A to $[0,2 \cdot \max(\text{data})]$. For all groups, this model was fit to 1) the slow process from the two-rate model, and 2) the reach data. It was also fit to each group's test trial data; 3) no-cursor reach deviations and both 4) active and 5) passive localizations. For the latter three kinds of fits, a zero was prepended to account for the fact that responses in these trials already changed through the previous training trial. The parameters were also bootstrapped (1k resamples per fit) across participants to get a 95% confidence interval for both parameters. The first trial where the modelled process based on the group average fell inside the bootstrapped confidence interval for the asymptote is taken as the saturation trial.

Results

Reach aftereffects

To test how quickly reach aftereffects emerge, 47 participants adapted to an imposed perturbation interleaved with no-cursor test trials. We began by investigating whether these test trials affected reach-training using a control group (N=32) that paused instead. Figure 2.3A shows the reach training performance for both groups. No-cursor reach trials, and two-rate model fits are shown in Fig 2.3B, and rates of change are listed in Table 2.1.

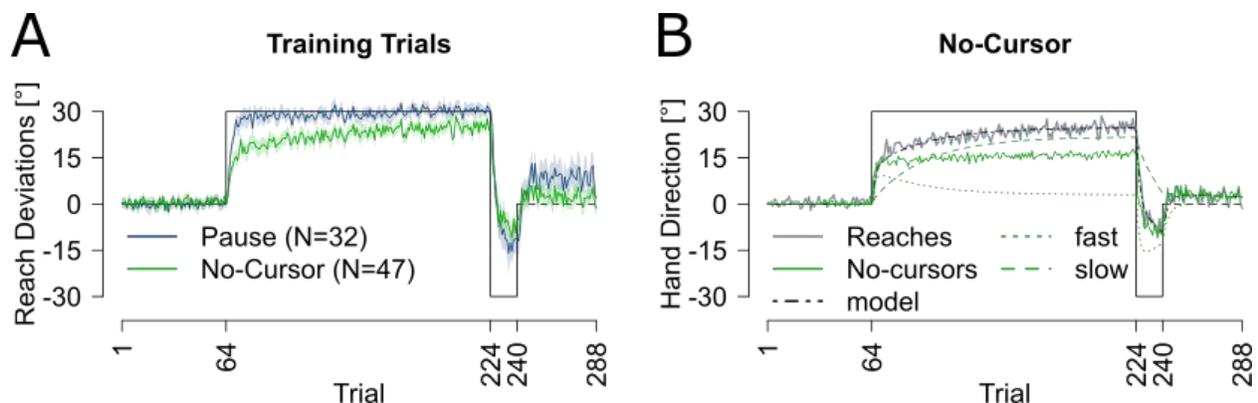


Figure 2.3. Performance across measures for pause and no-cursor groups. (a) Reach training performance averaged across all participants for the two groups. (b) Two-rate model fit (black and green dashed lines), and no-cursor test trials in solid green. For reference, reach performance for the no-cursor group is plotted again in grey. All solid lines are an average of all participants in that group, shaded regions are 95% confidence intervals. Trials included in analysis are as follows: R1 = trials 65–68; R1_Late = trials 221–224; R2 = trials 237–240; EC = 273–288.

		Rate of change			
		No-cursor	Pause	Active	Passive
Reach training	rate of change	13.8% [10.7% - 17.7%]	36.5% [28.3% - 49.8%]	15.4% [10.8% - 21.8%]	27.0% [21.4% - 34.8%]
	asymptote	23.2° [22.0° - 24.3°]	29.1° [28.5° - 29.7°]	24.7° [22.7° - 26.2°]	28.6° [27.8° - 29.5°]
	saturation trial	21 [16 - 27]	9 [6 - 12]	16 [11 - 23]	12 [9 - 15]
Slow process	rate of change	3.4% [3.1% - 3.8%]	2.8% [2.5% - 3.2%]	2.1% [1.9% - 2.4%]	3.5% [3.0% - 4.1%]

	<i>asymptote</i>	21.4° [19.8° - 23.0°]	27.2° [25.5° - 28.6°]	26.0° [23.9° - 27.8°]	25.2° [22.6° - 27.4°]
	<i>saturation trial</i>	74 [67 - 82]	96 [85 - 109]	117 [107 - 130]	64 [54 - 74]
No-cursor or localization	<i>rate of change</i>	56.9% [27.4% - 58.5%]	-	93.9% [51.3% - 95.7%]	100% [29.0% - 100%]
	<i>asymptote</i>	15.3° [13.8° - 16.9°]	-	9.8° [8.1° - 11.6°]	6.9° [5.7° - 8.2°]
	<i>saturation trial</i>	3 [1 - 3]	-	1 [1 - 3]	1 [1 - 6]

Table 2.1. Rate of change and asymptote for reach training trials and measures of implicit learning, for each of the experimental groups, calculated for the first rotation. Reach training trials are represented in the first three rows, then the slow process predicted by the model, with the final three rows being the implicit measure test trial associated with that training group. Averages with 95% CI are reported for all values.

Training Trials:

To investigate whether the type of intervening test trial affects training performance (Fig 2.3A), we conducted a mixed ANOVA with group (no-cursor or pause) and trial set (R1, R1_Late, R2 and EC, described in Fig 2.3 & 2.2). We found an effect of trial set [$F(3,186)=415.30$, $p<.001$, $\eta^2=.82$] and an interaction between trial set and group [$F(3,186)=11.78$, $p<.001$, $\eta^2=.11$]. The interaction seems to be driven by the slower learning and much smaller rebound in the no-cursor paradigm. Follow-up t-tests show a significant difference between the pause and no-cursor group during R1, R1_late, R2 and EC trials sets with $p<.01$. We fit the two-rate model to the averaged reach deviations for each group (see Fig 2.3B and Table 2.2). The model predicts average performance well for the pause group and reasonably well for the no-cursor group. The smaller learning rate parameter values for the no-cursor group versus the pause group (Table 2.2), are mimicked in the rates of change (Table 2.1), which may be explained by slight interference from the no-cursor trials. Nevertheless, the model fits warrant comparison between reach aftereffects and the model's slow process.

Two-Rate Model Parameters								
Group	Rs	Ls	Rf	Lf	MSE	Two-Rate AIC	One-Rate AIC	One-Rate likelihood
No-Cursor	0.991	0.036	0.737	0.148	3.061	13.901	19.11	0.074
Pause	1	0.055	0.825	0.226	8.345	19.293	25.697	0.041
Active Localization	0.999	0.03	0.76	0.158	4.053	15.605	27.004	0.003
Passive Localization	1	0.054	0.74	0.236	7.425	19.548	27.207	0.022

Table 2.2. Model parameters and goodness-of-fit estimates. All twoRate AIC's are smaller than respective oneRate AICs indicating a better model fit from a two-rate model. Relative likelihoods below .05 are bolded. Parameter values could vary between 0 and 1, inclusive.

Testing Trials:

We found reach aftereffects were present at the first trial set, after only 1-4 rotated training trials, compared to those of no-cursors from the aligned phase [$t(46)=20.97$, $p<.001$, $d=4.12$, $\eta^2=.82$, 10.94°]. Using an exponential decay model (see methods) we calculated a rate of change and the trial at which the no-cursor deviations are at asymptote, focusing on the first rotation. We found reach aftereffects had a rate of change of 56.9% (CI: 27.4% - 58.5%), attaining asymptote within 3 trials (see Table 2.1 for all rate of change values). Both the substantial rate of change and, early trial at which changes saturate in no-cursor reaches, i.e., the implicit reach aftereffects, show that implicit adaptation develops rapidly. In fact, aftereffects saturate well before reach training does (56.9% > 13.8%, 95% CI: 10.7% - 17.7%), which asymptotes only at the 21st trial for this group and 9th trial for the control, pause group.

Furthermore, the rate of change of the slow process (3.4%) is much lower than the rate of change of the reach aftereffects (56.9% > 3.4%, 95% CI: 3.1% - 3.8%). Additionally, fitting the two-rate model's slow process to the reach aftereffects, to see if the model's output still matches reaches increases the AIC from 13.9 to 29.17

significantly decreasing the fit (relative log-likelihood: 0.0005; see OSF <https://osf.io/9db8v/> for details). This all shows the rate of change in reach aftereffects is much higher than what would be expected of a slow, implicit process, or indeed that of the two-rate model's slow process.

Hand localization shifts

An additional 64 participants adapted to the same perturbation schedule, interleaved with test trials that measured estimates of the hand location after the trained hand was displaced by a robot manipulandum (passive localization, N=32, Fig 2.4A&D) or by the participant themselves (active localization, N=32, Fig 2.4A&C). We once again used the pause group as a control (Fig 2.4A).

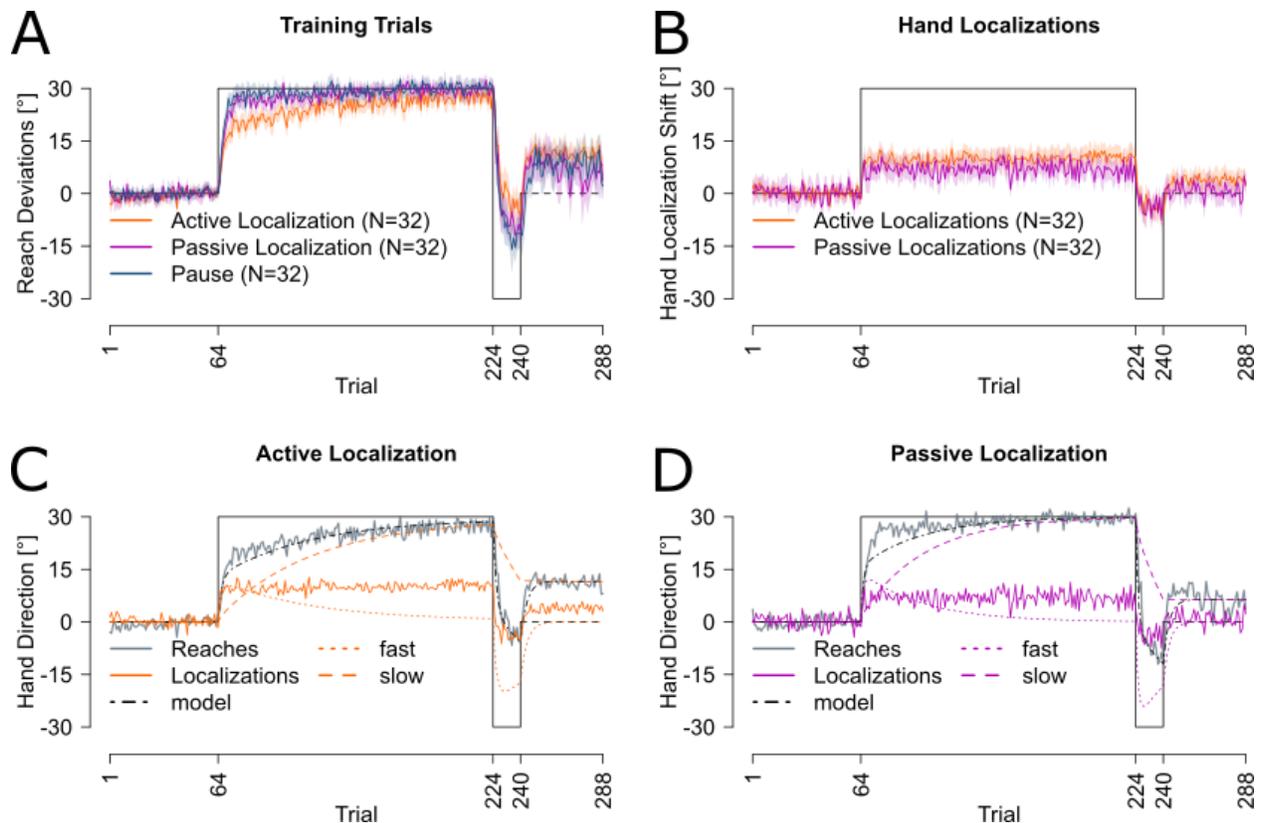


Figure 2.4. Performance across measures for passive, active and pause groups. (A) Reach training performance averaged across all participants for each corresponding group. (B) Hand localization performance for the two groups. (C,D) Model predictions for the active and passive localization groups. All solid lines are an average of all participants in that group, shaded regions are 95% confidence intervals.

Training Trials

We conducted an ANOVA with the same factors as the previous experiment, trial set and group (active localization, passive localization and pause) on training performance (Fig 2.4A). As expected, reach deviations varied across trial set [$F(3,279)=537.99$, $p<.001$, $\eta^2=.80$], and there was a significant interaction between trial set and group [$F(6,279)=8.29$, $p<.001$, $\eta^2=.11$], but no effect of group on its own [$F(2,93)=1.90$, $p=0.15$]. Follow-up ANOVAs show that learning was slower in active localization compared to the other conditions [all $p<.001$]. We also fit the two-rate model to the reach data from the passive and active localization groups, shown in Fig 2.4C&D. The model fits the reach data well, but as shown in Table 2.2, the learning rates for the active group are slightly lower than the passive or pause group. Importantly, the retention parameters are very similar across all three groups, indicating the same ability to retain what was learned. In summary, despite a small effect of test-type, the two-rate model explains the reach data well.

Test Trials

We also compare the time course of changes in estimating the location of the unseen, adapted hand across training: for the passive vs. active localization shown in Fig 2.4B. Estimates of hand position show a rapid shift on the first trial after the initial perturbation is introduced for both active (8.95°) and passive localizations (6.46°). These shifts do not increase with further training with both groups achieving 93.9% and

100% of asymptote within one rotated training trial. Seeing as changes in state estimates of hand location appear incredibly fast, these localization shifts cannot follow from motor adaptation. Instead, they directly result from the perturbation in a single trial.

Despite similarly quick shifts in hand localization (Fig 2.4B), a mixed ANOVA revealed a significant difference in hand estimates between the active and passive localization groups [$F(1,62)=6.28$, $p=0.014$, $\eta^2=.05$], across trial sets [$F(3,186)=96.97$, $p<.001$, $\eta^2=.43$] and an interaction between trial set and group [$F(3,186)=2.93$, $p=0.04$, $\eta^2=.02$]. Follow-up t-tests indicate larger shifts in felt hand position in the active localization group both during the initial [$t(51.43)=2.37$, $p=0.028$, $d=.59$, $\eta^2=.08$, 2.92°] and final [$t(61.78)=2.98$, $p=.016$, $d=.74$, $\eta^2=.11$, 4.35°] trial set of the first rotation and at the end of the error clamp phase [$t(61.99)=2.73$, $p=.016$, $d=.68$, $\eta^2=.11$, 3.5°]. Thus, even though the participants in the active localization group adapted their cursor movements slightly slower than the passive group, the active group showed a slightly larger shift in felt hand position, that didn't reach significance for the counter rotation [$t(58.93)=-0.15$, $p=.88$]. This small separation between active and passive localization shifts reflects the updates in the predicted sensory consequences that further shift active hand localization compared to passive ('t Hart & Henriques, 2016; Cameron et al., 2012; Mostafa et al., 2019).

More importantly, Fig 2.4C&D, show that these changes in state estimates are not captured by the slow process. To test this, we used the same, simple exponential decay model to quantify the rate of change in the passive and active localization data as well as in the models' slow processes. The rates of change are much higher for the localization data than the respective slow process [Passive: $3.4\% < 100\%$, 95% CI:

29.9% – 100%; Active: 2.1% < 93.9%, 95% CI: 63.2% - 100%]. Thus, shifts in hand localization in no way resemble the observable pattern of the slow process.

Given that the rate by which estimates of hand position changes do not match the slow process and saturate in 1 trial (see Table 2.1), we next tested whether these shifts could simply be described as a proportion of the perturbation. When the changes in hand position were fit with a linear regression estimating the proportion of the perturbation accounted for, we see a reasonable fit between actual hand location estimates and these simple models (see Fig 2.5A-B). The fitted slopes are consistent with previous studies, where the change in felt hand position was usually 20-30% of the perturbation (Cameron et al., 2012; Henriques & Cressman, 2012; Salomonczyk et al., 2011). Figure 2.5D&E shows a one-parameter model (black line) that estimates the size of the average localization shift as a proportion of the perturbation using all trials (colored lines). Even though the model over-estimates the size of change in hand localizations during the reversal period, it is clear that a stepwise function is a better fit than an exponential, further providing support for the conclusions that hand localizations shift incredibly fast, too fast to be the slow process in the two-rate model. The small over-estimate of this fit for reversal phase in the active localization group reflects what is a relatively slower rate of changes for this phase (for all measures, but not the slow process), which could partly reflect retrograde interference. Nonetheless, the change in localization during the reversal seems to occur even prior to the change in cursor-reach for this reversed shift of perturbation (compare curves within Fig 2.4C and 2.4D). Given that hand localization shifts occur before other changes, they are able to guide subsequent motor adaptation processes.

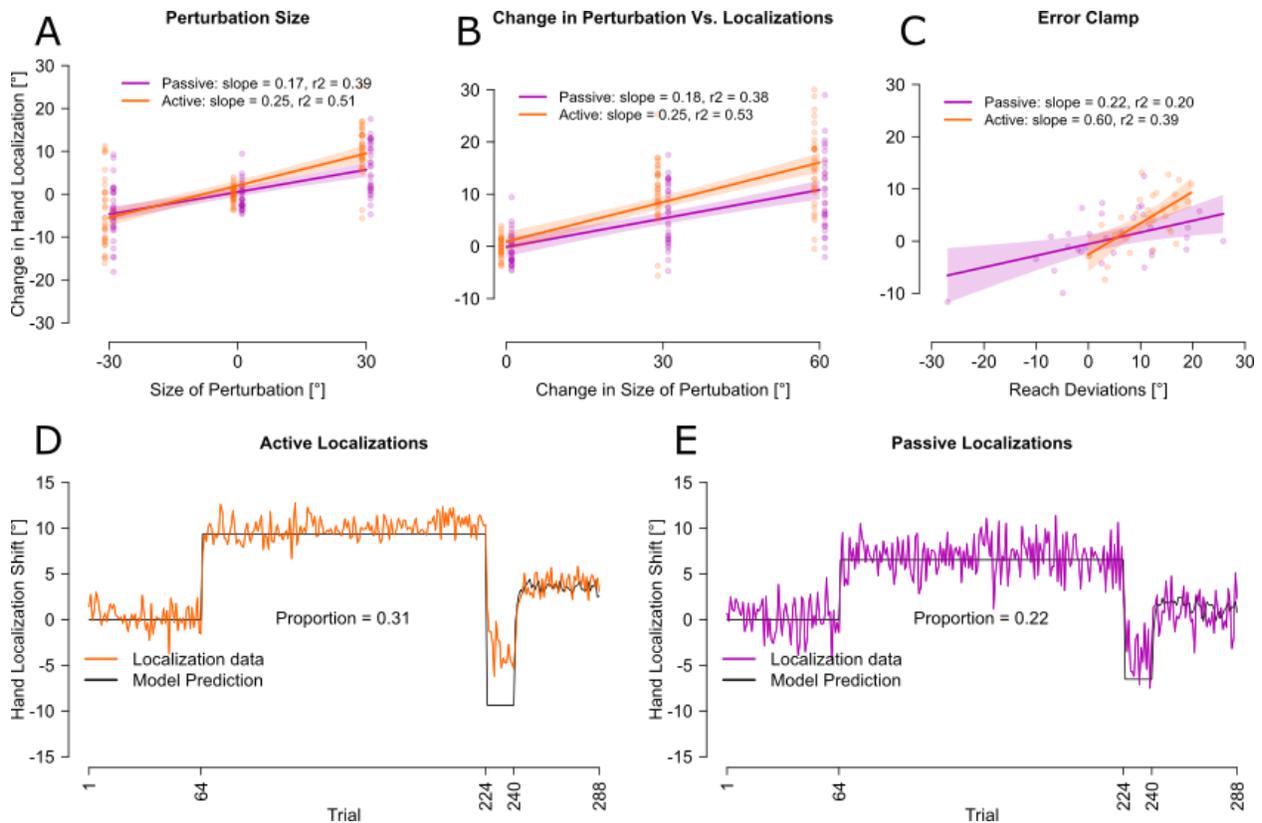


Figure 2.5. Linear and proportional fits between localization and error clamp trials. (A–C) Fits between localizations and either the size of the visual discrepancy (aligned = 0, first rotation = 30, second rotation = -30), the absolute change in size of visual discrepancy (aligned = 0, first rotation = 30, second rotation = 60) and the participants average performance on the final 16 error clamp trials. The shaded regions represent the 95% confidence interval around the regression line. The last four initial rotation trials, the last four reversal trials and the last four aligned training trials were used for figures (A,B). (D,E) The proportional models' prediction and the averaged participant performance for each localization test trial separately.

Implicit Measures of Learning

As both reach aftereffects and hand localization shifts are implicit and potentially driven by similar processes, we compared the first test trial after the first rotated training trial and found no significant difference between the reach aftereffects, and either of the active [$t(73.54)=-1.08$, $p=.28$] or passive [$t(59)=-1.81$, $p=.08$] localization test trials. This finding is consistent with the relatively small correlations between angle at peak velocity during error clamp trials and the corresponding estimates of hand location seen in Fig

2.5C. We speculate that these initial reach aftereffects may mainly reflect the changes in hand location estimates, or a similar training signal (Cameron et al., 2012; Cressman & Henriques, 2010; Salomonczyk et al., 2013), before additional sources of information emerge to create even larger shifts in reach aftereffects but no further shift in hand localizations.

Speed of Learning

While tangential to the main goal of this study, we found that intervening trials that involve active movements (no cursor, or active localization where participants moved their own trained hand) slowed down learning when compared to just passive hand displacements or a pause in time. We can in fact predict for individual participants whether they made self-generated movements in the interleaved testing trials or not for 118 / 143 participants (82%; chance=79/143 or 55%; $p < .001$ binomial exact test) based on a multiple logistic regression model without interactions, using the parameters of the two-rate model as predictors. The exponential decay model also predicts a much slower rate of change for reach training when the test trial involves an active movement (no-cursor: 13.8%, active localization 15.4%) compared to when it does not (pause: 26.5%, passive localization 27.0%). This shows that learning is slowed by having active intervening movements made in the absence of visual feedback. This means that our measures of the rate of change may be underestimating the real speed of implicit learning in some of the processes.

Discussion

While many studies measure and model the time course of reaches in response to a perturbation (McDougle et al., 2015; Ostry et al., 2010), very few investigate the emergence of other outcomes of training, such as reach aftereffects and changes in estimates of hand position, but see: (Ruttle et al., 2016, 2018; Zbib et al., 2016). In the current study, we measure implicit changes as reach aftereffects and estimates of the passively and actively displaced hand's position, at high temporal resolution. This is accomplished by following every reach training trial that has aligned, rotated or error-clamped cursor feedback with one test trial. We find that reach aftereffects and changes in estimates of hand position emerge and saturate rapidly, within 1-3 trials of visuomotor adaptation training (see Fig 2.6). That is much faster than when reach adaptation saturates (9 trials at best), let alone the two-rate model's slow process (64 trials at best). This suggests that implicit changes do not follow explicit changes and play an important role in initial learning. Indeed, changes in hand-localization are so fast, they can best be explained as a proportion of the visual-proprioceptive discrepancy experienced on the previous trial. In sum, given that our measures of implicit learning saturate within 1-3 trials, implicit learning can hardly be characterized as "slow".

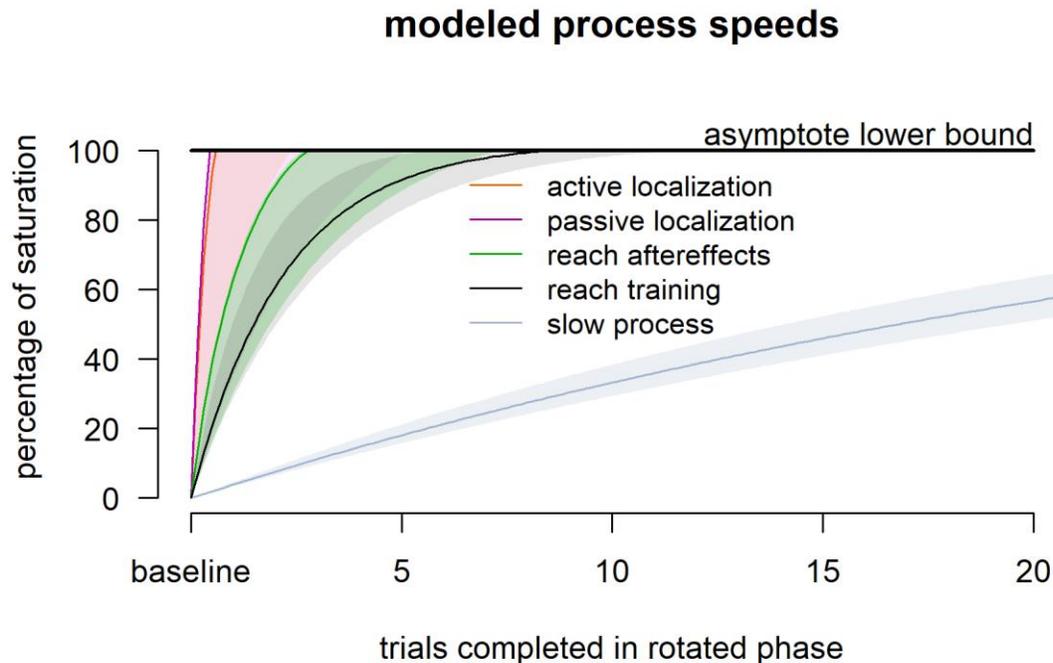


Figure 2.6. Overview of Results. For each of the five processes considered in the paper, the plot shows the change from baseline (0%) to the lower limit of the 95% confidence interval of the asymptote (100%). For the reach adaptation and the two-rate model's slow process, the highest rate of change is used. As is clear, the measures of implicit adaptation (reach aftereffects and hand localization shifts) are faster than adaptation and much faster than the model's slow process.

As expected, reach performance with a rotated cursor for all four groups adhered well to a model that consists of a fast and a slow process (McDougle et al., 2015).

Adaptation, and hence implicit processes in other studies are sometimes slower than what we found for our four groups, especially in the case where targets span the entire radial workspace (McDougle et al., 2015). However, given the fact that learning-induced changes in hand estimates and reach aftereffects saturate within one to three trials, i.e. before experiencing all four targets, it's unlikely that this saturation would have been much delayed or reduced if we tested more locations. Regardless, all other processes would likely have slowed down as well, so that our direct measures of implicit adaptation would still be faster. Of note is also that while we found that some of the

interleaved testing trials slowed down adaptation, the underlying implicit processes were still very fast.

Estimates of hand location are incredibly quick to shift, with participants only having to experience one rotated training trial to elicit the full shift. Hand localization responses are thought to measure the brain's state estimate of hand position and likely rely on at least two signals: an efferent-based predictive component and an afferent-based proprioceptive component, that both change during visuomotor rotation training (t Hart & Henriques, 2016; Mostafa et al., 2019). Active localization reflects both, and indeed exhibits slightly larger shifts than passive hand localization, which is consistent with previous findings (t Hart & Henriques, 2016; Mostafa et al., 2019), as is the size of the shift in hand localization of 20-30% of the rotation (Cressman & Henriques, 2009; Henriques & Cressman, 2012; Ruttle et al., 2018). We see here that a proportional fit seems to explain changes in hand estimates throughout the adaptation task, especially during the error-clamp phase where the size of the visual-proprioceptive discrepancy is determined by the size of the reach deviation. This is essentially a step-function which indicates that the process of changing estimates of hand location is qualitatively different from other processes of motor learning.

Reach aftereffects also emerge incredibly quickly, while not reaching asymptote as fast as shifts in hand localization. The similar size of aftereffects and hand localization shifts after just one rotated training trial potentially indicates a shared source. In addition, participants who perform no-cursor reaches with minimal instruction or more detailed instruction (to ensure strategy wasn't used) show similar rates and extents of learning of reach aftereffects (see OSF; <https://osf.io/9db8v/>), which is in line

with some previous findings (Modchalingam et al., 2019; Werner et al., 2015). If no-cursor reach deviations reflect implicit changes in state estimation, these arise much quicker than previously thought bolstering recent claims that the earliest wave of muscle activity during adaptation is influenced by implicit motor learning (Gu et al., 2019).

Other work on the time-course of implicit adaptation uses primarily two approaches. Either implicit adaptation is indirectly inferred from reach deviations and a measure of explicit learning (Bond & Taylor, 2015; McDougale et al., 2015), or it uses error-clamped feedback paradigms (Morehead et al., 2017). Results from such approaches indicate that implicit learning is slow, and we can only speculate here about why our findings are so different. In the first approach, subtracting a measure of explicit adaptation from training reach deviations relies on a largely untested assumption that implicit and explicit adaptation linearly add to produce behavior (McDougale et al., 2015; Smith et al., 2006). Aside from the effect the aiming task may have on adaptation (Leow et al., 2017; Maresch et al., 2020), this is not a biologically plausible mechanism, and it should not be surprising that an actual measure of implicit adaptation, as we use here, shows a different time course. Our results set the nature of the mechanism by which implicit and explicit adaptation are combined as a topic for future study.

In the second approach for measuring implicit adaptation, which uses error-clamped feedback to get at the time course of implicit adaptation, participants are instructed about the nature of the paradigm, prompted to ignore the visual feedback, and faced with unnaturally smooth reach trajectories throughout the task (Kim et al., 2019; Morehead et al., 2017). Since this context necessarily increases external error attribution it should also suppress implicit learning (Gastrock et al., 2020). This could

explain why error-clamped feedback paradigms slow down implicit adaptation compared to how it naturally occurs here. In sum, both approaches to assessing implicit adaptation have drawbacks, that straightforward interleaving of trials doesn't have, although our method does show some interference, potentially slowing down adaptation processes. It will remain an interesting challenge to unify results from all paradigms.

The results here raise a few other questions. We observe that reach aftereffects are as large as hand localization shifts after 1 trial of perturbed feedback, which may be an indication that hand localization shifts contribute to reach aftereffects. More compelling evidence comes from previous studies where a strong correlation between these measures was found (Cressman & Henriques, 2010; Modchalingam et al., 2019). We have shown that the size of both proprioceptive and predictive components of hand localization shifts can predict separate components of reach aftereffects (Gastrock et al., 2020). However, all evidence that hand localization shifts contribute to reach aftereffects is correlational, so that the mechanism remains unknown. In addition, while here we did manage to look at the time-course of implicit processes, the relevance for rehabilitation and skills training would lie in how these consolidate, as eventually we need to be able to move without exerting explicit control. That as little as 5 trials suffice for savings (Huberdeau et al., 2015), is hopeful and in line with the high speed of implicit processes we find here.

Conclusion

We show here that the conventionally implicit components of motor learning; no-cursor reach deviations, and changes in estimates of hand location emerge very rapidly.

The fast emergence of reach aftereffects and changes in hand estimates indicate implicit components of motor learning appear before or alongside explicit components of learning. Perhaps some implicit processes lead or maybe drive motor learning, unlike previously believed, as certainly they do not lag behind explicit processes. In addition, our results provide further evidence that implicit learning consists of at least two sub-processes that separately contribute to adaptation, and that both can be extremely fast.

Chapter 3: Reduced feedback barely slows down proprioceptive recalibration

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Abstract

Introducing altered visual feedback of the hand produces quick adaptation of reaching movements. Our lab has shown that the associated shifts in estimates of the felt position of the hand saturate within a few training trials. The current study investigates whether the rapid changes in felt hand position that occur during classic visuomotor adaptation are diminished or slowed when training feedback is reduced. We reduced feedback by either providing visual feedback only at the end of the reach (terminal feedback) or constraining hand movements to reduce motor adaptation related error signals such as sensory prediction errors and task errors (exposure). We measured changes as participants completed reaches with a 30° rotation, a -30° rotation and clamped visual feedback, with these two “impoverished” training conditions, along with classic visuomotor adaptation training, while continuously estimating their felt hand position. Training with terminal feedback slightly reduced the initial rate of change in overall adaptation. However, the rate of change in hand localization, as well as the asymptote of hand localization shifts in both the terminal feedback group and the exposure training group were not noticeably different from those in the classic training group. Taken together, shifts in felt hand position are rapid and robust responses to sensory mismatches and are at best slightly modulated when feedback is reduced. This

suggests that given the speed and invariance to the quality of feedback of proprioceptive recalibration, it could immediately contribute to all kinds of reach adaptation.

Introduction

Visuomotor adaptation leads not only to changes in motor behaviour but also changes in felt hand position (Barkley et al., 2014; Cressman & Henriques, 2010; Henriques & Cressman, 2012; Ruttle et al., 2021). Our lab has recently demonstrated that shifts in estimates of felt hand position during visuomotor adaptation develop surprisingly quickly (Ruttle et al., 2021). However, it is unknown whether this quick and robust rate of change can be slowed down, like in the case where the feedback during adaptation is impoverished. To test this, we use two training paradigms with reduced feedback that still lead to visuomotor adaptation: terminal feedback and cross-sensory exposure. We characterize both the rate of adaptation and shift in hand localization in these two paradigms and compare it with that produced during classical visuomotor adaptation.

In terminal feedback training the cursor representing the unseen hand is provided only at the end of the reach movement. Reducing visual feedback to the end of the reach during visuomotor rotation training has been shown in some studies to reduce the extent of learning and the magnitude of reach aftereffects (Barkley et al., 2014; Hinder et al., 2008, 2010; Taylor et al., 2014) although this is not always the case (Brudner et al., 2016; Heuer & Hegele, 2008; Rand & Rentsch, 2016). Whether terminal feedback also affects the rate of adaptation is usually not quantified. Compared to classic

continuous cursor feedback, training with terminal feedback has been shown to also reduce or slow down the changes in estimates of hand location (Barkley et al., 2014; Izawa & Shadmehr, 2011) but the rate of change has not been determined yet. Here we model learning on a trial-by-trial basis to be able to directly compare learning rates between terminal and continuous visual feedback.

Cross-sensory exposure training involves either passively moving the unseen hand or using a force-channel that deviates its direction, while the cursor moves directly to a target. Despite minimizing the motor or efferent signals involved, this passive exposure to a discrepancy between seen and felt hand location leads to similar or smaller reach aftereffects (Cressman & Henriques, 2010; Mostafa et al., 2019; Ruttle et al., 2018; Salomonczyk et al., 2013) and can facilitate subsequent adaptation to the same perturbation in a classic visuomotor paradigm (Bao et al., 2017; Sakamoto & Kondo, 2015; Tays et al., 2020). Not surprisingly, such training also leads to changes in hand localization, which are similar in size to those elicited when the reaches are self-generated during classical visuomotor adaptation. This suggests that this proprioceptive recalibration is primarily driven by the visual-proprioceptive mismatch between the hand and the cursor. We have previously measured hand localization shifts on a trial-by-trial basis, allowing us to assess the rate of change for these shifts. Given that these shifts in hand localization saturate within a single trial during classical visuomotor adaptation, our aim was to determine if a similar saturation rate occurs when the motor system is less engaged.

It is reasonable to assume that reducing and removing availability of certain types of feedback, like in terminal feedback or exposure training, should affect the time-

course and/or asymptotic level of adaptation. Central to this paper, it is unknown whether reducing this feedback can also slow down the rapid saturation of shifts in hand localization. It is possible that shifts in felt hand position develop so rapidly that they are unaffected by error information that generally takes time to fully saturate such as task error. Our goal is to quantify and model the rate by which these changes in felt hand position saturate on a trial-by-trial basis and how they compare across exposure, continuous or terminal feedback training. By measuring shifts in felt hand position after every training trial with these three feedback types, we can identify the role feedback has during ongoing proprioceptive recalibration.

Methods

Participants

96 (mean age=22.17, range=18-46, males=22) right-handed, healthy adults participated in this study, and gave prior, written, informed consent. All procedures were in accordance with institutional and international guidelines and were approved by the York Human Participants Review Subcommittee.

Apparatus

The experimental set-up is illustrated in Fig 3.1. While seated, participants held a vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand such that their thumb rested on top of the handle. A reflective screen was mounted horizontally, 14 cm above the robotic arm. A monitor (Samsung 510 N, 60 Hz) 28 cm above the robotic arm presented visual stimuli

via the reflective screen to appear in the same horizontal plane as the robotic arm. A Keytec touchscreen 2 cm above the robotic arm recorded localizations of the unseen thumb of the trained right hand, made the left hand's index finder (see (Cressman & Henriques, 2009) for more details). Subject's view of their training (right) arm was blocked by the reflective surface and a black cloth, draped between the touch screen and their right shoulder. The untrained, left hand was illuminated, so that any errors in reaching to the unseen, right target hand could not be attributed to errors in localizing the left, reaching hand.

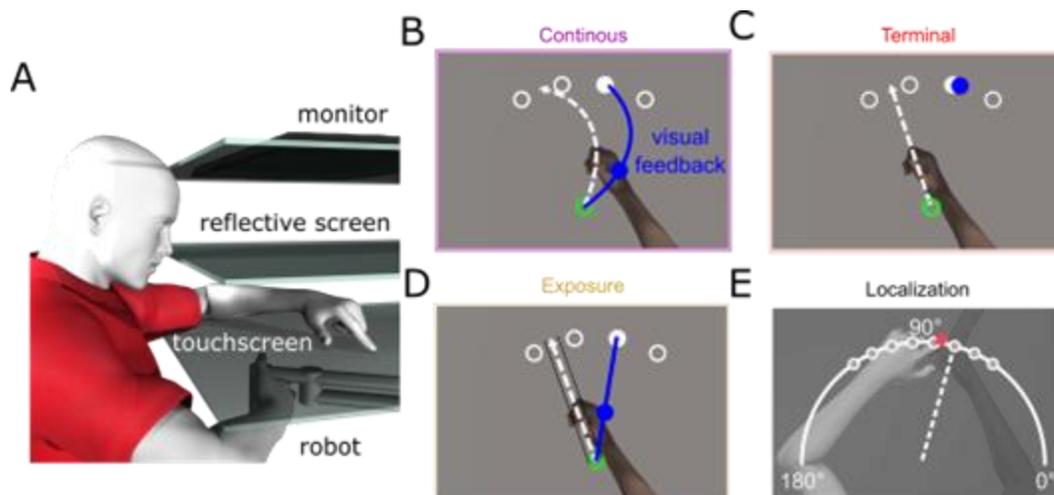


Figure 3.1. Experimental setup and design. **A:** Side view of the experimental set-up. The top layer is the monitor, middle layer is the reflective screen, and the bottom opaque layer is the touchscreen. The robot is depicted beneath with the participants' right hand grasping it. **B-D:** Top views of task specific set-ups. **B:** Continuous training trial. The home position is represented by a green circle with a 1 cm diameter; located approximately 20 cm in front of the subject. Targets are represented by white circles with a 1 cm diameter located 12 cm radially from the home position at 60°, 80°, 100° and 120°. Participants hand cursor was also a 1 cm diameter blue circle. **C:** Terminal training trial. The same hand cursor was only visible at the end of the movement for 500 ms to allow for comparison to the visible target. **D:** Exposure training trial. The robot constrained the participants movements (denoted by solid black lines either side of white dashed line), so they perfectly countered the rotation and only decided the speed of movement. **E:** Localization test trial. Participants were passively moved to one of the eight target locations, 55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°. Subsequently, participants used a touch screen to indicate on a white arc spanning 180° where their unseen right hand was.

Stimuli

Illustrated in Fig 3.1B-D, at the beginning of each trial, we displayed one of four potential targets, (white 1 cm diameter circles), 12 cm from the start position at 60°, 80°, 100° and 120°. The home position (green 1 cm circle) and the participants' hand cursor (blue 1 cm circle) were also visible at the beginning of the trial (for 2 of the 3 paradigms). During proprioceptive localization trials Fig 3.1E a white arc, 12 cm from the home position, was visible on the screen spanning from 0° to 180°. Participants were required to hold their hand still at the home position for 250 ms before any trial would begin.

Trial Types

Classic continuous training trials

Participants (N=32) reached as accurately as possible with their right hand to one of four possible target locations, while their hand cursor was continuously visible (Fig 3.1B). In all reaching trials, i.e., with cursor and with clamped cursor (explained below), participants had to reach out 12 cm from the home position to a force cushion within 800 ms. Participants received auditory feedback throughout training indicating if they met the distance-time criteria or not. The target would then disappear, and the robot manipulandum returned the right hand to the home position where they waited 250 ms for the next trial. The hand cursor was aligned with the hand for the first 64 training trials, then rotated 30° CW for 160 training trials and then rotated 30° CCW for 16 training trials. This was followed by 48 visual error-clamped trials, dashed lines in Fig 3.2, which were identical to the reach training trials except that the cursor always moved

on a straight line to the target. The distance of the visual error-clamped cursor from the home position was identical to the distance of the hand from the home position.

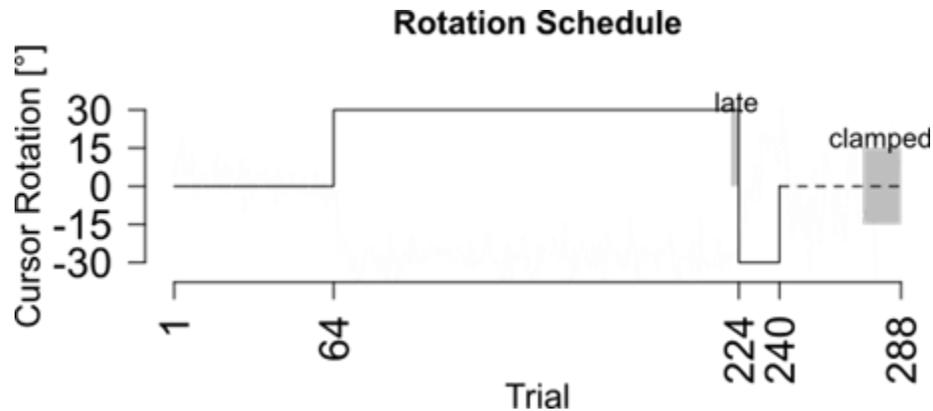


Figure 3.2. Experimental Schedule. Participants reached to visual targets with a perturbation denoted by the black line. The dotted line at the end of the paradigm signifies visually clamped trials where there was no visual error as the cursor always moved to the target regardless of the participants movement direction. The final 16 clamped trials were used in the rebound analysis trials: 273–288.

Terminal training trials

Terminal training trials were identical to classic training trials, except that the participants' (N=32) hand cursor was not visible during the entire reach movement, from the home position to the target (Fig 3.1C). Once the participant moved their hand 12 cm from the home position, the robot locked their hand in place and the hand cursor became visible for 500 ms for the participant to be able to see any potential movement errors. The auditory cues were present to encourage consistent speed throughout the experiment. These participants also experienced a phase of visual error clamped trials which were identical to the classic clamp trials, with the cursor being visible the entire trial, not just at the end.

Exposure training trials

Exposure training trials differ from those in the previous two paradigms (Fig 3.1D). Participants (N=32) were not in control of the direction they moved during reach training trials. The handle at the end of the robot arm they were grasping was constrained to a force channel, so participants only chose the speed of movement, not direction, removing any performance error. If they attempted to move outside of the pathway, a resistant force, proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s), was created perpendicular to the pathway (Henriques & Soechting, 2003). During the visual error clamp phase of the experiment, participants were instructed to actively move their hands, so these trials were identical to the previous two paradigms. Participants still heard the auditory feedback to encourage consistent speed across training paradigms.

Localization test trials

All three groups completed a passive localization of their hand position after every training trial. These proprioceptive localization trials (Fig 3.1E) were executed to one of two targets, 5° on either side of the previous training target. The localization targets were close to the preceding training targets to maximize generalization, but not on the same location to be able to detect if participants simply touched the remembered visual target from the previous trial. All eight hand-targets (55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°; one on each side of each of the training targets) were cycled through before being repeated. After the white arc appeared on the screen, participants' right unseen, adapted hand was dragged to one of the target locations. Then once their target hand was locked in place, participants used their visible, left index finger, to indicate on the touchscreen, along a 180° arc, where they believed their right,

stationary, unseen hand was. The arc was continuously visible until the touchscreen registered the participants estimate. We tested if localization responses were biased towards the preceding visual target in both the end of the aligned and the end of the rotated phase in all three conditions, but there was no bias in 5 of 6 tests. There is a 2.4° bias in the aligned phase of the terminal condition, which is much smaller than the 10° distance between the localization target pairs.

Data Analysis

We analyzed hand localization and reach training trials separately from each other, but their rates of change (see Table 3.1) can be compared.

Hand Localization: Estimates of hand location were based on the angular endpoint error between the movement endpoint of the right unseen hand and the left hands responses on the touchscreen, relative to the home position.

Reaching with a cursor and visual error-clamp trials: To quantify reach performance during training, the angular difference between a straight line from the home position to the target and a straight line from the home position and the point of maximum velocity is computed. This was calculated for all training trials both classic and terminal training but only for the error clamp trials for exposure training.

Analyses

All data was visually screened for incorrect trials by lab volunteers naïve to the purpose of the study. Subsequently, outliers of more than three standard deviations

across participants within each trial were also deleted, in total, we removed 2.4% of the trials. All measures were normalized, by subtracting out each subjects' average performance during the second half of the aligned session (trials 33-64). The same preprocessing steps were applied to both localization and reach trials.

To quantify the time courses of changes in reaching and localization trials, we fit an exponential decay model to the first rotation (trial 65-224) separately for hand localizations and reach data. In this model, the value of each process on the next trial (P_{t1}) is the current process' value (P_{t0}) minus the product of the rate of change (L) multiplied by the error on the current trial, which is the difference between the asymptote (A) and the process' value on the current trial (P_{t0}).

$$P_{t1} = P_{t0} - L * (A - P_{t0})$$

The parameter L was constrained to the range $[0,1]$, and the parameter A to $[0, 2 \cdot \max(\text{data})]$. We allowed for negative asymptotes indicating individuals had proprioceptive recalibration in the unexpected direction to ensure that all participants had a meaningful learning rate (4 of 96 participants showed this pattern of recalibration). For all paradigms using only the first rotations data (trials 65-224), the model was fit to 1) the localization data and 2) the reach data. For the localization data fit, a zero was prepended to account for the fact that responses in these trials already changed because of the previous training trial. The parameters were also bootstrapped (1k resamples per fit) across participants to get a 95% confidence interval for both parameters.

The decay model was used to fit a rate of change and asymptote for training and hand localization data for each of the feedback types. We then used the rate of change and bootstrapped 95% confidence interval of the mean for the asymptote to calculate the saturation trial for illustration purposes. The first trial where the mean response moved inside the confidence interval of the asymptote was considered the saturation trial (Cumming & Finch, 2005). We used the bootstrapped 95%CI to compare across the three types of feedback on three parameters (rate of change, asymptote and saturation trial) describing the time courses. Parameter values which don't overlap with the CIs of those for the other groups indicate significant differences (Cumming & Finch, 2005). This allows us to not only characterize the rate of change but detect even small differences, across feedback conditions that would normally be obscured when comparing the average of a block of trials. We used Bayesian statistics to compare learning rates and asymptotes across feedback types and to zero. In cases where we did not have a decay model parameter such as the rebound phase of training, we averaged the last 16 trials and did simple Bayes Factors to identify equivalence or significant differences. Bayes Factors are the ratio of how likely the alternative hypothesis (there is a difference) is over how likely the null hypothesis (there is equivalence) is, given a non-informative prior and the data. With $BF_{10} = 1$ both are equally likely. Within the interval $\frac{1}{3}$ to 3 (either hypothesis is up to 3 times more likely than the other) there is only anecdotal evidence (Jeffreys, 1961; Rouder et al., 2009). However, a $BF_{10} > 3$ or $BF_{10} < \frac{1}{3}$ (or 0.333) is considered moderate evidence in favor of the alternative hypothesis or the null hypothesis, respectively, whereas values of $BF_{10} > 10$ or $BF_{10} < 0.1$ are considered strong evidence.

Similar to our previous study (Ruttle et al., 2021) we applied a simple proportional model that stipulates the size of shift in hand estimates will be a proportion of the size of the visual-distortion. We also fit a one-rate model to the localization data and computed AIC's for both simple models, where the smaller AIC by at least two was considered the superior model.

The datasets for the current study are available on Open Science Framework, <https://osf.io/6q2zd/> while the code and analysis scripts are available on github <https://github.com/JennR1990/VisualFeedback>.

Results

We used multiple approaches to investigate if reducing sensory prediction and performance errors during training slows the rapid changes in estimates of hand location or reduces rate of adaptation in motor learning. Specifically, we used an exponential decay model to compute rates of change and asymptotes (and their bootstrapped 95% confidence intervals), as reported in Table 3.1, for localization and reaches. Figure 3.3 shows all estimates of hand location across the three feedback groups (Fig 3.3A&B) as well as reach training trials for both the continuous and terminal groups and the visual error clamp trials for the exposure paradigm (Fig 3.3C&D). The saturation-timepoint occurs for the first trial where the signal as modelled by its rate of change is equal to or greater than the lower bound of the 95% CI for its asymptote. These saturation timepoints are also reported in Table 3.1 and depicted in Fig 3.3E&F.

Bootstrapped Decay Model Parameters				
		Continuous	Terminal	Exposure
Localization	<i>rate of change</i>	100%	43.5%	69%

		[29.0% - 100%]	[7% - 100%]	[47% - 100%]
	<i>asymptote</i>	6.9° [5.9° - 8.0°]	6.3° [5.3° - 7.8°]	5.1° [3.8° - 6.4°]
	<i>saturation trial</i>	1 [1 - 7]	4 [1 - 23]	2 [1 - 3]
Reach training	<i>rate of change</i>	27.0% [20.1% - 32.8%]	14.2% [10.0% - 20.0%]	-
	<i>asymptote</i>	28.6° [27.8° - 29.5°]	27.1° [26.1° - 29.7°]	-
	<i>saturation trial</i>	12 [10 - 16]	19 [13 - 27]	-

Table 3.1. Adaptation estimates for localization trials and reach training trials. Rate of change estimates, asymptote and average trial participants reached asymptote are provided for each training condition and estimates of hand location, this was computed on the averaged participant data. Bootstrapped 95% confidence intervals are included for each estimate. Parameters were estimated using an exponential decay model.

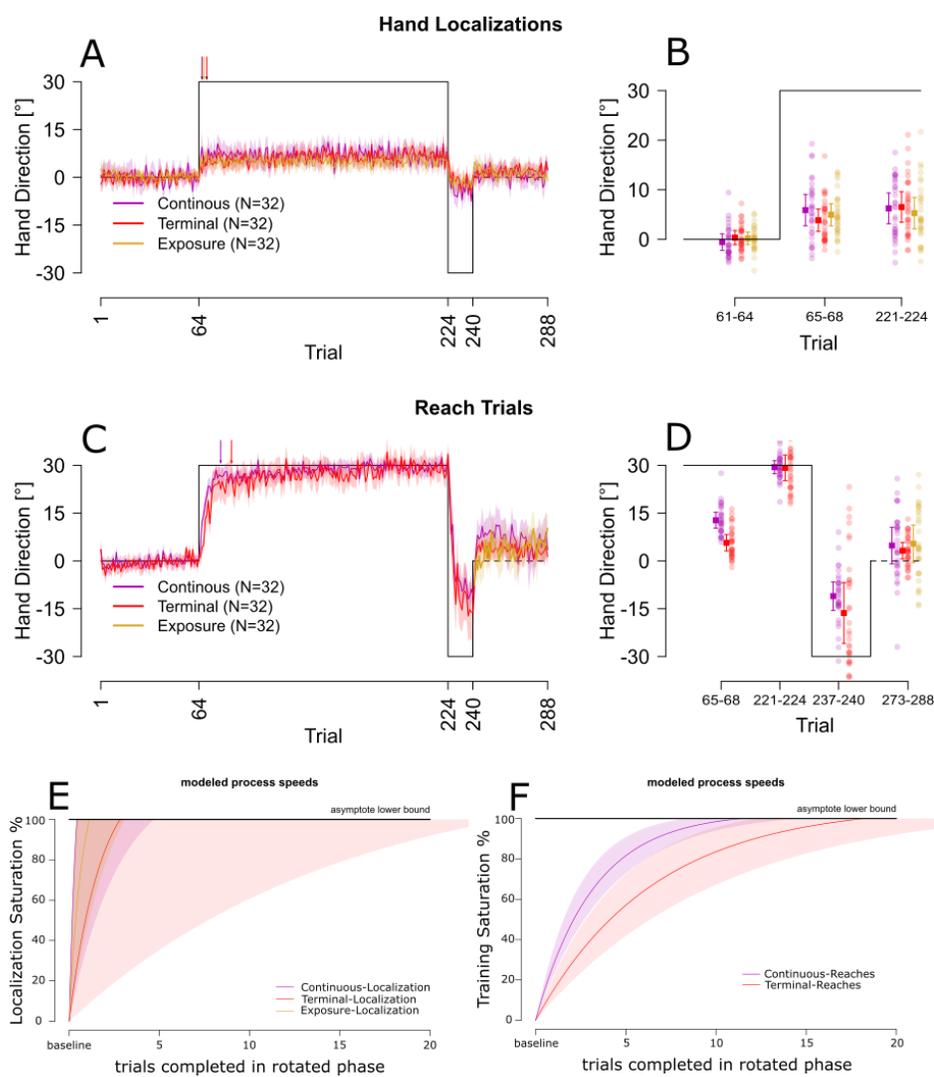


Figure 3.3. Localization and reach trials for all feedback types. A. Estimates of hand location throughout the course of training. The solid-colored lines are the deviations between actual and indicated hand position averaged across all participants within a paradigm, the corresponding shaded regions are 95% confidence intervals. Colored arrows indicate the trial participants reached asymptote on average, saturation trial. B. Close-up of estimates of hand location for different time points in the training schedule. Individual participant data are coded by color along side paradigm averages with error bars representing ± 2 SE. C. Endpoint error for all three paradigms across the entire training paradigm. Solid lines are the averages across participants within each paradigm, and the corresponding shaded regions are the 95% confidence intervals. Colored arrows indicate the average trial at which participants reached asymptote, saturation trial. D. Average reach direction during different time points of the training schedule. Individual data is shown around the mean for each paradigm. E & F. Saturation trial depicted as a curve. E. Localization. F. Reach saturation trials. The shaded regions in both E & F represent the 95% confidence intervals.

Speed of Estimates of hand location

The main focus of this study is to compare the speed of proprioceptive recalibration across feedback types. Following every training trial (analysis below), we measured changes in hand estimates by having participants indicate the felt location of their unseen right hand after it was passively displaced. All three feedback groups produced robust shifts in felt hand position of $\sim 6^\circ$, (asymptotes in Table 3.1) that were significantly different from baseline ($BF_{10} > 1000$ for all three asymptotes), but fairly similar across all training conditions ($BF_{10}=0.26$). More importantly, the rates of change were very high resulting in the shift saturating within 1-4 rotated training trials regardless of training as shown in Table 3.1 (rate of change, saturation trials) and depicted by the colored arrows in Fig 3.3A. While the very rapid shift in hand localization in the continuous group appears to saturate even faster than those of the exposure and terminal feedback groups, their bootstrapped confidence intervals for the rate of change and saturation overlap suggesting no significant effect of feedback on the speed by which proprioception recalibrates. However, when we calculate saturation trial (Table 3.1) we can see these hand localization shifts take on average four trials for terminal, compared to only one for continuous and two for exposure. Bayesian statistics on learning rates show anecdotal support for a difference between continuous and terminal

($BF_{10}=1.9$) and support similarity between continuous and exposure ($BF_{10}=.26$). Thus, the type of feedback had no or at best minimal effect on rate of change of proprioceptive recalibration. In summary, proprioceptive recalibration emerged and saturated surprisingly quickly even in the reduced feedback-training groups.

Speed of visuomotor adaptation

As is customary, we wanted to ensure overall adaptation had occurred and whether adaptation differed across the different feedback groups. Participants in the exposure training group were not in control of movement direction during the first three phases of the experiment and thus were not included in this analysis. As reported in Table 3.1, rates of change in the initial learning phase are faster for continuous training [27%, 95%CI: 20.1% - 32.8%] than for the terminal training paradigm [14.2%, 95%CI 10.0% - 20.0%], which is evidenced by mean learning rate for continuous training being outside the confidence interval of the terminal training. Moreover, adaptation saturated at trial 12 for continuous (at 28.6°) and at trial 19 for terminal training (27.1°) as reported in Table 3.1 and indicated by arrows in Fig 3.3C and plotted in Fig 3.3F. This is reflected in the average degree of compensation in the early phase of training (Fig 3.3D&F) which shows that compensation for terminal feedback (5°) was lower than that for continuous feedback (12°). However, a closer inspection of these trial-by-trial reaches in Fig 3.3C shows that while continuous feedback reaches maximum compensation by the 12th trial (purple arrow), by that same trial for the terminal feedback shows that compensation is merely a few degrees or 10% behind. This last 10% compensation is what requires the additional seven training trials to reach a similar asymptotic level.

Despite the slower rate of adaptation in the terminal feedback group the asymptote was equivalent for terminal and continuous feedback ($BF_{10}=0.25$, shows moderate evidence for the null hypothesis) which can be seen in Fig 3.3C and in the overlapping CI for asymptote for reach training in Table 3.1. Together, these results indicate terminal feedback reduces learning rate, but extent of learning is comparable after ~20 trials.

To test if the participants with exposure feedback produced motor changes, we used the reach deviations in the visual error-clamp phase since this was the only time the exposure training group controlled the direction of their hand movements. Bayes Factors₁₀ of > 3 indicate moderate evidence for a rebound in these error-clamped trials relative to baseline for all three groups (C= 4.8°, T=3.2°, E=5.4°, far right of Fig 3.3C&D). There was also moderate evidence that they are the same across feedback groups ($BF_{10}=0.14$). This result shows that there was adaptation in the exposure training group, and that at least during the error-clamp phase this was comparable to that in the other groups.

Our earlier work suggests that proprioceptive recalibration is driven by the visual-proprioceptive discrepancy (Cressman & Henriques, 2010; Mostafa et al., 2019; Salomonczyk et al., 2013), which for the visually-clamped trials, is equal to the size of the rebound which varies across individual participants. Hence, here we investigate the relationship between the size of the hand localization shift and the size of this rebound (Fig 3.4D). A simple linear regression showed a moderate positive relationship between reach deviation during error clamp trials and estimates of hand location for all three training paradigms. Regression values are: Continuous $R^2=.22$, $F(1,30)=8.51$, $p=.006$,

Terminal $R^2=0.15$, $F(1,30)=5.19$, $p=0.03$ & Exposure $R^2=0.13$, $F(1,30)=4.59$, $p=0.04$. The fitted slopes (β s in Fig 3.4D) all indicate that proprioceptive recalibration is around 20% of the rotation, as we found earlier (Ruttle et al., 2021). We also fit a simple model that suggests shifts in estimates of hand location are directly proportional to the visual distortion during regular cursor training (Fig 3.4A-C). We find the proportions suggested by the model are visually similar to the beta values given by the regression between reach deviations during the clamp phase and shifts in estimates of hand location. The proportional model also provides a better fit than just a simple one-rate model fit to the localization data based on all AIC's being smaller for the proportional model (Continuous=17.68<25.52; Terminal=16.26<22.63; Exposure=12.15<22.73).

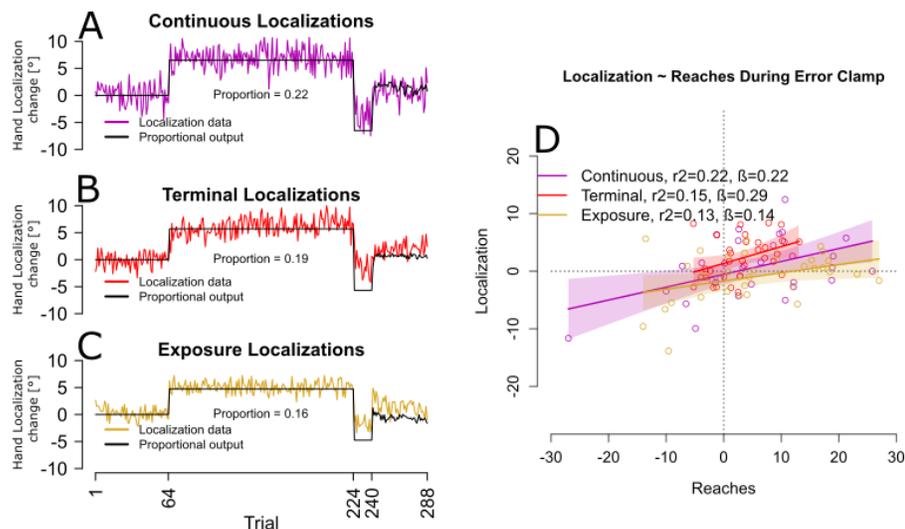


Figure 3.4. Visuo-proprioceptive discrepancy. A-C. A simple proportional model, that says the size of the shifts in hand estimates should be directly related to the size of the visual distortion, is applied to each set of localization data visible in figure 3. D. Comparison of reach deviations and shifts in hand location during error clamp. Each training paradigm has its own color, and each dot represents one participant. The regression line and the 95% confidence interval around the regression line is included in the corresponding color.

Discussion

We have previously shown that changes in estimates of unseen hand location saturate after a single trial of classic visuomotor adaptation with a continuously visible cursor. Here we measure the extent that this surprisingly rapid saturation may be slowed down with reduced feedback during training. We reduced feedback with terminal feedback or with robot constrained movements in an exposure paradigm. By measuring estimates of unseen hand position after every training trial, we captured the time course of proprioceptive recalibration in finer detail. Training with terminal feedback or with passive exposure of a 30° rotation only slightly slowed the saturation of these shifts in proprioceptive estimate of hand position by a few trials, although not significantly. On average, the terminal group took 4 trials (1-23), the exposure group took 2 trials (1-3) compared to 1 trial (1-7) for continuous feedback, but an equally large shift in felt hand position. We found that even with reduced feedback, changes in felt hand position saturate very quickly during training, perhaps earlier than motor adaptation saturates.

A secondary finding is that motor adaptation was slowed down when feedback was reduced to only the endpoint position, requiring 19 (13-27) trials for participants to reach saturation for terminal adaptation compared to only 12 (10-16) trials for classical visuomotor adaptation. Nonetheless, final adaptation was equal for the terminal feedback and continuous feedback groups, and all visual feedback types, including exposure training, produced the same rebounds. In short, motor adaptation also saturated fairly quickly with only a small reduction in the speed of these changes.

Learning-induced Changes in Hand Localizations

Following the completion of every training trial participants indicated the felt position of their then passively displaced hand. Shifts in felt hand position have been shown to be implicit (Modchalingam et al., 2019) and driven by the visual-proprioceptive mismatch between visible cursor location and felt position of the hand (Henriques & Cressman, 2012; Mostafa et al., 2019; Salomonczyk et al., 2013). Previous work in our lab and others has shown that the shift in felt hand position is a robust feature of learning under various conditions (Cameron et al., 2012; Gastrock et al., 2020; Henriques & Cressman, 2012; Izawa & Shadmehr, 2011; Ruttle et al., 2018, 2021). Here we were able to go a step further by measuring shifts in felt hand position after every training trial so that we can accurately compare the rate of change of hand localization between various kinds of training feedback.

As in the classic continuous-cursor training, the changes in unseen hand location estimates were rapid; with most participants for all groups saturating within a few trials. Nonetheless, terminal feedback required a few additional trials for changes in hand localization to reach a similar asymptote compared to continuous training. In our previous study comparing terminal and continuous feedback training, we found that proprioceptive recalibration (change in estimates of hand location) required a third block of 99 trials before achieving the same magnitude of proprioceptive recalibration (Barkley et al., 2014). This is most likely because the method for measuring perceived hand location used in the previous study was a two-alternative force choice (2-AFC) method involving 50 trials to get a single estimate. While the 2-AFC method does an equivalent job of measuring the magnitude of proprioceptive recalibration as the method used in this and other studies, it requires far more training to overcome decay during

measurement (Clayton et al., 2014; Ruttle et al., 2016; Zbib et al., 2016). The method used in the current study is able to measure hand localization shifts much faster with the same consistency (Clayton et al., 2014).

Exposure training led to a similar rate of change in hand localization as classic visuomotor training, requiring only one more training trial to reach asymptote. This is consistent with our previous study (Ruttle et al., 2018), where we found a similar rate and size of changes in estimates of hand location, and reach aftereffects, only after every 6-12 cursor-rotation training trials. In this previous paper, the average proprioceptive recalibration for exposure training was 10° , which is larger than the 5° - 7° shift usually seen in both our exposure (Cressman & Henriques, 2010; Mostafa et al., 2019; Salomonczyk et al., 2013) and classic training paradigms (Barkley et al., 2014; Modchalingam et al., 2019; Ruttle et al., 2016), including those measured in the current study. However, all these shifts in perceived hand location are within a reasonable range and really emphasize the robustness and rapidness of changes in felt hand position that co-occur when experiencing altered visual feedback of the hand.

The position of our hand is crucial in reach adaptation: both the starting position and the goal of the movement are defined by it. It may very well be possible that reach adaptation is, to some degree, driven by our sense of limb position: proprioception, even when it is recalibrated (Tsay et al., 2022). We have previously shown that proprioception can recalibrate so quickly, that it fully precedes reach adaptation (Ruttle et al., 2021). In such cases it is a signal capable of driving reach adaptation. Since the speed of hand localization shifts in exposure training is indistinguishable from that in continuous training, this could suggest that in any situation with a visuo-proprioceptive

discrepancy and proprioceptive recalibration, the shifted hand position could be driving some part of reach adaptation. That is: before sensory prediction error or task errors have had a chance to influence reach directions. Since we see recalibrated proprioception in a wide variety of tasks, such as when people are told about the perturbation (Modchalingam et al., 2019) or can clearly see where perturbation comes from (Gastrock et al., 2020) and told to ignore it (Tsay et al., 2020) the current results may indicate that proprioceptive recalibration happens in time for it to drive reach adaptation under many varying conditions. Of course, it has not yet been shown that recalibrated proprioception causally drives reach adaptation, so this remains speculation.

Adaptation to Varying Types of Feedback

While not the main focus of this study, the data allows a glance at the processes underlying motor adaptation as well, by testing how they respond to various kinds of feedback. Humans are very visually dominant beings and favour vision over many other senses for guiding reaching movements. Thus, it is not surprising that reducing visual feedback of the reach to the end of the reaching movement, when adapting to a visual perturbation can result in poorer learning performance compared to when the cursor is continuously visible. Nonetheless, many studies, including ours, find that given enough training trials similar levels of asymptote are achieved for both training paradigms (Brudner et al., 2016; Heuer & Hegele, 2008; Rand & Rentsch, 2016; Schween & Hegele, 2017; Song et al., 2020; Wijeyaratnam et al., 2019), although in some cases, learning extent is smaller (Barkley et al., 2014). The exact difference in the rate of the learning is not usually measured or reported in previous studies; few studies compare

whether the average first block of trials differ between the different paradigms (Taylor et al., 2014). In the current study, when we fit a single exponential to the two training paradigms, we find that compensation for a terminal feedback visuomotor rotation is only half as fast as that for a continuous distortion (14.2% vs 27%) and takes 58% more training trials (19 vs 12) to saturate. By the 12th trial, however, compensation produced with terminal feedback is only 10% lower than those for continuous. The rate of learning could explain conflicting results regarding whether performance in terminal and continuous feedback training paradigms differ. Taken together, this indicates the same mechanisms may facilitate learning in these conditions, but the reduced feedback merely diminishes the overall speed by which motor and sensory changes hit asymptote levels.

During reaching trials in the clamp phase, participants showed small but significant rebounds that were similar in all three training groups, including in the exposure group where the preceding training did not involve active hand movements. This confirms that as in our previous studies using exposure training (Cressman & Henriques, 2010; Mostafa et al., 2019; Ruttle et al., 2018; Salomonczyk et al., 2013), that visual-proprioceptive discrepancies are sufficient to lead to changes in hand movements.

Conclusion

Extending our previous work, here we show that regardless of available feedback type, changes in felt hand position appear incredibly quickly. Reducing feedback did not slow down proprioceptive recalibration. The impact was greater for reach adaptation,

with rate of adaptation for terminal being slower than continuous. With similar asymptotes, the extent of learning was significant regardless of training paradigm. In conclusion, changes in felt hand position, are a rapid and resilient feature of adaptation which saturates before reach training trials, regardless of feedback during visuomotor training.

Chapter 4: Proprioceptive recalibration is unaffected by varied rotations

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Abstract

Visuomotor adaptation leads to changes in movement kinematics as well as estimates of hand position. The process of adapting to a visual misalignment of the hand of 30° or more leads to a rapid change in felt hand position of ~6°. Here, we test if frequently changing the size and sign of the rotation will produce smaller or slower shifts in the felt hand position as the uncertainty in the rotation increases. We changed the size and sign of the visual rotation between -30° and +30° in steps of 15° every 12 trials and probed shifts in felt hand position after every training trial to see if these shifts occurred as fast as previously found. We applied an exponential decay rate model to identify asymptotes and the learning rates for each block. We find that robust shifts in felt hand position appear incredibly quick throughout each training block. We see an increase in rates of change, but no change in the extent of adaptation for reaching training, indicating evidence of structural learning. Overall, we find that visual recalibration of hand-proprioception is incredibly robust and has the potential to lead reach adaptation given the rapid changes in state estimates.

Introduction

Reach adaptation can occur quickly and in response to many perturbations, including force fields, displacing prisms, and visuomotor rotations (Krakauer et al., 2019). For visuomotor adaptation, rapid changes in felt hand position also emerge.

Previous studies have shown that felt hand position shifts about 6° of a 30° visual distortion; this occurs when the visuomotor training experienced is a rotation or a lateral shift (Cressman & Henriques, 2009). The visually-induced changes in proprioceptive estimates occur when the visual distortion is introduced abruptly and gradually, with terminal feedback and for rotations as large as 60° (Modchalingam et al., 2019). These changes in felt hand position occur even during passive-exposure training, when the hand cursor moves directly towards the target while the robot either moves or constrains hand movement based on the rotation size, thereby removing volitional movement or performance errors (Cressman & Henriques, 2010; Ruttle et al., 2022). Given our recent findings that these changes in felt hand position, on average, can saturate within a single trial of continuous altered visual feedback and within four trials where the cursor is only visible at the end of the reaching movement, we wanted to investigate further how robust and quick these perceptual changes are. Specifically, the aim of the current study was to test if these rapid visually-induced changes in felt hand direction continue to occur rapidly even when the size and direction of the visual perturbation change every 12 or so trials.

The speed of reach adaptation is also affected by previous training to different perturbations. It is reduced when participants must adapt to a visual perturbation in the opposite direction within ~5 hours of adapting to the first rotation, suggesting that adapting to one visuomotor rotation (e.g. 30° CW) interferes with adaptation to a second rotation in the opposite direction (e.g. 30° CCW) (Krakauer & Shadmehr, 2006). In contrast, if the second visuomotor adaptation is in the same direction (even for different magnitudes), even after a period of rest in between, adaptation occurs quicker; this

faster re-learning is known as savings (Coltman et al., 2021). Thus, the changes in the direction of the visuomotor rotation can decrease or increase the learning rate of adaptation for subsequent visuomotor rotations.

Adaptation to a series of perturbations that vary in direction and size has a different effect on subsequent adaptation. For example, when changing the size and direction of the visuomotor rotation every 6-20 trials and then including a final test to one or a short series of perturbations after a short washout period (where the cursor is aligned with hand movement), the rate of adaptation of this final perturbation is usually faster compared to a naïve group who are adapting to the same test perturbation for the first time (Braun et al., 2009a, 2009b; Coltman et al., 2021; Seidler, 2004, 2007; Turnham et al., 2012). This consistent result suggests that participants may learn the structure of the environment during training to the varied perturbation, and is called structural learning (Braun et al., 2009a, 2009b; Coltman et al., 2021; Seidler, 2004, 2007; Turnham et al., 2012). This form of learning has also been shown to extend to gain and sequence learning (Seidler, 2004).

However, these studies usually did not investigate the learning rates during training with the random rotation phases since their focus is on the final learning phase following a washout period. While not the main goal of the current study, given our sensitive method of the rate of change and our large sample size of participants who were all given the same set of varied visuomotor rotation, we also measure whether structural learning for reach adaptation emerges within the training phases as well.

It is not clear whether structural learning for reach adaptation would also affect proprioceptive recalibration. Given the variability and increased uncertainty of the

rotation, the rate of change or extent of these shifts in felt hand position may diminish for subsequent blocks of visuomotor rotation, likely due to less weight being placed on the visual feedback from the preceding trials. Alternately, given the quick response of estimates of felt hand position to previously altered visual feedback of their hand, it is possible that the rate of change and extent responds to the most recent visual experience and thus is largely immune to the history of changes in perturbation.

Methods

Participants

32 (mean age=20.38, range=18-34, males=9) right-handed, healthy adults participated in this study and gave prior, written, informed consent. All procedures were in accordance with institutional and international guidelines and were approved by the York Human Participants Review Subcommittee.

Apparatus

The experimental setup is illustrated in Fig 4.1A. While seated, participants held a vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand such that their thumb rested on top of the handle. A reflective screen was mounted horizontally, 14 cm above the robotic arm. A monitor (Samsung 510 N, 60 Hz), which was 28 cm above the robotic arm presented visual stimuli via the reflective screen to appear in the same horizontal plane as the robotic arm. A Keytec touchscreen 2 cm above the robotic arm recorded localization endpoints of the left index finger to the unseen right thumb targets. The participant's

view of their training (right) arm was blocked by the reflective surface, and a black cloth draped between the touch screen and their right shoulder. The untrained left hand was illuminated so that any errors in reaching to the unseen, right target thumb could not be attributed to errors in localizing the left, reaching hand.

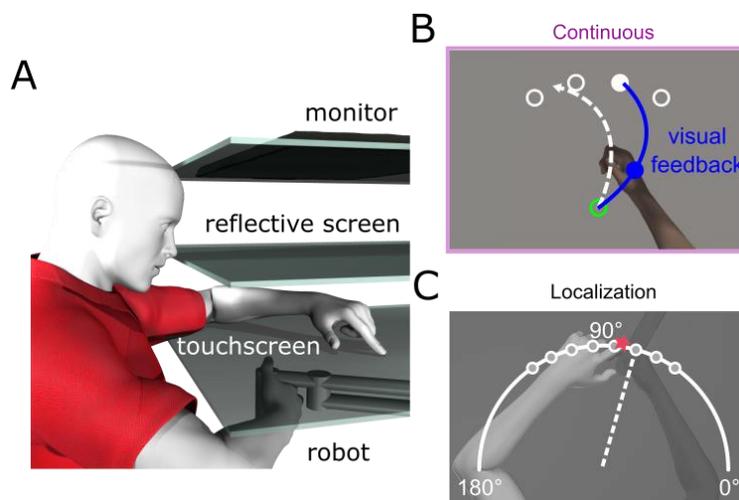


Figure 4.1. Experimental setup and design. **A:** Side view of the experimental set-up. The top layer is the monitor, middle layer is the reflective screen, and the bottom opaque layer is the touchscreen. The robot is depicted beneath with the participants' right hand grasping it. **B&C:** Top views of task specific set-ups. **B:** Continuous training trial. The home position is represented by a green circle with a 1 cm diameter; located approximately 20 cm in front of the subject. Targets are represented by white circles with a 1 cm diameter located 12 cm radially from the home position at 60°, 80°, 100° and 120°. Participants hand cursor was also a 1 cm diameter blue circle. **C:** Localization test trial. Participants were passively moved to one of the eight target locations, 55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°. Subsequently, participants used a touchscreen to indicate on a white arc, spanning 180°, where their unseen right hand was.

Stimuli

At the beginning of each reach trial Fig 4.1B, one of four potential targets was displayed, (white 1 cm diameter circles), 12 cm from the start position at 60°, 80°, 100° and 120°. The home position (green 1 cm circle) and the participant's hand cursor (blue 1 cm circle) were also visible at the beginning of the trial. During proprioceptive localization trials, Fig 4.1C, a white arc, 12 cm from the home position, was visible on the screen spanning from 0° to 180°. Participants were required to hold their hand still at the home position for 250 ms before any trial would begin.

Trial Types

Training trials

Participants (N=32) reached as accurately as possible with their right hand to one of four possible target locations while their hand cursor was continuously visible (Fig 4.1B). In all reaching trials, i.e., with a cursor and with a clamped cursor, participants had to reach 12 cm away from the home position to a force cushion within 800 ms. Participants received auditory feedback throughout training indicating if they met the distance-time criteria or not. The target would then disappear, and the robot manipulandum returned the right hand to the home position, where they waited 250 ms for the next trial. The hand cursor was aligned with the hand for the first 48 training trials; then the rotation changed every 12 trials to one of 5 possible rotation sizes and directions (-30, -15, 0, 15, 30).

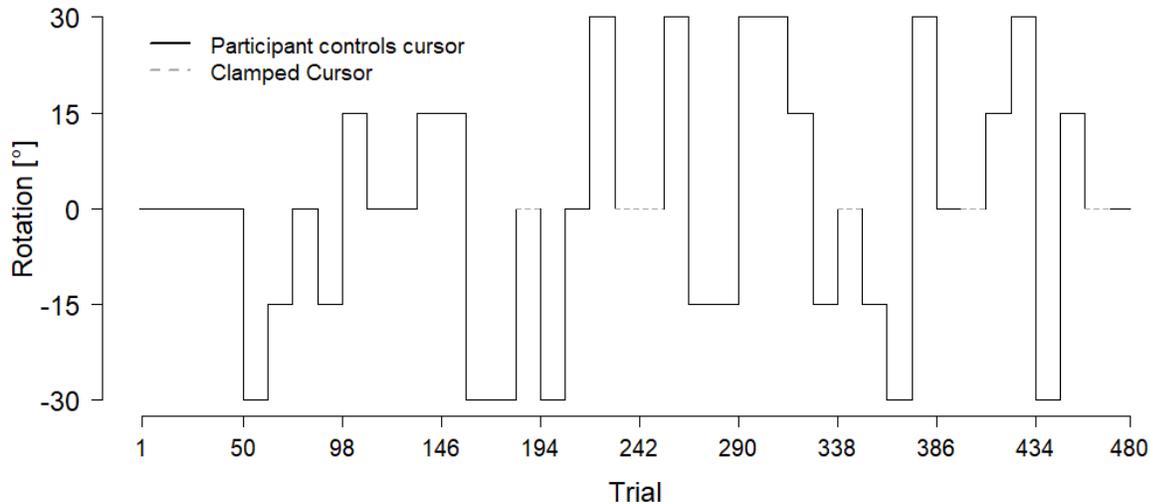


Figure 4.2. Experimental Schedule. Participants reached to visual targets with a perturbation denoted by the black line. The dotted line throughout the paradigm signifies clamped trials where there was no visual error as the cursor always moved to the target regardless of the participants movement direction.

Clamp trials

The trial structure is the same as training trials, except that the cursor moved directly to the target regardless of the direction the participant moved their hand. The cursors' distance from the home position was tied to the distance the participant moved, but all visual task error was removed as the cursor moved perfectly to the target. Hence, “clamped” refers to the fact the visual error has been clamped or removed. These trials are useful for measuring implicit driven changes in reach direction without giving error-feedback and are shown as dashed lines in Fig 4.2. For the purpose of this dissertation, performance in clamp trials was not analyzed.

Localization test trials

In the proprioceptive localization trials (Fig 4.1C), the robot passively moved the unseen, right-trained hand to one of the two locations, 5° on either side of the previous training target. The participants then used the index finger of their left untrained, visible hand to indicate the felt location of the unseen right hand, specifically the thumb. The localization targets were close to the preceding training targets to maximize generalization but not in the same location to be able to detect if participants simply touched the remembered visual target from the previous trial. All eight hand-targets (55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°; one on each side of each of the training targets) were cycled through before being repeated. After the white arc appeared on the screen, the participants' right unseen, adapted hand was dragged to one of the target locations. Once their target hand was locked in place, participants used their visible left index finger to indicate on the touchscreen, along a 180° arc, where they believed their right, stationary, unseen hand was. The arc was continuously visible until the touchscreen registered the participant's estimate. These passive localization trials followed every training trial, such that these hand-localization trials were interleaved with the cursor trials described above.

Data Analysis

We analyzed reach training and hand localization trials separately, but their rates of change (see Table 4.1) can be compared.

Reaching with a cursor and clamp trials: To quantify reach performance during training, the angular difference between a straight line from the home position to the target and a straight line from the home position and the point of maximum velocity is computed.

Hand Localization: Estimates of hand location were based on the angular endpoint error between the movement endpoint of the unseen right hand and the left-hand responses on the touchscreen relative to the home position.

Analyses

All data were visually screened for incorrect trials by lab volunteers naïve to the purpose of the study. Subsequently, outliers of more than three standard deviations across participants within each trial were also deleted, resulting in 2.8% of all trials being deleted. All measures were normalized by training target location by subtracting out each subject's average performance during the aligned session (e.g. trials 1-49). All subsequent analyses ignored the target location.

Exponential decay function

In order to obtain the rates of change and asymptotes for both reaches and hand localization, we fitted an exponential decay function. The value of each process on the next trial (P_{t1}) is the current process' value (P_{t0}) minus the product of the rate of change (L) multiplied by the error on the current trial, which is the difference between the asymptote (A) and the process' value on the current trial (P_{t0}).

$$P_{t1} = P_{t0} - L * (A - P_{t0})$$

The parameter L was constrained to the range $[0,1]$, and the parameter A to $[0,2 \cdot \max(\text{data})]$. Since rotations are in a random order, participants did not start each block in a non-adapted state. To account for this, the starting point of the fits for each block took into account the reach and localization endpoints (the average across the last four trials) of the previous block. This is illustrated in Fig 4.3, and the effects demonstrated in Fig 4.4 for averaged reach data (green) and their exponential fits (blue) for the first and last four unique rotation blocks. Most blocks were 12 trials, but when the rotation was repeated, 24 trials were used as a single block.

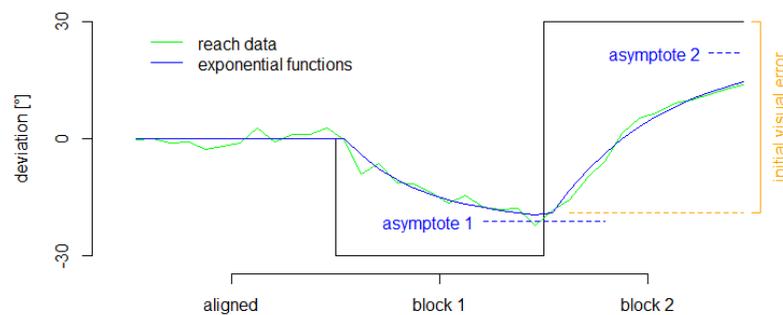


Figure 4.3. Accounting for successive reach adaptation. Simulated reach data shown in green. The exponential fits are shown in blue while the initial visual error for the second block is shown in orange: which is the difference between the rotation and the endpoint of the previous block (indicated by the dashed orange line). The learning rates, used to create this illustration are slightly decreased to show the difference between endpoint and asymptote.

For localization data, a zero was prepended to account for the fact that responses in these trials had already changed through the previous training trial. The parameters were also bootstrapped (1k resamples per fit) across participants to get a 95% confidence interval for both parameters. The first trial, where the modelled process based on the group average fell inside the bootstrapped confidence interval for the asymptote, is taken as the saturation trial.

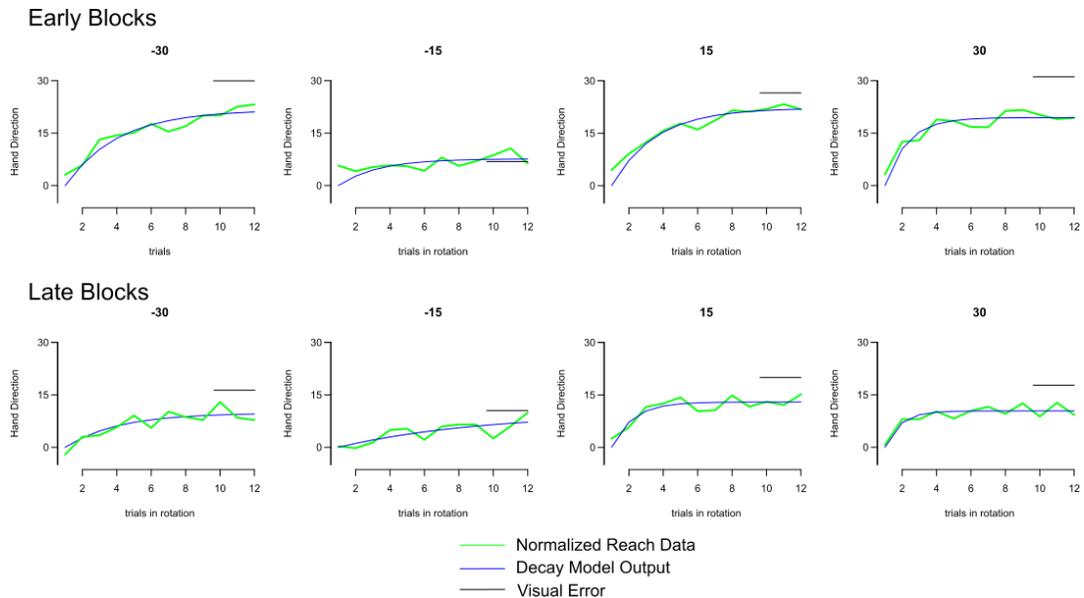


Figure 4.4. Reach and Exponential Fit Data. Reach data (green) and exponential fits (blue) for the first (top row) and last four (bottom row) unique blocks. The endpoint of the previous block was subtracted from the next block to force all blocks to start close to zero. The results are normalized so that all changes are in the same direction.

Considering that most of the time, participants were only given 12 trials per block the asymptote value for reach adaptation for these blocks likely underestimates the potential extent of learning. Nonetheless, as reported in the Result sections, the asymptotes are still quite high, reflecting an average compensation of 71% of the visual error for each block and 70% for the fit value at trial 12. In comparison, the average compensation from ten studies ($N = 501$) from our labs and others, with training blocks of at least 90 trials for rotations between 15° and 60° , is $86\% \pm 20\%$ (’t Hart et al., 2022). Nonetheless, we realize that more training trials would have likely led to both larger asymptotes and greater magnitudes of learning for reaches, like that found after over 100 training trials in study 1 of this dissertation ($> 95\%$); which was on the higher end of the typical adaptation range. However, given that analyses in this study are within blocks, these values should be sufficient to quantify whether rates of change or asymptotes increase or decrease across a series of random visuomotor rotations.

To transform the raw asymptote values into compensation values, we divided each asymptote by the size of the initial visual error, as illustrated in orange in Fig 4.3. To determine whether training with a series of random rotations affects speed and extent of changes in reaches and felt hand position, simple linear regressions were performed on the asymptotes and learning rates over training blocks.

One-Rate and Two-Rate Models

Another way to describe the learning curve mathematically is to implement a state space model that describes the time course as a function of learning and retention rate. A state-space model with a single process using a learning and retention rate is equivalent to an exponential function. However, a state-space model using two processes can explain a larger set of phenomena in motor adaptation (Smith et al., 2006). Instead of fitting each block, we fitted one-rate and two-rate models to all 480 reach trials simultaneously.

The two-rate model postulates the reaching behaviour exhibited on trial t (X_{t1}), is the sum of the output of the slow ($X_{s,t1}$) and fast process ($X_{f,t1}$) on the same trial:

$$X_{t1} = X_{s,t1} + X_{f,t1}$$

Both processes learn from errors on the previous trial (e_{t0}) by means of a learning rate (L_s and L_f), and they each retain some of their previous state ($X_{s,t0}$ and $X_{f,t0}$) by means of their retention rates (R_s and R_f):

$$X_{s,t1} = L_s * e_{t0} + R_s * X_{s,t0}$$

$$X_{f,t1} = L_f * e_{t0} + R_f * X_{f,t0}$$

The model is further constrained by making sure the learning rate of the slow process is lower than that of the fast process: $L_s < L_f$, and by having the retention rate of the slow process be larger than that of the fast process: $R_s > R_f$. We constrained the parameters to the range $[0,1]$.

The one-rate model postulates the reaching behaviour exhibited on trial t (X_{t1}), is:

$$X_{t1} = L * e_{t0} + R * X_{t0}$$

This process learns from errors on the previous trial (e_{t0}) by means of a learning rate (L), and it retains some of its previous state (X_{t0}) by means of a retention rates (R):

The datasets for the current study are available on Open Science Framework, <https://osf.io/sgfaj/> while the code and analysis scripts are available on GitHub https://github.com/JennR1990/Varied_Prop_Adaptation.

Results

We show the direction changes in felt hand position (red) along with changes in movement direction (blue) in Fig 4.5, along with the size and direction of the cursor deviation (solid black line), which was normalized so that all changes are in the same direction. From this figure, we can see that both the perceived and produced hand motion appear to respond quickly to changes in cursor deviations, and the extent of the changes relative to the perturbation magnitude.

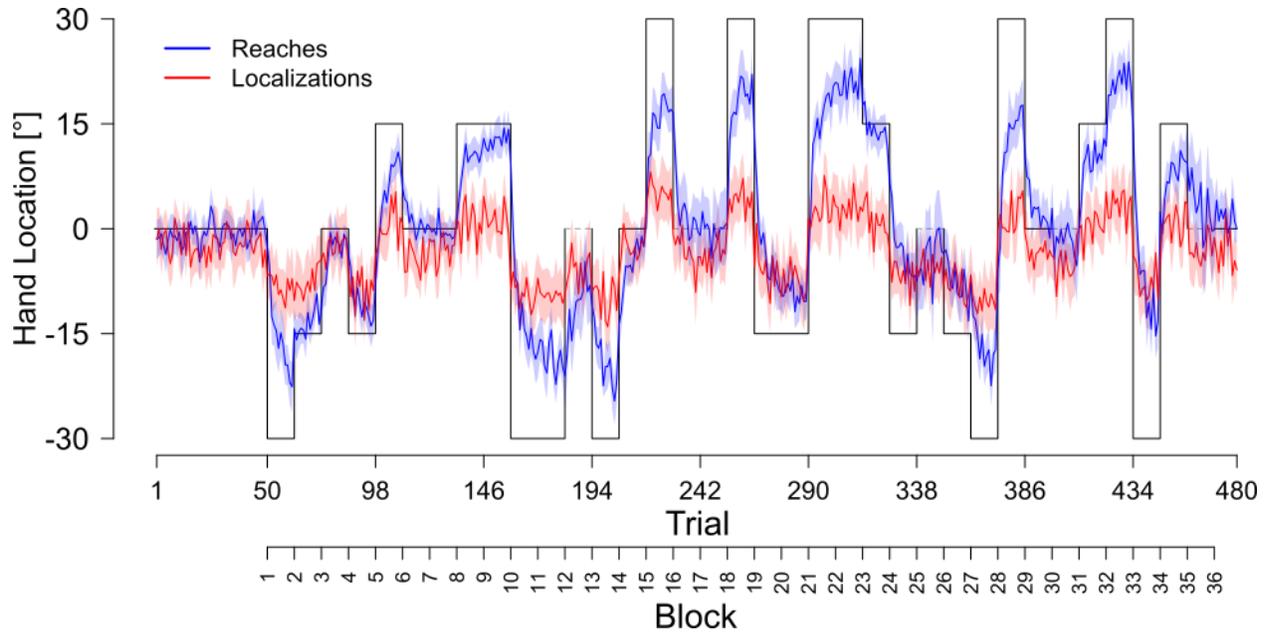


Figure 4.5. Overall localization and reach data. The rotation is shown with black with average localization data in red and the confidence interval for localization data in transparent red. The average reach data is shown in blue and 95% confidence interval is shown in transparent blue. Hand localizations are actually in the opposite direction of the hand-cursor movements, but have been normalized so all changes are in the same direction.

To quantify the speed of these changes, we used the decay function described earlier to estimate rates of change and asymptotes in response to a variable visuomotor rotation schedule for both shifts in hand location (in red for Fig 4.6) and changes in reach direction (in blue). There were two blocks where the rotation went from $\pm 30^\circ$ to $\pm 15^\circ$ without changing sign; these blocks resulted in inflated asymptote values and learning rates. We have chosen not to include those two blocks (2 and 23) in our analysis which is shown as greyed-out confidence intervals in Fig 4.6A&B.

Estimates of hand location

As expected, for shifts in felt hand location, the asymptote value for the first block of rotated-cursor training (block 1 for Fig 4.6A, red lines) was about 30% of the initial visual error, as found in our previous studies. More importantly, for the purpose of this paper, this asymptote value (denoted as a percentage of the relative visual error in Fig

4.6A) did not change much for the subsequent set of trials, even when the visuomotor perturbation changed in direction. When we ignore the inflated asymptotes produced by the “stepped” order of visuomotor rotations, as described above (blocks 2 and 23, greyed out in the figure), we see that the asymptotic shifts were around the typical 25-30% mark. A simple linear regression model comparing the size of the asymptote across blocks shows no relationship [$F(1,16)=0.003$, $P=0.95$]. That is, the relative size of these shifts in felt hand position did not vary across the experiment as may be expected with diminished sensitivity following these regular changes in visual perturbation. In summary, the magnitude of these visually-induced shifts in hand localization persisted despite repeated changes in the size and magnitude of the visual perturbation.

Next, we investigated whether the rapid change in these felt estimates of hand position was reduced following repeated changes in the visuomotor perturbation. As expected, the speed by which people misestimate the location of their felt hand occurred quite quickly (within 2-3 trials), although not as rapidly as in our previous studies (which required only one trial) in the first set of training trials (red dot in block one in Fig 4.6B). We found that the speed by which shifts in hand localization saturated did not slow even after a series of training with random visuomotor perturbations (red dots after block 1 in Fig 4.6B). This can be demonstrated by the absence of a linear relationship between rates of changes and blocks [$F(1,16)=0.13$, $P=0.77$], indicating no significant increase or decrease in the rate of shift in felt hand position across blocks. Overall, shifts in felt hand position are robust and occur very rapidly in response to previous visual experience, even when the rotation varies across trials.

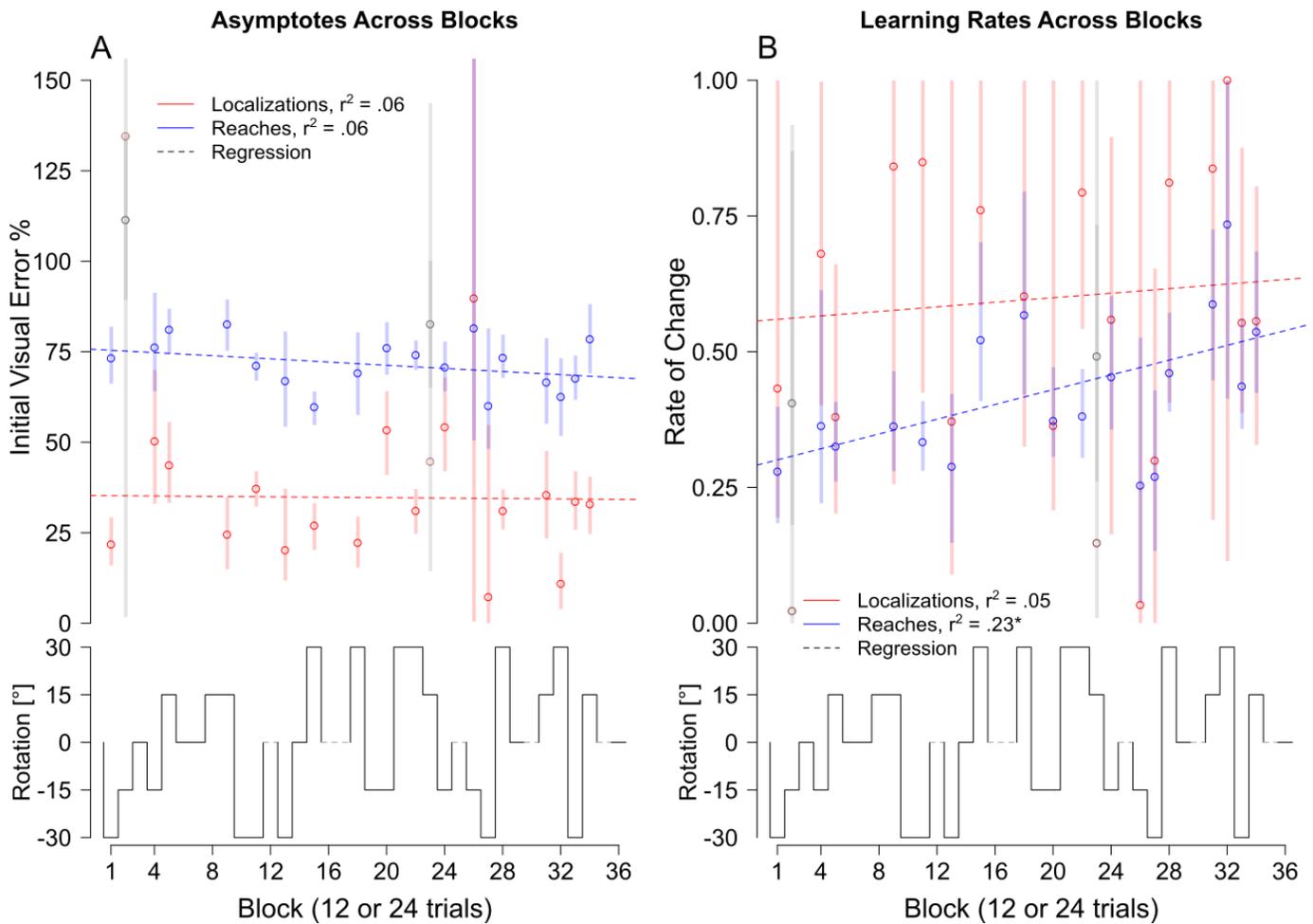


Figure 4.6. Asymptotes and Learning rates for Localization and reach data. **A.** The decay function was used to estimate an asymptote value for each of the blocks of interest. The model was bootstrapped 1000 trials to create 95% confidence intervals which are the shaded regions around each average dot. Localization data is shown in red and reach data is shown in blue. Their corresponding regression lines are also displayed in the respective colors. **B.** Learning rates estimated by the decay model are shown in red for the localization data and blue for the reach data with their corresponding 95% confidence intervals and regression lines. Rotation schedule with block and trial indicated are shown below the asymptote and rate of change values. Clamp and aligned blocks were not included in the analysis but are shown in the schedule for completeness as in Figure 4.2. These blocks are seen as blank spaces in panels A and B.

Reach Adaptation

As the rotation was consistent for 12 trials at a time, we expected to see some learning. However, it is not clear how the amount and rate of learning may also change across the series of random rotation blocks. Asymptote values from the decay model for each block, shown in Fig 4.6A as blue dots, show incomplete but consistent reach

adaptation across the entire experiment. The simple linear regression on asymptote values in Fig 4.6A across the series of blocks of random perturbation shows no significant relationship [$F(1,16)=1.75$, $P=0.21$], indicating participants consistently adapted to $\sim 71\%$ (± 6.9) of the distortion across all blocks. This suggests that reach adaptation occurred to a similar degree across all blocks, even in the face of a varied rotation schedule.

As we did for the estimates of hand location, we looked at the rate of change in reaching trials. The rate of change or speed of learning is typically impacted when adaptation is followed by training either to a single rotation or a series of rotations. Based on the relative rate of change shown in Fig 4.6B, participants adapted their reaches to the cursor rotations rather quickly across all blocks. We see an increase in the rate of change as a factor of time [$F(1,16)=6.12$, $P=0.021$, slope = 0.007], indicating the participants are learning faster across the blocks. In fact, the rate of change doubled in size between the first and last blocks. Overall, changing the rotation every 12 trials progressively increases the learning speed but not the amount of learning, as consistent with structural learning.

With the previous regression pointing to a change in the learning speed over time, we also applied a popular state-space model with both one rate or two rates to the data to see which one was better at predicting adaptation. The oneRate model had a worse mean squared error (oneRate MSE=9.49) than the twoRate model (twoRate MSE=6.93). The twoRate model, which includes both a slow and fast process, can better predict the data than a model with only oneRate, but without a variable learning rate cannot explain the increase in learning we see with the decay rate model.

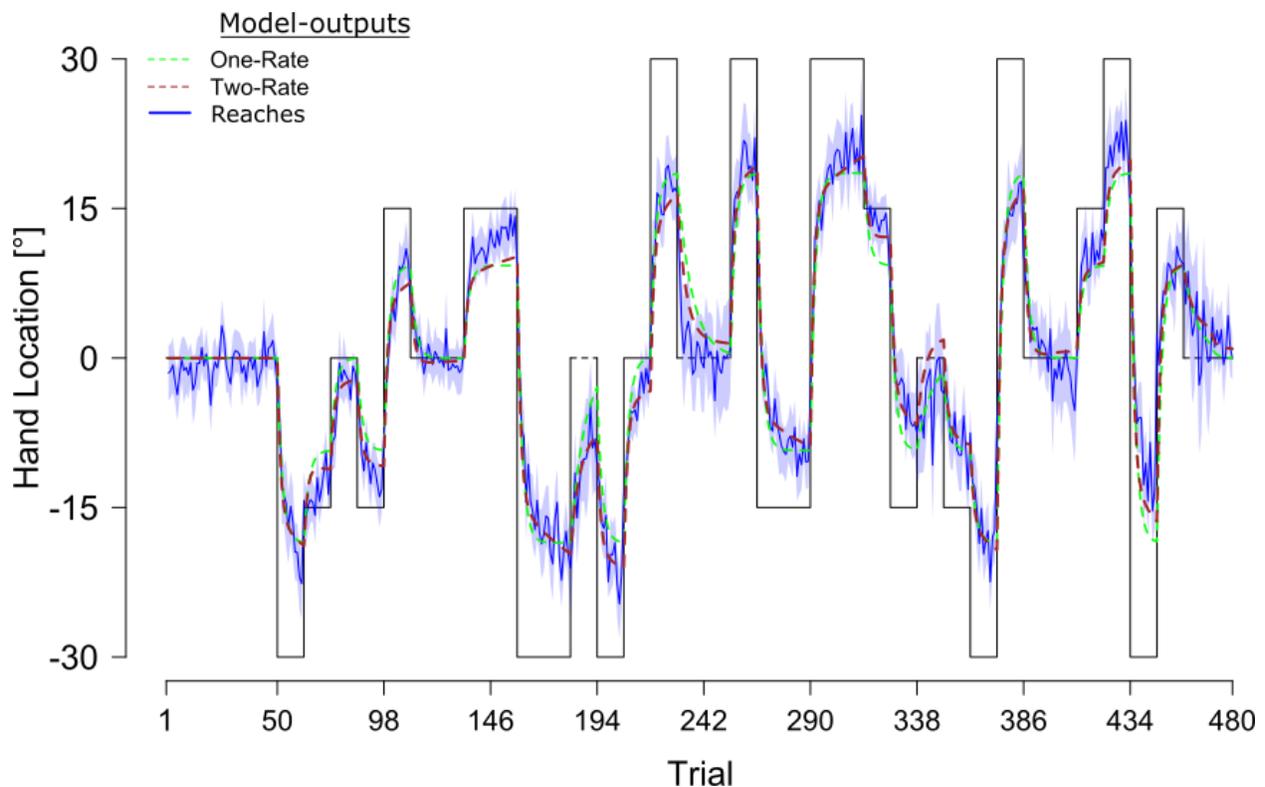


Figure 4.7. State-Space Model outputs. The one-rate and two-rate models applied to all reach data, where the two-rate model did a better job at predicting reach performance.

Discussion

By changing the rotation every 12 training trials, we could assess whether the speed and extent by which reach adaptation and proprioceptive recalibration are sensitive to regular but random changes in visual perturbation. Participants showed substantial learning of each rotation introduced, learning ~71% of the relative distortion, which in turn led to large shifts in felt hand position ~30% of the distortion. More importantly, we found that training with random variations of visuomotor distortions did not slow down the change for hand localization, which continued to respond rapidly to

the prior visual experience of the cursor. As consistent with structural learning, we found that the rate of change increased for reach adaptation.

Robust shifts in proprioception

Previous research has shown that consistent shifts in felt hand position occur whether training with a hand cursor that is constantly visible, visible only at the end of the reach trial, or they have no active control over their trained hand (Barkley et al., 2014; Henriques & Cressman, 2012; Ruttle et al., 2022). Here we went a step further and showed that even when the rotation is unpredictable and constantly changing, shifts in subsequent felt hand position develop to the same degree and speed throughout training. This provides further evidence that these shifts in felt hand position occur whenever the nervous system is exposed to a visual-proprioceptive mismatch. Because these shifts appear so rapidly, they may partly drive motor adaptation as hand position is required for the nervous system to make movement vectors. Additionally, this suggests that proprioceptive recalibration relies on the immediately preceding visual-proprioceptive mismatch and not the history of mismatches that have been experienced. This is unlike adaptation, which tends to depend on the history of perturbations.

Although we wanted to investigate whether the rapid visual recalibration of hand proprioception could be reduced or slowed down given the constant change in direction and size of the visual perturbation, it is possible that introducing the perturbation as steps could have also led to larger misestimates of hand position. In an older study from our lab (Salomonczyk et al., 2011), where we increased the rotation in steps from 30° to 50° then finally to 70°, the size of the shift in felt hand position also increased from 6° to

about 15° keeping it at a steady 20% of the rotation. In contrast to a more recent study from our lab that showed an abrupt rotation, without steps, of 60° does not lead to larger shifts (Modchalingam et al., 2019). Given that the changes in steps, this could have led to larger shifts, and indeed in some blocks, we did find greater recalibration than the typical 20-25% found in our other studies. However, this was not consistent enough to determine the kind of steps necessary to facilitate the amount of recalibration. Further research is necessary to disentangle these possibilities.

Speed and magnitude of motor adaptation over blocks of random rotations

The advantage of also measuring so many participants and in the same random perturbation is that we could, as a secondary goal, investigate structural learning within the training paradigm rather than having to add extra training phases and control groups. As mentioned in the introduction, other studies with variable visuomotor rotations mostly measure the final phase of adaptation after a washout period and compare the learning rate across groups that experienced the random perturbation and with those that experienced a consistent perturbation and no training at all (Bond & Taylor, 2017; Braun et al., 2009a, 2009b; Coltman et al., 2021; Seidler, 2004, 2007). This approach largely ignores all the training data except for the last phase. As well, the majority of the studies introduced a unique series of random visuomotor rotations and so did not attempt to measure learning at the group level (Bond & Taylor, 2017; Coltman et al., 2021). However, one such study, besides analyzing the final training phases, also reported evidence of greater learning in the final block compared to the first block of the training phases of random visuomotor rotation between +/- 60° every 16 trials (Turnham et al., 2012). But the relative size and speed of adaptation were not

reported during the main training phase that spanned over 1000 trials. Using the same series of rotations for all participants (N=32) and applying the decay rate model allowed us to get a more reliable and better measure of the rate and amount of learning during the entire training phase. In this way, we were able to measure structural learning, faster learning across subsequent blocks, and show it emerges surprisingly quickly within the series of random rotation variation training of only 400 trials and for an overall smaller range of rotations. Thus, our study may be the first to show the evolution of structural learning within the training phases and in such a short time frame.

Despite faster learning across blocks, we did not find any evidence for changes in the magnitude of such learning across blocks. This cannot be attributed to our asymptote values for short blocks of reach training underestimating the magnitude of potential learning. None of the structural learning studies described above found greater learning extent in their final training phase. Structural learning only appears to facilitate the rate of learning and not the extent.

Proprioceptive recalibration shows no structural learning

It is not surprising that structural learning did not appear to impact either the rate or size of proprioceptive recalibration. One reason could be that changes in hand localization already emerged so quickly and appeared capped in size that structural learning for the motor component does not add anything. The visual-proprioceptive mismatch that likely drives the changes in proprioceptive estimates appears to work on a different scale, and these signals are not the same as those that lead to structural

learning. Indeed, the results from Bond and Taylor (2017) suggest that structural learning is mainly strategy-driven.

State-space models and structural learning

Other studies have used a state-space model to determine the contributions of the fast and slow processes in structural learning, which are assumed to reflect explicit and implicit processes, respectively (Coltman et al., 2021; Turnham et al., 2012). Their results could not verify if random rotation training was more implicit or explicit. This could reflect what may be an erroneous assumption that the fast and slow processes map onto explicit and implicit components of learning. The state-space model also has limitations making it hard to identify more subtle changes. The two-rate model has been criticized for having a constant learning rate and thus unable to capture adaptation to random rotations (Braun et al., 2009b). We also found that the two-rate state space model could not pick up on the small but significant increase in learning rate over blocks. Supporting the idea that the model is unable to capture these finer changes and models with dynamic learning rates should be prioritized for explaining more complex adaptation paradigms.

Conclusion

We showed that even with uncertainty in the visual cursor, shifts in felt hand position in response to a visual distortion in the preceding trials are incredibly fast and robust. This provides support for shifts in felt hand position being able to drive reach adaptation. Rates of change in reach trials increased across rotation blocks, indicating that varying visuomotor rotations can produce structural learning in reach adaptation.

However, this did not have a significant impact on shifts in felt hand position, highlighting that the motor system is incredibly plastic in the face of changing environments.

Chapter 5: General Discussion

My main research goal was to first; quantify the speed by which implicit changes emerge during motor learning and then explore what factors impact the speed and size of these implicit changes. Motor learning is driven by many different things, like error signals and explicit strategies. Here we measured reach aftereffects and shifts in hand localization on a trial-by-trial basis, which had not been done before. Most studies quantified these implicit measures of motor learning after a substantial number of training trials. By measuring them on a fine time scale, I was able to directly investigate and model the time course of both learning and their associated implicit changes.

Research on implicit measures of adaptation assumed that reach aftereffects and shifts in felt hand position take many trials to reach asymptote during classic training. This may have been an artifact of the way they were studied, mostly being measured after prolonged training and not throughout training. The unique training schedule we employed allowed us to probe implicit changes in motor learning at a much finer scale than had been done before. We could not only look at the overall extent of change in implicit learning but also how these changes evolved over time. We were also the first to fit exponential decay functions to the implicit trials as well as the cursor reach trials, which provided a rate of change that is much more precise and comparable across trial types. Previous research used simpler analysis that could not directly answer questions on the speed of learning beyond comparing learning curves during cursor reach trials. Here we could quantify the speed of change in cursor reach trials and proprioceptive recalibration and reach aftereffects.

In experiment 1, I measured reach aftereffects and shifts in felt hand position after every reach-training trial. Both appeared much quicker than previously thought. Hand localizations were measured both actively and passively; participants either moved their hand to a target location or had their hand moved by the robot. Both conditions showed immediate shifts in felt hand position, with slightly larger shifts for the active condition than the passive condition. This study extended current research in implicit learning and showed that using a finer time scale allowed for a more in-depth look at these key measures of implicit learning. It was also the first time we applied a decay rate model to the data to extract a rate of change and asymptote value that was comparable across tasks.

My master's research showed that both reach aftereffects and shifts in felt hand position appear within six training trials, and the size of shifts in felt hand position was consistent after this point, as there was no further increase with additional training trials (Ruttle et al., 2018). This was the case for both classic training, where participants had full control and vision of the cursor during reaches as well as during an exposure condition where participants' reaching hand was constrained to a channel. Hence, the cursor always moved straight to the target, removing task error. Task error is thought to be a more explicit error signal during training as participants are aware of whether they achieved the target or not. When the target is moved into the participants reaching path or the target is enlarged to remove task error, implicit learning in the form of reach aftereffects has been found to be smaller than regular training (Leow et al., 2018). We also found the same pattern of results, with smaller aftereffects for exposure training than classic, indicating that exposure training reduces task errors similar to other

methods (Ruttle et al., 2018). Shifts in felt hand position were unexpectedly larger in the exposure training condition than in the classic training condition. In experiment 2, I found a similar-sized shift in both the exposure and classic training condition. I also found these changes appeared and hit asymptote even faster than in my master's research when measured at a finer time scale.

In experiment 2, I also reduced access to sensory prediction errors by providing only terminal visual feedback; participants only received performance feedback at the end of the reach trial. Consequently, this removed the ability to compare the seen and felt hand position during the reaching movement. Previous research has shown that the degree of reach adaptation and implicit learning, measured by reach aftereffects, was smaller for terminal feedback training (Barkley et al., 2014; Hinder et al., 2008, 2010; Taylor et al., 2014), although some studies have shown equivalent learning and aftereffects (Brudner et al., 2016; Heuer & Hegele, 2008; Rand & Rentsch, 2016). In experiment 2, we found similar adaptation extents in classic and terminal training conditions. Instead of looking at reach aftereffects, we investigated shifts in felt hand position and found similar speeds and sizes of shifts. Once again, observing learning and shifts in felt hand position on a trial-by-trial basis allowed us to quantify adaptation and implicit changes better.

The final study in this dissertation tried to push the limits of proprioceptive recalibration by changing the size and direction of the rotation every 12 trials. Previous studies on varied rotations rarely look at implicit components of adaptation and generally look at adaptation on a consistent rotation after the varied rotation training. Here we calculated a rate of change and asymptote value for each rotation block for

both cursor training trials and shifts in felt hand position. We found consistent asymptotes and rates of change in shifts in felt hand position and an increase in the rate of change for reach adaptation. This study provided additional evidence that shifts in felt hand position are a robust component of implicit learning and are a potentially driving force in adaptation.

Speed of reach adaptation

When participants are given a continuous vision of their hand cursor and control over their movement directions, reach adaptation is fast and consistent. Learning speed is slowed by many things, such as simply increasing the number of targets from one to eight, reducing access to error information during the reach trial, and by altering the intertrial interval (Barkley et al., 2014; Hulst et al., 2021; Kim et al., 2015; Krakauer et al., 1999; Ruttle et al., 2021, 2022). Overall, reach adaptation is thought to be a balance between learning and forgetting. By altering the training conditions, the amount of learning or forgetting on each trial can be changed to see an overall slowing of learning. In all three of my studies, we changed the learning environment subtly to see how we could impact this balance of learning and forgetting.

In the first study, four groups of participants completed reach trials, where the cursor was visible the entire reach trial. This continuous training condition should allow for the most learning as they can use error information during the whole reach and compare their expected and actual hand and endpoint locations. By changing what occurred between training trials, we were able to change the amount of forgetting that happened. We can group the intertrial behaviours into two groups; active behaviour and

passive behaviour. Half the participants completed active behaviour: either a no-cursor reach or an active movement to a hand localization target; importantly, both trials provided no performance information. In the passive behaviour groups, participants either sat still with their hand at the home position for 2 secs (pause group) or their hand was passively moved to a hand localization target. Those in the active behaviour group showed significantly reduced and slower learning than those in the passive behaviour group (Table 2.1 from Ruttle et al., 2021). This result suggests that these active behaviours, even in the absence of visual feedback, increase the amount of forgetting between training trials. All groups reached at least 75% compensation, but it took significantly more time for the active behaviours group to reach this level of asymptote.

A study by (Kim et al., 2015) found that participants that had to learn an opposing rotation on every other trial but to targets in a slightly different workspace also learned slower than those with a longer intertrial interval. These participants did receive feedback on performance for these intervening trials, unlike our groups, but both of our groups and their alternating group completed an active movement between the training trials of interest and showed this slower learning rate. Of course, this group was also trying to adapt to this opposite rotation; thus, the slower learning could have been due to interference, as was concluded by the authors. Thus, more research is necessary to replicate our tertiary but novel finding that intervening in active movements, even in the absence of visual feedback, could interfere with the learning rate.

In my second study, all participants completed a passive intervening behaviour, which was shown previously to not interfere with the speed of reach adaptation. However, we altered the error information available during training trials. One group

received continuous visual feedback on cursor position, while another group was only given this information at the completion of the reaching movement. As has been shown in some previous studies looking at terminal visual feedback, we saw slightly slower learning for this group compared to the continuous vision group (Barkley et al., 2014; Bernier et al., 2005; Hinder et al., 2010; Wijeyaratnam et al., 2019).

Reach adaptation has been said to involve both feedforward and feedback control mechanisms (Raichin et al., 2021). Specifically, this is the ability to execute a motor plan reliably and adjust the motor plan while moving. Studies to disentangle these two mechanisms use terminal and continuous visual feedback, assuming that by not providing continuous feedback of the cursor, the information required for feedback control is significantly reduced (Hinder et al., 2010; Raichin et al., 2021; Wijeyaratnam et al., 2019). Additionally, when knowledge of performance is only given at the end of the movement, this is thought to emphasize feedforward control, and proprioceptive feedback, which may be more critical because it is not overshadowed by visual feedback (Bernier et al., 2005). By emphasizing feedforward control and proprioceptive feedback, implicit adaptation may be increased, as seen in reach aftereffects (Bernier et al., 2005; Shabbott & Sainburg, 2010), although this is not always the case (Hinder et al., 2010). We did not measure reach aftereffects in our terminal feedback condition. However, we did measure angular error during clamp trials at the end of the experiment, which have been used to probe aftereffects (Criscimagna-Hemminger & Shadmehr, 2008). We found no increase in aftereffects for the terminal visual feedback group, but this could be due to a few reasons. Primarily, we required participants to reach the target quickly, and we took the angle at peak velocity as our measure of angular

deviation, before they could make any alterations in their movement based on feedback control. We also used a study design, which included a counter-rotation block before the clamped block. Overall, it is not surprising that feedforward control is present in both continuous and terminal training paradigms, and terminal visual feedback training produces fast learning, even without access to feedback control mechanisms.

Reach aftereffects and clamp trials

We introduced clamp trials in our three studies to fit a state-space model to our data. Clamp trials are those trials where the cursor moved with the distance of the hand but only directly to the target, and during such trials, reaches continue to deviate in a way consistent with compensating for the rotation. Thus, reaches during visually-clamped trials share some similarities with no-cursor reaches and, therefore, could partly reflect implicit learning. For this reason, we can cautiously interpret the absence of any difference in the size of the clamp errors for continuous, terminal, and exposure feedback groups in our study 2 as suggesting a similar amount of implicit learning. This is consistent with previous studies that measured no-cursor aftereffects, which failed to find differences in aftereffects after terminal and continuous training with a rotated cursor (Heuer & Hegele, 2008; Song et al., 2020). Yet other studies have found slightly smaller aftereffects when adapting to terminal feedback (Barkley et al., 2014; Brudner et al., 2016; Hinder et al., 2008; Schween & Hegele, 2017; Taylor et al., 2014). These mixed results may be because any difference in adaptation and aftereffects between terminal and continuous may be too small to be reliably elicited, especially in small sample sizes. Moreover, smaller reach aftereffects do not necessarily mean less implicit contribution but merely reflect the quality of the error signals that drive implicit learning.

Whether reducing visual feedback to the end of the reach also affects the time course of these implicit changes is still an open question.

Shifts in felt hand position

One common thread across all the studies in this dissertation is the measurement of change in felt hand position. We were able to show how quickly altered visual training can recalibrate proprioception, even reduced access to error information, or when visual perturbation does not remain consistent. Although the size of the change is smaller, the speed with which vision recalibrates proprioception outpaces learning in cursor training trials and reach aftereffects. This observation suggests that proprioception could be a driving force in adaptation, which is what has been suggested by a recent model proposed by (Tsay et al., 2022). This model suggests that one of the main error signals involved in reach adaptation is the difference between actual and expected proprioceptive information at the end of the reach. Study three shows that even when the rotation is changed every 12 trials, participants shift where they estimate their hand location incredibly quickly to help reduce the visual-proprioceptive discrepancy and align their expected and actual hand locations. In the study two, participants were not in control of the direction they moved their hand but still produced robust shifts in felt hand position, indicating that this recalibration occurs even without volitional control of reach direction. In summary, it is clear that proprioception is very sensitive to vision and recalibrates incredibly quickly in the face of misaligned visual information and likely contributes to reach adaptation more than previously thought.

Conclusion

In conclusion, this dissertation is the first to the time course of proprioceptive recalibration in detail. We showed that regardless of the intervening trials, access to error information, or consistency of the rotation schedule, reach adaptation occurs quickly and produces robust shifts in felt hand position, and implicit components of learning appear much faster than previously thought. Study one shows how active localization trials produce slightly larger shifts in felt hand position, potentially indicating recalibration in not only proprioception but also prediction and that implicit changes appear much faster than previously believed. Study two shows that even with altered error information during training trials, reach adaptation occurs quickly and still produces large shifts in passive hand localizations. Finally, study three shows that even changing the size and direction of the cursor rotation has little impact on shift in felt hand position, the latter of which still appears incredibly quickly and to the same size as the previous two studies. We did find evidence for structural learning in the rates of change for reach adaptation, which emerged within a relatively small series of random visuomotor rotations and thus more quickly than assumed. However, we confirm that a greater magnitude of adaptation did not accompany a faster rate of learning. Together these studies provide strong evidence that implicit changes due to misaligned visual feedback appear far quicker than previously thought and cannot be slowed or reduced by altering the visuomotor training paradigm.

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Appendix A: Disclaimer for Coauthored Chapters

Chapter 2&3 in this dissertation has been published with my supervisor Denise Y.P.

Henriques and Marius 't Hart a postdoc in our lab as co-authors.

Denise, Marius 't Hart, and I conceived and designed the experimental methodology, created the experimental methods and stimuli. Experiments were programmed by Alireza Tajadod (Chapter 2) and Abdul Adeshine (Chapter 3 & 4). I performed the experiments and collected the data for all chapters. I analyzed all the data and wrote the manuscripts.