The Effects of Error-Sensitivity and Perturbation Schedules on the Slow and Fast Processes in Reach Adaptation

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ABSTRACT

Adapting movements to our ever-changing environment likely involves many neural processes, and the two-rate model (Smith et al., 2006) nicely demonstrates that at least two processes are involved, called the “fast” and “slow” process, which work in parallel to contribute to our motor output. The fast process is quick to learn but also quick to forget, whereas the slow process is slow to learn, but retains the learnt adaptation for much longer. This model explains a rebound phenomena, where people revert to reaching as if they were still adapted to the initially learned rotation, when doing error-clamped trials after a short reversal of the adapted perturbation. It is the slow process that is the greatest contributor to this rebound effect. Later work has also mapped the fast and slow processes onto the explicit and implicit components of motor learning, respectively. Here, we were interested in whether there would be any behavioural learning differences between a perturbation that was introduced abruptly compared to gradually. We used a within-subjects design where all participants (N=32) adapted to the same 30-degree rotation introduced both gradually and abruptly. A perturbation that is introduced gradually should rely more on implicit learning than an abrupt perturbation, and therefore lead to larger rebounds. However, we found no effect on the size of the rebound. In attempt to tease out more of the explicit component of the abrupt condition, we did a follow-up experiment using the same paradigm, except this time participants (N=32) adapted to a 60-degree rotation. Similarly, we found no significant differences between the abrupt and gradual conditions on the size of the rebound. This led us to believe that the way the perturbation is introduced does not affect the size of the rebound. As a second study, we also ran this same paradigm with a 30-degree rotation in an immersive virtual reality setup. Our results show no significant differences in the extent of learning or rebound between the tablet and stylus setup compared to the virtual reality setup, which confirms that it is feasible to use a more naturalistic 3-D virtual reality environment for running visuomotor adaptation experiments in the future.

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INTRODUCTION

One of the most fundamental functions of the human brain is to control and adapt movements to our ever-changing environments. Motor adaptation is the ability to modify our movement to changes in both the environment and our body. Our capacity for motor adaptation can be observed in several situations, whether it is adjusting to a new tool or changes in muscle fatigue. The learning required to adapt to a change in the body or environment that is introduced abruptly, such as adjusting to a new tool, is thought to be different than adapting to similar change or perturbation that is introduced gradually, such as changes in muscle fatigue. How our sensorimotor systems respond to small but growing changes compared to abrupt changes likely involves different neural processes, yet the nature of these processes and how they contribute to adaptation is largely unknown.

Producing a goal-directed movement, like a reach movement, requires a number of computations that involves specifying the necessary inverse kinematics and dynamics to produce the motor command to send to the muscles. A copy of this motor command, or efference copy, is also sent to other motor-related brain areas and used to simulate or predict the consequences of these movements. These simulations or predictions help overcome delays with sensory feedback, and serves as a way to store knowledge, sometimes known as a forward model, necessary for planning and producing movements and interacting with our environment. Perturbations, like those mentioned above, when first introduced, not only lead to errors in the movements but errors in these predicted consequences of action. Repeated practice leads to modifications of these forward models in order to correctly predict the actions under these perturbed or changed circumstances. This in turn is believed to be used to update necessary computations in order to produce movement (Blakemore et al., 1998). This information can be stored and later recalled when the circumstances (i.e. using a specific tool) comes up again.

All brain areas that are involved in producing movement, are likely also involved in adapting and learning new movements, however the cerebellum is thought to be a particularly important brain area for coordinating and adapting movements. The cerebellum receives input from sensory systems of the spinal cord and from other parts of the brain, including the cerebral cortex, and integrates these inputs to fine-tune motor activity. The cerebellum contains as many neurons as the rest of the brain, and therefore is a power-house for the kind of computations necessary to coordinate precise and timely voluntary movements, and likely houses many of the forward models or predictive sensorimotor mappings necessary to produce smooth, coordinated movements. This is despite that the fact that the cerebellum does not generate movements. Instead it calibrates the detailed forms of movement, and modifies movements in response to systematic changes or perturbation in our environment.

Patients with hereditary cerebellar ataxia show a decrement in motor adaptation, which is believed to be the result of a deficit in the ability to process the discrepancy between predicted and measured sensory consequences (Tseng et al., 2007; Maschke et al., 2004; Izawa et al., 2012). Damage to other brain areas does not systemically disrupt adaptation to the same degree as the cerebellum. Patients with damage to the basal ganglia, such as those seen with Huntington's (Smith & Shadmehr, 2005) or Parkinson's disease (Contreras-Vidal & Buch, 2003) show an intact ability to adapt.

Patients with cerebral damage post-stroke show locomotor adaptation on a split-belt treadmill as well, whereas patients with cerebellar damage do not (Reisman et al., 2007). Recent transcranial direct current stimulation (tDCS) evidence has shown that increased excitability of the cerebellum causes an increased rate of motor adaptation (Galea et al., 2011). These studies provide support for the specific role of the cerebellum in motor adaptation.

Motor Adaptation

The typical reach paradigms used to test motor adaptation in a lab setting involve perturbing the movement of the hand in one of two ways: (1) perturb the movement dynamics by applying a systematic force on the hand, termed a force-field paradigm (2) perturb the movement kinematics by altering visual feedback of the hand movement direction, termed a visuomotor adaptation paradigm (Krakauer et al., 2000). In a visuomotor adaptation, the visual feedback of the hand movement can be altered either using prism goggles, or by manipulating a cursor representing your actual hand movement (Figure 1). A hand-cursor reach adaptation is typically introduced using either a gain or a rotation. In this study, we use the latter approach to elicit motor adaptation. This means that when the actual hand is moved straight to a target, the motion of the cursor, which represents that hand, is rotated to the left or right. The goal is to move the unseen hand in the opposite direction of the rotation in order to continue to get the cursor straight to the target. A visuomotor adaptation can be performed using several different apparatus, typically with a tablet and stylus setup, however recent work has attempted to induce this same visuomotor adaptation in virtual reality (Anglin et al., 2017; Groen & Werkhoven, 2006; Carter et al., 2016; Messier et al., 2007). One study has compared whether visuomotor rotation adaptation was similar in virtual reality compared to a more conventional training using a tablet and stylus (Anglin et al., 2017). There results showed a similar timecourse of adaptation for both experimental setups, although the authors found that the mechanisms by which the adaptation was occurring may have differed. Virtual reality has been used to induce a prism adaptation, or lateral shift of the visual field in both neurologically typical people (Groen & Werkhoven, 2006), as well as people with unilateral spatial neglect (Carter et al., 2016). It has also been used in a reach-adaptation paradigm with subjects who have Parkinson's disease (Messier et al., 2007). Virtual reality allows for the freedom to create experiments that are more ecologically valid, while still maintaining the control of a laboratory setting. Although this technology is relatively novel, this immersive 3-D setting is a promising tool to aid in our ability to test these complex systems further.

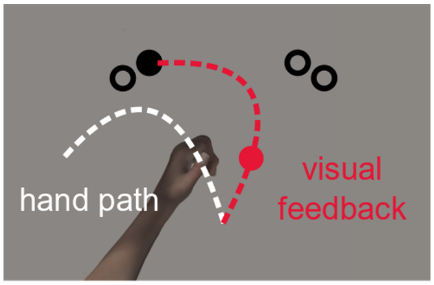

Figure 1. **Hand-cursor reach**. The cursor representing the hand is rotated by 30^o. Visual targets here are presented either 40 or 50 degrees from the midline on either the left or right side of the workspace. The white path initially goes straight to the black target, but the red cursor veers off 30^o clockwise. Once adapted, this is corrected such that the white hand path is moving 30^o in the opposite direction and the cursor is moving straight to the target.

Previous research has established that when reaching to a single target where the cursor is rotated by 30^o, the learning rate is relatively quick, such that participants are able to return to baseline levels within 20 trials for a single target (Krakauer et al., 2000). This learning curve, which is seen as a negatively accelerated exponential function, is produced as an outcome of plotting performance as a function of time. Besides measuring the rate and magnitude of learning during training, motor learning can also be gauged by using measures of generalization, savings, and reach aftereffects. Generalization is the degree in which training in one direction transfers to novel locations. This measure provides insight into the representation of new sensorimotor mapping (Ghilardi et al., 1995). During a visuomotor adaptation, learning has been shown to generalize almost fully across distances but less so for directions (Krakauer et al., 2000). Savings refers to the improved rate of relearning due to prior learning, which is evident even after behaviour of the original learning have been forgotten. Savings have previously been investigated using the Pavlovian eyelid conditioning (Schneiderman et al., 1962; Medina et al., 2001), and has been demonstrated in both visuomotor and force-field motor learning paradigms as well (Caithness et al., 2004; Krakauer & Shadmehr, 2006). When the perturbation is removed after reach-training with rotated visual feedback, the adaptation persists and the movements continue to deviate; this is known as reach aftereffects. This robust measure is used to reflect implicit learning or learning that occurs unconsciously since the hand-perturbation is absent. Reach aftereffects are also used to examine the phenomena of a rebound. When people who are adapted to one perturbation are briefly exposed to an opposing perturbation, they continue to make reaches in the opposite direction of the first perturbation when they are no longer given error feedback. This can only be explained if there is some memory of the initial perturbation that persists while adapting to the second perturbation (Smith et al., 2006). This provides evidence that there are at least two processes involved in motor adaptation, and measures of this rebound can be used to assess these processes.

Abrupt versus Gradual Motor Learning

The rate by which a change or a perturbation is introduced during training has been shown to also affect adaptation performance. Previous studies have used a visuomotor adaptation task to compare adaptation to a perturbation that is introduced gradually with the same perturbation that is introduced abruptly (Kagerer et al., 1997; Ingram et al., 2000). Kagerer et al. (1997) had participants make reaching movements with a hand-cursor, where the movement of the cursor was rotated by 90^o. In the abrupt condition the full 90^o rotation was introduced within 1 trial, and in the gradual condition the rotation was introduced in increments of 10^o with blocks of 60 trials until they received the same 90^o rotation. Ingram et al. (2000) altered the visual feedback of the hand by applying a gain between the actual hand movement and the cursor movement. In the abrupt condition a gain of 1.5 was introduced on the first trial of training, and in the gradual condition the gain was increased incrementally over the 80 trials of training until it reached the same gain of 1.5 on the last trial. Both studies found more adaptation in the gradual condition compared to the abrupt condition, as seen with larger aftereffects once the perturbation was removed after training. In line with these results, similar effects were found using prism adaptation (Michel et al., 2007). Participants had to perform a visual pointing task with an optical shift introduced either abruptly or gradually, and found that the gradually introduced perturbation led to greater aftereffects. Kluzik et al. (2008) used a force-field adaptation task in which a robot manipulandum perturbed the participant's reaching movement, and found that transfer of learning to a free space increased from 40% to 60% when the force-perturbation was gradually introduced compared to when it was abruptly introduced during training. The authors found that the gradual condition led to broader generalization of the reach adaptation. These studies suggest that gradual, smaller trial-to-trial errors which lead to larger reach aftereffects and broader generalization may suggest that implicit changes associated with learning may be greater.

Although results from several studies have shown that the way a perturbation is introduced, either abruptly or gradually, can affect adaptation, there is also evidence for the contrary. The authors from the Kagerer et al. (1997) study did a follow-up, looking at the difference in adaptation when children with developmental coordination disorder are exposed to a 60^o visuomotor adaptation introduced abruptly or gradually (Kagerer et al., 2006). In the typically developing children, there was no significant difference between the adaptation conditions, whereas the children with developmental coordination disorder showed larger aftereffects in the abrupt condition compared to the gradual. Similar to Kagerer et al. (1997), Buch et al. (2003) used a hand-cursor visuomotor adaptation where the cursor was rotated by 90^o, introduced either abruptly or gradually. However, results from this study show no significant difference in the aftereffects between the abrupt and gradual conditions (Buch et al., 2003). In addition to using a visuomotor adaptation paradigm, previous research has also tested this using a dynamic force-field task (Klassen et al., 2005; Criscimagna-Hemminger et al., 2010). To assess adaptation, Klassen et al. (2005) tested retention of learning a day later on the same visuomotor and force-field perturbation. Results show no significant difference between the abrupt and gradual conditions for either the visuomotor or force-field paradigm. Using a force-field paradigm, similar aftereffects were observed between the abrupt and gradual conditions in both healthy controls and patients with mild cerebellar ataxia (Criscimagna-Hemminger et al., 2010). However, this was not true for the patients with severe cerebellar ataxia. A later study tested this same question using a visuomotor adaptation and found no differences between the abrupt and gradual conditions in either the patients with cerebellar ataxia or the healthy controls (Schlerf et al., 2013). Intermanual transfer; adapting to a 30^o visuomotor perturbation with one limb and having a substantial benefit when performing with the untrained limb, also does not seem to be affected by whether the perturbation is introduced either abruptly or gradually (Taylor et al., 2011). In addition to reaching tasks, these results have also been replicated using a locomotor adaptation task (Hussain & Morton, 2014). They measured adaptation and retention of altered interlimb symmetry during walking with a perturbation introduced either abruptly or gradually. One day after training, results show no significant difference between the groups in retention, re-adaptation, or aftereffects. Looking at the whole picture, it is still unclear whether the rate by which perturbation is introduced can affect adaptation performance, and this may partly depend on the magnitude of the perturbation.

In addition to the behavioural evidence, previous neurophysiological research has further attempted to delineate the difference between gradual and abrupt learning of a perturbation. Both the cerebellum (Robertson & Miall, 1999; Schlerf et al., 2012) and basal ganglia (Werner et al., 2014) have been shown to have differential contributions to visuomotor adaptation depending on how the perturbation is introduced. Robertson & Miall (1999) had a monkey reach with a 15^{o} rotation introduced either abruptly or gradually. This was done with and without the administration of a lignocaine infusion to inactivate the dendate nucleus. In the control condition, without the infusion, there was no difference between the abrupt and gradual conditions. In the abrupt condition there was no difference between the control and the inactivation of the dendate nucleus, whereas in the gradual condition there was a significant difference. With the inactivation of the dendate nucleus during the gradual condition, the monkey was unable to fully adapt to the perturbation, as seen with the consistently large performance errors. Using TMS, Schlerf et al. (2012) also found differences in the role of the cerebellum, specifically in the cerebellar-M1 connectivity, when adapting to an abrupt versus gradually introduced perturbation. When adapting to an abrupt perturbation, where errors are large, there is an overall decrease in the level of cerebellar inhibition during the early stage. Later in adaptation, where errors are small, cerebellar inhibition increases back to baseline. However, this modulation of cerebellar inhibition was not seen in the gradual condition, where the errors were consistently small. Werner et al. (2014) used functional magnetic resonance imaging to show the crucial role that the cerebellum plays in the early adaptation to a large, abrupt error. These authors found greater activation of the cerebellar and cingulate cortex in the abrupt condition compared to the gradual condition, but interestingly no difference in the behavioural aftereffects. Reviewing the literature, it is still unclear whether the way a perturbation is introduced, either abruptly or gradually, affects adaptation performance. Although there may be some underlying differences in the neural mechanisms involved, the delineation between these conditions, at least in regards to behavioural effects, is still blurred.

Although visuomotor adaptation has traditionally been described as an implicit process of learning, recent evidence suggest that even for visuomotor adaptation, explicit learning can contribute to early stages of error correction (Taylor et al., 2014; Bond & Taylor, 2015), at least for an abrupt perturbation. These studies were able to tease apart the explicit process from the implicit by having participants indicate their intended aiming direction before beginning each movement. During early phases of adaptation, when errors are large and salient, the explicit process seems to be the predominant component of motor learning. Although as the adaptation gradually progresses, the explicit process decreases and the implicit becomes the primary component. These findings allude to the fact that adapting to an abrupt perturbation may be more explicit, which differs from a gradually introduced perturbation that may be more implicit. Although the size of the rotation is thought not to affect the extent of implicit learning, a larger rotation may elicit a greater contribution of the explicit component (Bond & Taylor, 2015, Modchalingam et al., 2019). Investigating these explicit and implicit components of learning will add to our understanding of whether a perturbation introduced abruptly or gradually can affect adaptation performance.

Two-Rate Model of Motor Learning

In neuroscience, a common model used to describe learning rates involves two processes (Smith et al., 2006). This model suggests that there are a fast and slow process that work in parallel, and both continuously contribute to our motor output. The fast process is quick to learn, but also quick to forget, whereas the slow process learns much slower, but also retains the learnt adaptation for much longer. This model was developed based on both force-field and saccade adaptation paradigms (Smith et al., 2006). It was able to explain the rebound phenomena, described above, i.e. the retention of compensation for a previous perturbation, after some interference, when error feedback is removed. When there is no longer error feedback, the reaches do not just return back to baseline, but they continue to partly compensate for the first perturbation. Again, this means that there must be some memory of the first perturbation that persists even when adapting to a second perturbation. This model has been shown to explain similar patterns of learning in visuomotor adaptation as well.

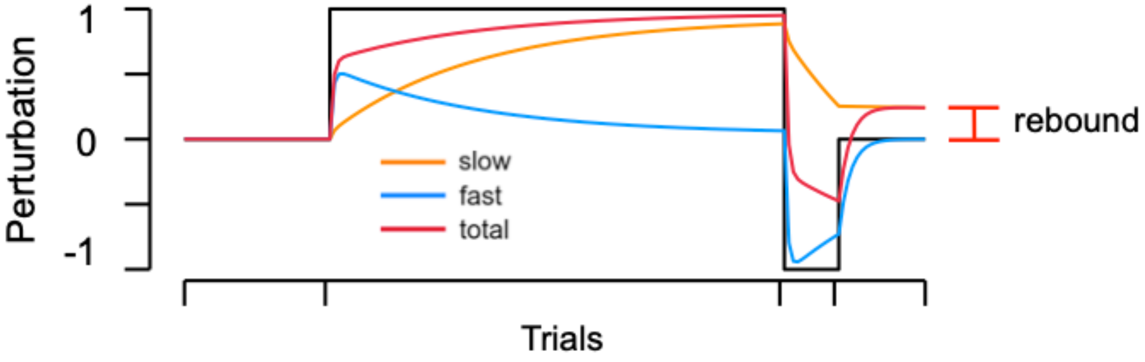

Figure 2. **The two-rate model.** The perturbation schedule is in the solid black line. The blue line is the fast process, which is quick to learn in both the training and reversal phase, but then also forgets quickly. The orange line is the slow process, which is slow to learn during the training phase, but is also the greatest contributor to the rebound. The fast and slow process work in conjunction to produce the total motor output, in red. Here, the y-axis has been normalized to the size of the perturbation.

McDougle et al. (2015) used this paradigm and attempted to equate the explicit and implicit processes of learning to the fast and slow processes of the two-rate model, respectively. They found that the fast process closely mapped onto the explicit learning pattern, and, in their approach, the slow process approximately resembled the implicit component of learning. Although previous studies have used this two-rate model as a tool to examine the explicit and implicit components of motor learning, it has yet to be investigated whether this model can account for any differences in learning when adapting to abruptly and gradually introduced perturbations. This is because abruptly and gradually introduced perturbations supposedly elicit different amounts of explicit and implicit learning. Given that the explicit component likely depends on large salient error signals, we can assume that when errors are small, or gradually introduced, it might not evoke explicit knowledge and thus adaptation likely reflects mainly the implicit component, whereas an abrupt perturbation likely has contributions from both. If the fast and slow processes indeed reflect explicit and implicit learning, and if abruptly and gradually introduced perturbations elicit different levels of explicit and implicit adaptation, then the two-rate model should explain any differences in the course of adaptation we can observe when the same perturbations is introduced abruptly or gradually. If there is a greater contribution of the implicit component when a perturbation is introduced gradually, then there should be a greater contribution of the slow process as well.

Objectives

The main objective of this study was to examine any differences in motor performance when responding to a perturbation that is introduced abruptly compared to gradually, using a within-subjects design. If the fast and slow processes of the two-rate model do map onto the explicit and implicit processes of motor learning, and abruptly and gradually introduced perturbations elicit different amounts of explicit and implicit learning, then differences in model fits on data from abruptly or gradually introduced perturbations should reflect the differences in explicit and implicit contributions to adaptation. To test this hypothesis, participants received a visuomotor adaptation where the rotation was introduced either abruptly, within one trial, or gradually, over 40 trials. Both conditions began with an aligned phase, followed by a training phase, where the 30-degree or 60-degree visuomotor (hand-cursor) rotation was introduced. After the initial training session, a brief exposure to the opposing rotation, and a set of trials with error-clamped feedback was performed. All participants adapted to the same perturbation magnitude (either 30° or 60°) twice: once introduced abruptly, and once gradually, albeit with opposing rotation directions, while reaching to different targets and in counterbalanced order. We quantify the magnitude of the rebound for each condition and each participant. Since the rebound emerges from an interaction between the fast and the slow process, it should change in size if abruptly or gradually introduced rotations affect the fast and slow process. Experiments were conducted both using a standard digitizing tablet and in an immersive virtual reality setup (separate groups). The secondary goal of this experiment was to test the feasibility of running similar experiments in a more naturalistic, ecologically valid setting, like that produced in the immersive virtual reality setup.

METHODS

Participants

Ninety-six students from York University participated in this study. There were thirty-two subjects who participated in each of the 3 groups (tablet30, tablet60, VR30). Of this, 2 participants were removed from the tablet30 group, 3 participants were removed from the tablet60 group, and 11 participants were removed from the VR30 group. These participants were excluded as a result of not having learned the perturbation. All participants reported having normal or corrected-to-normal vision. The protocols used in this study were approved by the York Human Participants Review Sub-committee. All participants gave prior informed written consent, and were naive to the purpose of the study. Participants were recruited using the York University undergraduate research pools, and were given course credit for participation.

Apparatus

Participants received one of two versions of the experiment, either the tablet version (n = 64), or the VR version (n = 32). The equipment used in the tablet version (Figure 2) was a laptop (Dell Inc.), computer monitor (Dell Inc. 20”, 30 Hz refresh rate, 1680 x 1050 resolution), mirror, tablet (Wacom Intuos Pro, 311 x 216 mm), and stylus. The visual stimuli were projected from the downward facing monitor onto the mirror, such that the stimuli were perceived to be in the same horizontal plane as the tablet below (Figure 2A).

In the VR version (Figure 3), the visual environment was presented via a head mounted display (Rift CV1, Oculus VR; 90 Hz refresh rate, 1080 x 1200 resolution per eye), the participants reached using a hand-held controller (Touch, Oculus VR), whose motion was tracked using 3 infrared Oculus cameras that were included with the system (see Shum et al., 2019). Although there was no touch-based position tracking like the tablet used in this setup, the Oculus Rift has been shown to have excellent accuracy, up to 1cm, and jitter of >0.35mm with only 1 position sensor (Borrego et al., 2018). In both experiments, participants were seated at a height-adjustable chair in front of the apparatus.

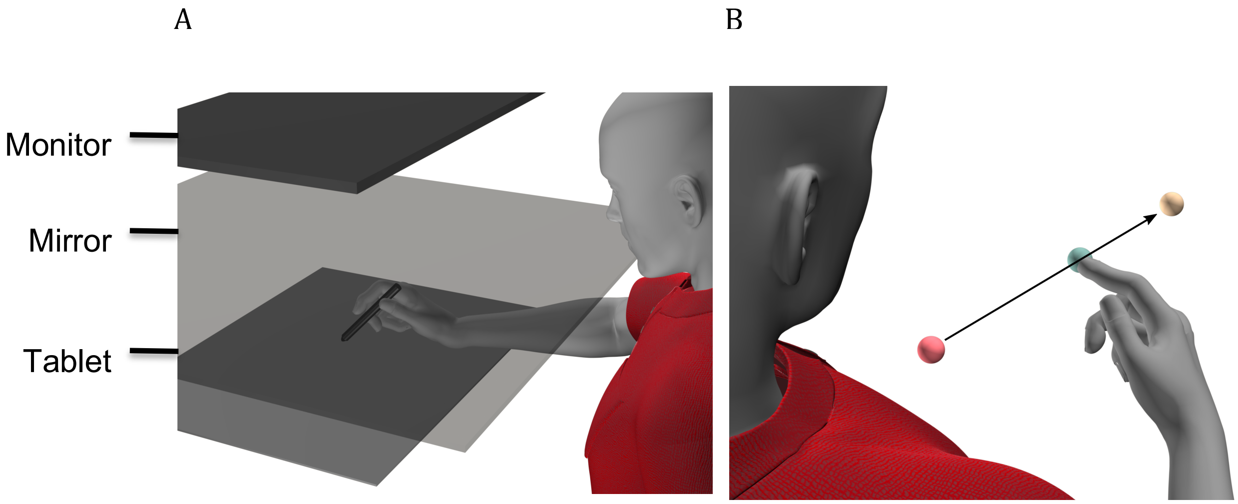

Figure 3. **Experimental setup**. (A) Depiction of the tablet experiment. The monitor was located 28 cm above the reflective surface, and the reflective surface was located 26 cm above the tablet. (B) Depiction of the virtual reality task.

Procedure

In both versions of the experiment completed with digitizing tablet, participants received continuous visual feedback of their unseen hand position via a white cursor; a 1 cm circle/sphere. Participants were instructed to make reaching movements from the home position to the visual target as quickly and accurately as possible. The visual target was a 1 cm circle/sphere, and was located 10 cm away from the home position. In both versions, the visual targets were presented either 40° or 50° from the midline on either the left or right side of the workspace (Figure 1). Once the target was acquired, the trial would end, and the participant would return back to the home position.

Participants performed two visuomotor adaptation tasks sequentially, one where the perturbation during training was introduced abruptly, and one where it was introduced gradually. Both conditions were comprised of 4 different phases: aligned, training, reversal, error-clamp (Figure 3). Both conditions started with the aligned phase, where the cursor represented the true location of the participant's unseen right hand. During the training phase, the cursor representing the participant's unseen right hand was rotated around the home position. Participants were asked to make a straight reach to a specific target in the workspace. The cursor representing their actual hand position was then rotated either clockwise or counterclockwise, for which the participant had to reach in the opposite direction to compensate for this perturbation. For the abrupt condition, the cursor was rotated by 30° or 60° for the entire training phase (different groups adapted to the smaller 30° rotation or the larger 60° one). For the gradual condition, the perturbation ramped up to a 30° rotation in increments of 0.75 degrees or to a 60° rotation in increments of 1.5°, such that it took 40 trials to get to the full rotation, and continued at the full rotation for the remaining 60 trials of the training phase (Figure 3). During the reversal phase, participants were exposed to an equal rotation in the opposite direction from the training phase. During the final error-clamp phase, the cursor would always move in the direction of the target irrespective of the participant's actual reach direction. There was always an equal distance between the home position and the cursor, and between the home position and the actual hand. During this phase, participants received no visual feedback of their hand location on the way back to the home position. However, to help participants return to the home position for the tablet version, an arrow at the home position indicating the direction of their actual hand location, guided most of the return to the home position. Once they were near the home position, the cursor representing their unseen hand location would also appear again. For the VR version, a semi-transparent sphere centered on the home position would appear, and decrease in size as the participant got closer to the home position. In real space, participants were given a physical home position that they were instructed to hold with their left hand as a proprioceptive marker to return to. Magnets were also attached to both the controller and the physical home position to ensure that participants were able to return to the same position and orientation. In both abrupt and gradual conditions, participants were given 32 trials of an aligned phase, 100 trials of the training phase, 12 trials of a reversal phase, and 20 trials with error-clamped feedback (Figure 3).

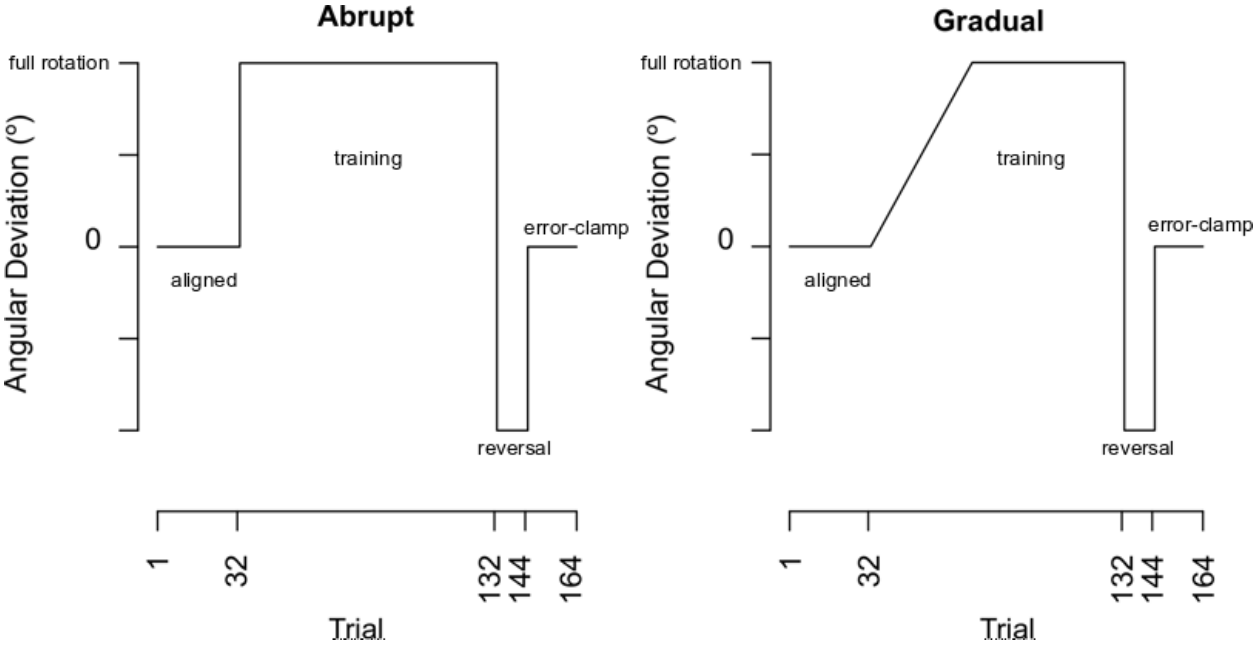

Figure 4. **Procedure.** Overview of a counter-clockwise perturbation schedule introduced abruptly and gradually. A full rotation during the training phase could be either 30° or 60°, and the reversal phase would be of equal magnitude (30° or 60°) and in the opposite direction of the training phase.

Design

For all three groups (30° digitizing tablet, 60° digitizing tablet, 30° VR setups), the experiment was a within-subjects design, such that all participants completed both abrupt and gradual conditions. The experiment began with a familiarization phase, which comprised of 8 aligned trials and 8 error-clamp trials. Next, participants completed one of the two visuomotor adaptation tasks (e.g. abrupt), followed by a mandatory break, and finished by completing the other visuomotor adaptation task (e.g. gradual). The following variables were counterbalanced across participants: the order of the conditions (abrupt or gradual), the side of the workspace that the targets appeared (left or right, See Figure 1), and the direction of the rotation (clockwise or counterclockwise). Therefore, participants received one of eight possible variations of the experiment. Counterbalancing the side of the workspace and direction of the rotation was performed to avoid transfer.

Data Analysis

The aim of this study was to test if abrupt and gradual perturbation schedules result in different visuomotor adaptation. If abruptly or gradually introduced rotations affect the relative contribution of implicit and explicit adaptation, and if implicit and explicit adaptation map on to the slow and fast process of the two-rate model respectively, there should be performance differences between abrupt and gradually introduced perturbations as well.

In order to assess performance throughout the task, for each reaching movement, we calculated the angular reach deviation at the point of maximum hand velocity. Angular reach deviation is the angular difference between a straight line from the start position to the target position, and a straight line intersecting the start position and the position of the participant’s hand. For comparisons that include both 30° and 60° groups, we converted the angular reach deviation to a percentage of adaptation by dividing it by the rotation size.

Before addressing the main objectives, we first checked for any order effects from the within-subjects design. In order to assess this, we performed two separate ANOVAs using only the data from the abrupt condition. We ran three separate 3 x 2 ANOVAs with groups (30° digitizing tablet, 60° digitalizing tablet, 30° VR setups) and order as our between-subject factors, first on the initial block of the training phase (trials

32-36), the second block (trials 37-40) of the training phase, and the final block (trials 129-132) of the training phase. In case there is no significant main effect of order or interaction, we could conclude that there were no (strong) order effects.

After ruling out possible order effects, we compared the extent of learning (final block of training) and the performance on last block (last 4 trials) of the reversal phase across gradual and abrupt training conditions for the different groups. Our first objective was to assess any reach-adaptation differences in the abrupt and gradual conditions, which we used only the data from the standard digitizing tablet setup. Our secondary objective was to assess the feasibility of running this experiment in VR. Since it did not make sense to compare the 30° VR group with the 60° digitizing tablet group, we opted to split these groups into pairs for two mixed-design 2 x 2 ANOVAs with first consisting of the Groups 30° and 60° digitizing tablet in order to test the effect of rotation magnitude, and the other ANOVA consisting of the Groups 30° digitizing tablet and 30° VR to test for experimental setup. This made a total of four 2 x 2 ANOVAs for each of the dependent variables.

Once we compared the training and reversal performance for these two conditions, we next investigated the magnitude of the rebound. As described in the introduction, the rebound represents the retention of compensation for a previous perturbation, after some interference, when error feedback is removed. Here, we calculated rebound by taking the average angular reach deviation of the last 10 error clamp trials. First we confirmed that the rebounds were present and were significantly greater than 0 by performing three one sample t-tests, one for each group. Once that had been established, we could proceed to examine whether there were any differences in the rebounds between the abrupt and gradual conditions. Like for the extent of training and reversal performance, we ran two separate 2 x 2 ANOVAs for groups with the same setup but different rotations, and the two groups with the same rotation but different experimental setups across abrupt and gradual conditions. To examine any null effects in the rebound, we also measured the Bayes Factor to determine the strength of evidence in favor of the null hypothesis. This was performed between the abrupt and gradual conditions for each group.

All results were reported using an alpha level of .05 significance, and any significant main effects or interactions were followed up by the appropriate pairwise comparisons, and the family-wise correction were implemented.

All data was processed and analyzed using R version 3.5.1.

RESULTS

In this study, we used a within-subjects design such that all participants adapted to both an abrupt and gradually introduced perturbation. As seen in Figure 4, all participants included were able to adapt to the first perturbation during the training phase. The following statistics and figures will examine whether there are differences in the extent of learning or rebounds between the abrupt and gradual condition. They will also investigate whether the size of the rotation or setup used to run these experiments had an effect on the extent of learning or rebounds as well.

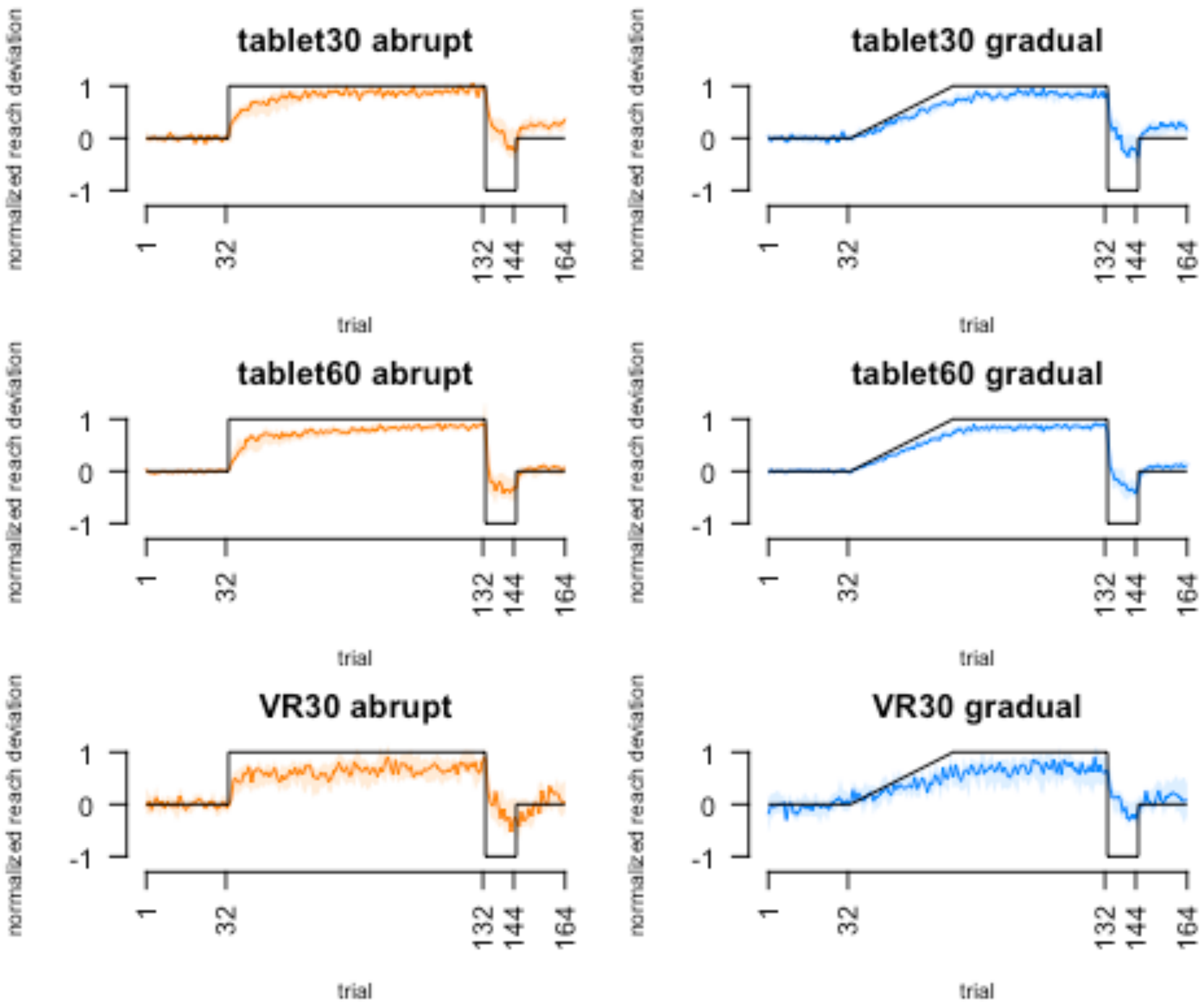

Figure 5: **Performance of all groups during adaptation for each of the abrupt and gradual conditions.** The data in orange here represents the mean angular reach deviations of the abrupt condition, whereas the data in blue represents the mean angular reach deviations of gradual condition. All of the data has been normalized to the size of the rotation. The lightly shaded area in each graph represents the 95% confidence intervals.

Order Effects

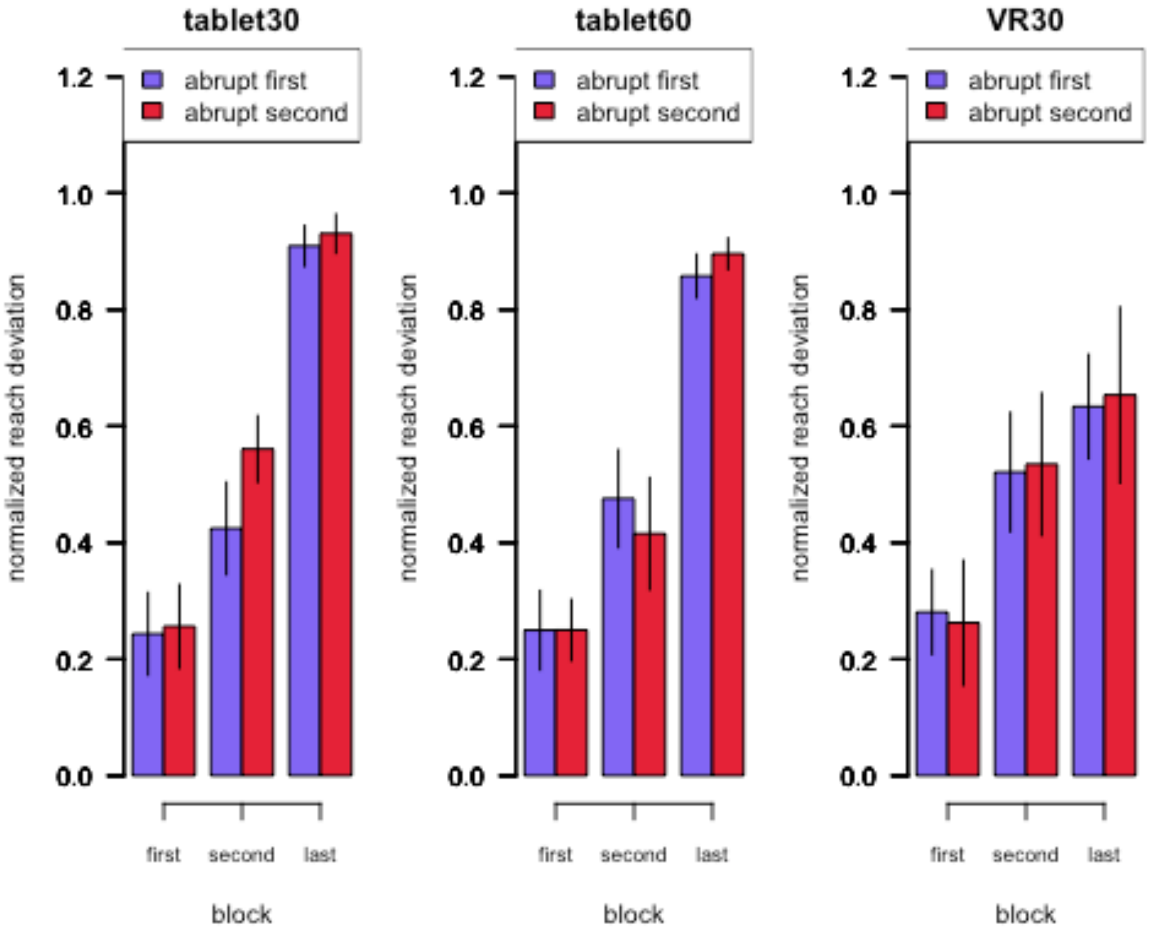

Figure 6: **Order effects of the within-subjects design for all groups:** This was done only on data from the abrupt condition. Performance is shown for the 3 groups (30° digitizing tablet, 60° digitalizing tablet, 30° VR setups), during the first, second, and last blocks of the training phase. The purple bars here represent the mean reach deviations of the participants who performed the abrupt condition first, and the red bars represent the mean reach deviations of the participants who performed the abrupt condition second. All of the data has been normalized to the size of the rotation. The error bars here represent the SEM.

Before we could address our main question of whether there were learning differences in the abrupt and gradual conditions, we first had to rule out any effects of order with our within-subjects design. The most sensitive way to check for order effect is to compare learning in the abrupt condition for participants who did this condition first, to those who did it second (after the gradual condition). We analyzed the first block of the training phase (trials 33-36), the second block (trials 37-40) of the training phase, and the final block (trials 129-132) of the training phase. We performed three 3x2 ANOVAs, one for each block (first, second, last), with Order and Group (tablet30, tablet60, VR30) as our between subjects factors. In the first block, there was no main effect of Order (F(1,71) = 0.0001, p>0.991), Group (F(1,71) = 0.052, p>0.948), or interaction (F(1,71) = 0.021, p>0.978). In the second block, there was also no main effect of Order (F(1, 71) = 0.233, p>0.630), Group (F(1,71) = 0.414, p>0.662), or interaction (F(1,71) = 0.726, p>0.486). In the last block, there was no main effect of Order (F(1,71) = 0.310, p>0.578), however there was a main effect of Group (F(1,71) = 10.539, p<0.001), but also no interaction effect (F(1,71) = 0.015, p>0.984). In short, this confirms that there were no significant differences in the order in which the conditions were performed, as seen in Fig. 5, and we were able to move forward in addressing our main research questions.

Extent of Learning

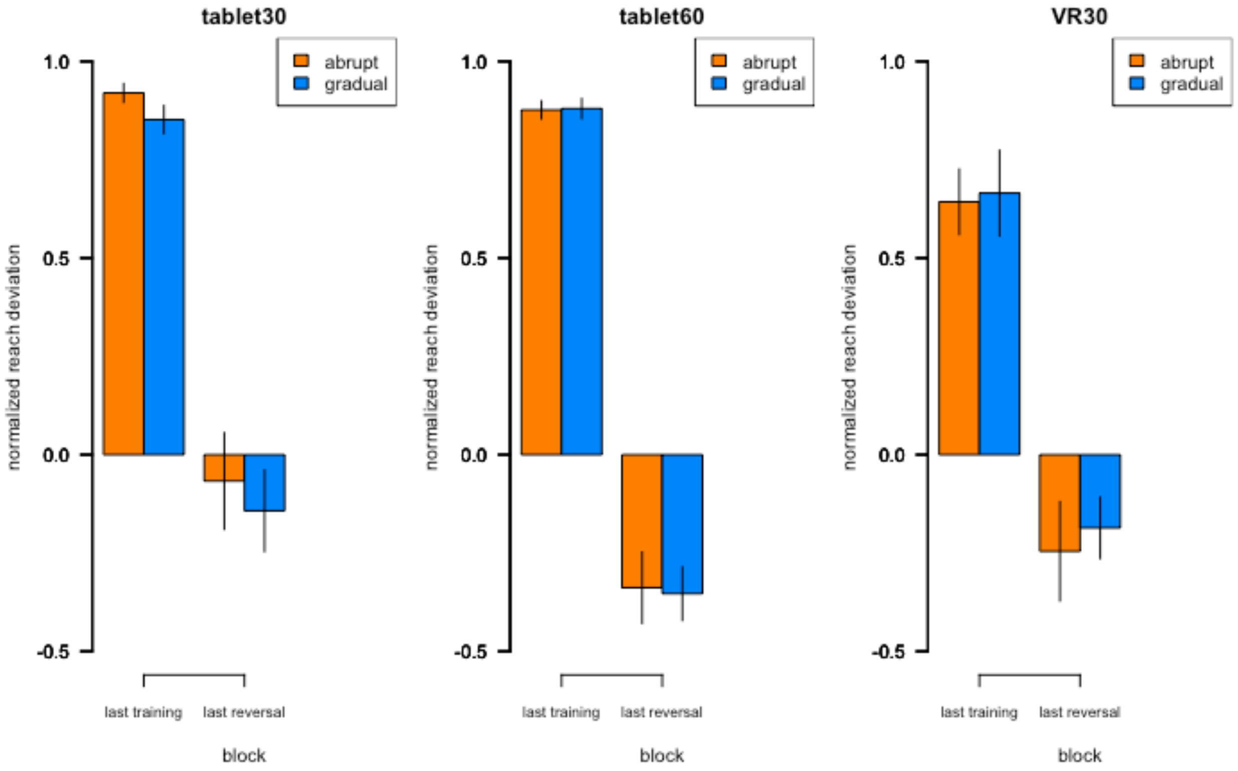

Figure 7: **Extent of learning for the abrupt and gradual conditions.** Performance is shown for the 3 groups (30° digitizing tablet, 60° digitalizing tablet, 30° VR setups) during the last training and last reversal blocks. The orange bars here represent the mean reach deviations of the abrupt condition, and the blue bars represent the mean reach deviations of gradual condition. All of the data has been normalized to the size of the rotation. The error bars here represent the SEM.

Since we ruled out any order effects, we proceeded to examine the extent of learning between the abrupt and gradual conditions (Fig 4 and 6). As a secondary objective, we were also curious to see whether the magnitude of the rotation, or difference in tablet and VR setups had an effect on the extent of learning. For instance, any differences between adaptation to a gradual or abrupt perturbation may be larger or only evident when the rotation is larger (30° vs 60°). In order to do this, we performed 4 mixed-design 2x2 ANOVAs on the last block of the training phase and the last block of the reversal phase with Group as our between subjects factor and Condition (abrupt, gradual) as our within-subjects factor. When looking at the performance in the last block of training for the groups with different setups (tablet30 and VR30), there was no main effect of Condition (F(1,47) = 0.311, p>0.578). Although there was an effect of Group (F(1,47) = 14.566, p<0.001), there was also no interaction effect (F(1,47) = 0.556, p>0.458). Looking at the same groups during the last block of the reversal phase, there were also no effect of Condition (F(1,47) = 0.066, p>0.798), Group (F(1,47) = 0.662, p>0.419) or interaction (F(1,47) = 0.522, p>0.472). When looking at the performance of the groups with different rotation magnitudes (tablet30 and tablet60) in the last block of the training phase, there was no effect of Condition (main effect; (F(1,56) = 1.669, p>0.201), Group (F(1,56) = 0.066, p>0.797), or interaction (F(1,56) = 1.889, p>0.174). Similarly, in the last block of the reversal phase, there were no effects of Condition (F(1,56) = 0.454, p>0.502), Group (F(1,56) = 3.851, p>0.054), or interaction (F(1,56) = 0.193, p>0.661). Although in these tablet30 and tablet60 groups, there was a trend towards significance in this last block of the reversal phase, it did not quite reach significance. These results show that there were no significant differences between the abrupt and gradual conditions in the extent of learning for any of the groups (see Fig. 6). Although there was a significant difference of the tablet and VR setups during the last block of the training phase, there were no significant differences seen during the last block of the reversal phase. These results also suggest that the magnitude of the rotation size has no significant effect on the extent of learning.

Rebounds

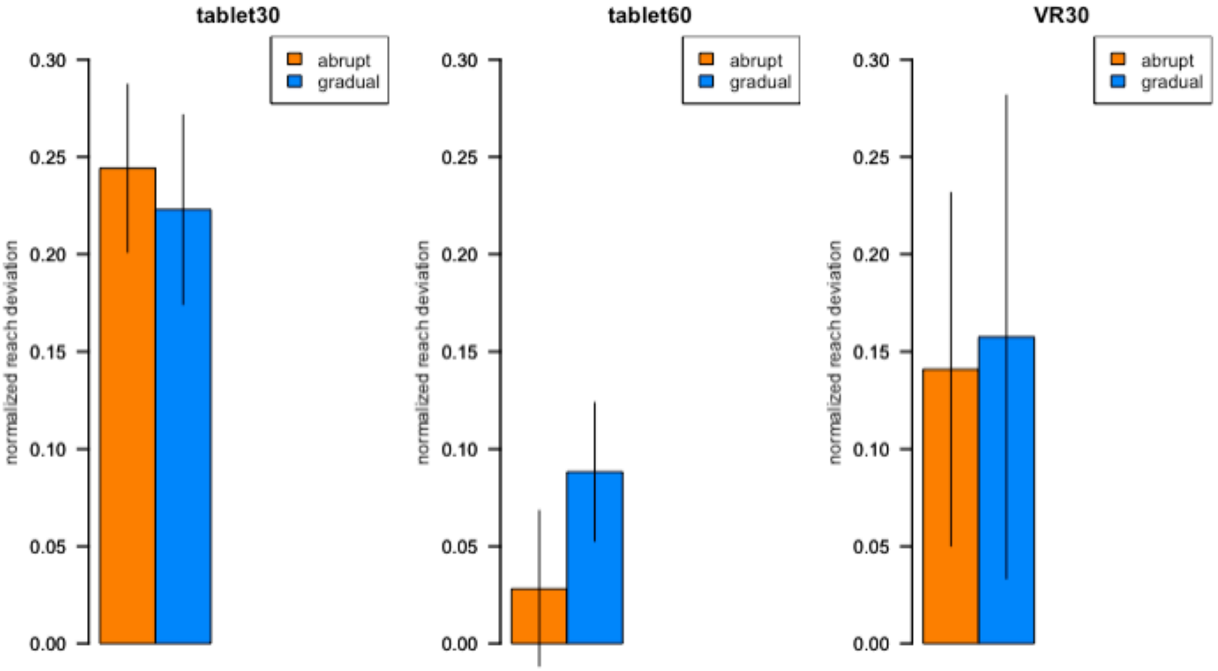

Figure 8: **Rebounds for the abrupt and gradual conditions.** Performance is shown for the 3 groups (30° digitizing tablet, 60° digitalizing tablet, 30° VR setups). The orange bars here represent the mean reach deviations of the abrupt condition, and the blue bars represent the mean reach deviations of gradual condition. All of the data has been normalized to the size of the rotation. The error bars here represent the SEM.

Having confirmed that there were no significant differences in the effect of order or extent of learning between the abrupt and gradual conditions, we moved on to addressing our main research question, whether there were behavioural differences in the rebound between the abrupt and gradual conditions (see Fig 7). However before we could get to that, we first had to confirm that the rebounds existed and were significantly greater than 0 with three one-tailed one sample t-tests. The rebounds were significantly greater than 0 in all of the tablet30 ($p<0.001$), tablet60 ($p<0.022$), and VR30 groups ($p<0.036$). These were uncorrected for multiple comparisons because they were planned comparisons and belong to different families. After we established that there were rebounds for every group, we proceeded to investigate the difference in rebounds between the abrupt and gradual conditions. Additionally to the extent of learning, we were also curious whether the magnitude of the rotation, or difference in tablet and VR setups had an effect on the rebound. We performed two mixed-design 2x2 ANOVAs with Group as our between subjects factor and Condition as our within-subjects factor. There were no significant differences in the abrupt and gradual conditions when looking at the tablet30 and VR30 groups, (main effect; F(1,47) = 0.009, p>0.921), or with the tablet30 and tablet60 groups (main effect; F(1,57) = 0.249, p>0.618). There was also no interaction when comparing the groups of different setups (F(1,47)= 0.075, p>0.784), or in the groups of different rotation magnitudes (F(1,57)=1.178), p>0.281). Although there was no main effect of Group with the tablet30 and VR30 groups (F(1,47) = 1.194, p>0.279), there was an effect of Group with the tablet30 and tablet60 groups (F(1,57)=14.256, p<0.001). All of these angular hand deviations were normalized relative to the rotation size, however since implicit learning has been shown to cap at 15 degrees (Modchalingam et al., 2019), it also made sense to test the rebounds in the tablet30 and tablet60 groups before they were normalized. Interestingly, if we compare the rebounds before normalization, there were no effects of Group (F(1,57)=3.124, p>0.082), Condition (F(1,57)=0.703, p>0.404), or interaction (F(1,57)=1.511, p>0.223). As illustrated in Figure 7, there were no significant differences in the rebound between the abrupt and gradual conditions for any of the groups. These results also suggest that the setup being used has no significant effect on the rebound, and before normalization, neither does the size of the rotation. Since there were no significant differences in the rebound between the abrupt and gradual conditions, we also tested the Bayes Factor to determine the strength of evidence in favour of this null hypothesis. In the tablet30 group, there was a Bayes Factor of 0.209, for the tablet60 group, there was a Bayes Factor of 0.367, and for the VR30 group there was a Bayes Factor of 0.239. This implies that there was moderate evidence in favour of the null hypothesis for the tablet30 and VR30 groups, and less, but also adequate evidence in favour of the null hypothesis for the tablet60 group.

In sum, we found no significant differences in the rebounds between the abrupt and gradual conditions across all three groups (tablet30, tablet60, VR30). In addressing our secondary objectives, we found no significant differences between the tablet and stylus setup compared to the VR setup in either the learning during the last block of the training phase or the rebounds, however there were differences in the last block of the reversal phase. Before the reach deviations were normalized to the rotation, we also found no significant differences in the rebounds between the groups who adapted to different rotation sizes (tablet30 and tablet60). After the reach deviations were normalized to the size of the rotation, these same tablet30 and tablet60 groups had no significant difference in the extent of learning either. These results, that there was no difference between the abrupt and gradual conditions, were true regardless of the rotation size or setup being used.

DISCUSSION

We investigated the reach-adaptation differences when compensating for a perturbation that is introduced abruptly compared to gradually in a visuomotor adaptation. We found that, contrary to our original hypotheses, there were no significant differences in the rebounds between the abrupt and gradual conditions. This was true when adapting to both a 30-degree and 60-degree perturbation using the tablet and stylus setup, as well as when adapting to a 30-degree rotation in VR. As we will discuss below, although these main findings were not what we were expecting, they do align with previous research and have implications in understanding the processes involved in abrupt versus gradual motor learning.

Abrupt versus Gradual Motor Learning

We found that the way a perturbation was introduced, either abruptly or gradually, had no effect on the rebound or the extent of learning. In reviewing the literature on this topic, it is evident that the differentiation between these abrupt and gradual conditions, at least behaviourally, is still unclear. Previous research has shown both behavioural (Kagerer et al., 1997, Ingram et al., 2000, Michel et al., 2007, Kluzik et al., 2008) and neurophysiological (Robertson & Miall, 1999, Schlerf et al., 2012, Werner et al., 2014) differences between a perturbation that is introduced abruptly compared to gradually. Although our findings opposed our initial thoughts that the way a perturbation was introduced would affect adaptation performance, previous studies have found similar results as well. In fact, previously presented work in our lab also supported this idea that there may not be behavioural differences when adapting to a perturbation that is introduced either abruptly or gradually (‘t Hart et al., 2018). Participants who were exposed to a 45° visuomotor adaption both abruptly and gradually showed no significant differences in the reach aftereffects. This was true for the younger adults, as well as older adults. In addition to our lab, previous research from other labs also provides evidence to support the fact that the rate at which a perturbation is introduced may not affect adaptation. Previous studies found no difference in reach aftereffects between abruptly and gradually introduced rotation with a 90° rotation (Buch et al., 2003), in typically developed children adapting to a 60° rotation (Kagerer et al., 2006), or in people with mild cerebellar ataxia (Crisimagna-Hemminger et al., 2010, Schlerf et al., 2013). The findings from these previous studies are commonly using reach aftereffects once the perturbation has been removed as their measure of adaptation, but there is also research that uses retention as their measure of adaptation. Others have also found no difference in retention between a perturbation that was introduced abruptly compared to gradually in reaching tasks such as a visuomotor hand-cursor adaptation or force-field paradigm (Klassen et al., 2005), as well as in a locomotor adaptation task (Hussain & Morton, 2014). In sum, although our results contradicted our initial hypotheses, there are still several previous studies that have similar findings, that there are no significant behavioural differences in adaptation between a perturbation that was introduced abruptly compared to gradually. Although it is not fully settled, our study provides a significant contribution to the conversation about whether the way a perturbation is introduced affects adaptation performance.

Admittedly, there are difficulties with interpreting null results. The absence of evidence is not necessarily evidence of absence, meaning that just because we found no statistically significant differences between the abrupt and gradual conditions, does not mean that there were no differences at all. One way we enhanced the statistical power in this study was using a within-subjects design to increase our number of participants in each condition. Other studies using a visuomotor adaptation paradigm have previously used a much smaller sample size. Kagerer et al. (1997) had 5 subjects for each abrupt and gradual condition, Buch et al. (2000) had 5 subjects per condition, Klassen et al. (2005) had 8 subjects per condition, and Kagerer et al. (2006) had 10 subjects perform both conditions. In our study we had 32 subjects perform both abrupt and gradual conditions, and this was true for all of three groups (tablet30, tablet60, VR30). Although there are always struggles with understanding null findings, our within-subjects design and large sample size give some addition strength to the interpretation of our results.

The Fast and Slow Processes

Our original idea that there would be a greater contribution of the slow process, and therefore larger rebound, in the gradual condition compared to the abrupt condition was based on two assumptions. The first assumption was that the explicit and implicit components of motor learning map onto the fast and slow processes of the two-rate model (McDougle et al., 2015). The next was that abrupt and gradually introduced perturbations elicit different amounts of explicit and implicit learning. Since explicit learning likely depends on large salient errors, when errors are small, or gradually introduced, it might not evoke explicit knowledge and thus mainly drive the implicit component. If there was a greater contribution of the implicit component when a perturbation is introduced gradually, then there should have been a greater contribution of the slow process as well. As explained earlier, the high retention rate of the slow process is the reason we still have some memory of the first perturbation even after adapting to a second perturbation. Therefore, if there were a greater contribution of the slow processes in the gradual condition, there should have also been a larger rebound in the gradual condition as well. Given that our results showed no significant difference in the rebounds between an abruptly or gradually introduced perturbation, we can conclude that at least one, if not both, of these assumptions are likely untrue.

Size of the Rotation

The implicit component of motor learning is thought to cap at 15°, regardless of the rotation magnitude (Kim et al., 2018, Morehead et al., 2017, Modchalingam et al., 2019). The fact that our results show no significant differences in the rebound between rotation sizes of 30 degrees compared to 60 degrees *before* normalization, provides further evidence that the size of the rotation likely does not affect the extent of implicit learning. Now that we know there is no effect of rotation size on implicit learning, we know that a larger rotation likely just recruits more explicit learning (Bond & Taylor, 2015; Heuer & Hegele, 2008; Neville & Cressman, 2018; Werner et al., 2015). This understanding could have implications on how we investigate the explicit and implicit components of learning, and consequently fast and slow processes of the two-rate model, in the future.

Feasibility of the VR set-up

As our secondary objective, we also wanted to test whether it was feasible to test these experiments in a more ecologically valid setting such as VR. We found no significant performance differences between the standard tablet and stylus setup compared to our novel virtual reality setup during the last block of the reversal phase and rebound, however there were significant differences in the last block of the training phase. Although, in using our outlier removal criteria, there were 11 more participants who had to be removed from the VR group compared to the tablet group. Previously, we have only explored visuomotor adaptation in a 2-D plane. In real life, the chance of restricting a reach to strictly a 2-D space is still unrealistic. Now that we have tested the feasibility of running reach adaptation experiments in VR, it opens up the possibilities of testing in a more naturalistic 3-D environment as well. It also allows us to start turning our experiments into virtual games, which could have a positive effect on the motivation of our participants during testing. In applying this research outside of the lab, there are several studies that provide evidence to show that VR can be used to promote motor learning in a clinical rehabilitation setting (see review Porras et al., 2018). Rehabilitation through the use of virtual reality has shown to enhance the gait and overall physical performance of people with Parkinson’s disease (Mirelman et al., 2011), as well as improve the gross motor function for children with cerebral palsy (Massetti et al., 2014). Although there is still a lot of research that needs to be done using virtual reality in the field of motor learning, this emerging technology does seem to be a promising resource to aid in our ability to test and improve these complex motor systems.

Future Studies

In this study, we did not directly test the explicit and implicit components of motor learning. In future studies, it might be beneficial to add a test of explicit and implicit learning during these experiments as well. Rather than focusing on the implicit component of adaptation, we could directly test explicit learning. One common way to do this is known as an aiming task, where we ask participants where they are going to aim their reach relative to the target before they actually make the movement. Getting this information on the relative contribution of explicit learning would add supplementary evidence for the fact that adapting to a gradual perturbation with small errors is indeed eliciting more implicit learning, compared to an abrupt perturbation with large errors, which should have contribution from both implicit and explicit learning. Another manipulation that would be interesting to change would be to alter the way the rotation is introduced further by introducing a condition in between the gradual and abrupt conditions. In the current study, the gradual condition for the 30-degree rotation had a ramp increasing the perturbation by 0.75 degrees each trial, whereas the abrupt condition changed to the full rotation within 1 trial. With a different condition, we could introduce the perturbation in steps instead, and test how this would affect the rebound and the learning processes. These different step sizes may elicit different components of explicit and implicit learning as well. The errors at each step will be a little larger and more salient than the gradual condition, which will recruit more explicit learning at the beginning of adaptation. Although at each step, participants will also consolidate more and more of their adaptation, which could elicit a greater contribution of implicit learning. Not only would it be interesting to see how the contributions of explicit and implicit learning are modulated throughout adaptation of this different condition, but it would also be intriguing to see how these processes map onto the fast and slow processes of the two-rate model as well. This could help explain some of the mixed findings in the literature, and add to our understanding of the different processes involved motor learning.

Conclusion

Our main finding here was that there were no significant differences in adaptation between a perturbation that was introduced abruptly or gradually. One major take-away from this study is that maybe we should not be so quick to equate the fast and slow processes of the two-rate model to the explicit and implicit components of motor learning. In regards to our secondary objectives, we also found that the neither the magnitude of the rotation, nor the different setups had an effect on both the extent of learning during the last block of the reversal phase and the rebound. However, there was a significant difference between the setups in the last block of the training phase. This lack of difference in the rebound provides further support for the idea that the size of the rotation may not affect the extent of implicit learning. These findings also show that these types of visuomotor learning experiments can be tested in a more naturalistic VR setting, which allows all sorts of new research questions.

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