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RESEARCH ARTICLE

Motor adaptation does not differ when a perturbation is introduced abruptly or gradually

Ambika Bansal[1,4] · **Bernard Marius 't Hart**[1] · **Udai Cauchan**[1] · **Thomas Eggert**[2] · **Andreas Straube**[3] · **Denise Y. P. Henriques**[1,4]

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Abstract
People continuously adapt their movements to ever-changing circumstances, and particularly in skills training and rehabilitation, it is crucial that we understand how to optimize implicit adaptation in order for these processes to require as little conscious effort as possible. Although it is generally assumed that the way to do this is by introducing perturbations gradually, the literature is ambivalent on the effectiveness of this approach. Here, we tested whether there are differences in motor performance when adapting to an abrupt compared to a ramped visuomotor rotation. Using a within-subjects design, we tested this question under 3 different rotation sizes: 30-degrees, 45-degrees, and 60-degrees, as well as in 3 different populations: younger adults, older adults, and patients with mild cerebellar ataxia. We find no significant differences in either the behavioural outcomes, or model fits, between abrupt and gradual learning across any of the different conditions. Neither age, nor cerebellar ataxia had any significant effect on error-sensitivity either. These findings together indicate that error-sensitivity is not modulated by introducing a perturbation abruptly compared to gradually, and is also unaffected by age or mild cerebellar ataxia.

Keywords Visuomotor adaptation · Motor learning · Two-rate model · Cerebellar ataxia · Older adults

Introduction

One of the most fundamental functions of the human brain is to adapt movements to our ever-changing environment or body. Understanding how to reduce the effort it takes to make these adaptations, by capitalizing on our powerful implicit learning processes, will be highly beneficial to rehabilitation and skills training. Here, we ask if adapting to small but gradual changes compared to abrupt changes modulates the effort it takes to adapt to them. We look at perturbations of different sizes and the effects of age and mild cerebellar ataxia on implicit adaptation.

Abrupt versus gradual motor learning

It is assumed that adapting to an abrupt perturbation is more effortful and explicit, whereas a gradually introduced perturbation may be more implicit (Taylor et al. 2014; Bond and Taylor 2015). Gradually and abruptly introduced perturbations do sometimes result in different aftereffects, a hallmark of implicit learning, in visuomotor adaptation (Kagerer et al. 1997; Ingram et al. 2000), force-field adaptation (Kluzik et al. 2008), and prism adaptation (Michel et al. 2007). However, these effects do not generally replicate (Buch et al. 2003; Klassen et al. 2005), even when done by the same lab (Kagerer et al. 2006). Three recent papers have tested the notion that the way a perturbation is introduced affects the underlying learning processes differently in younger adults (Coltman et al. 2021; Alhussein

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✉ Bernard Marius 't Hart
thartbm@gmail.com

[1] Centre for Vision Research, York University, Toronto, 4700 Keele Street, Toronto, ON M3J 1P3, Canada

[2] Department of Neurology, LMU University Hospital, LMU Munich, Fraunhoferstr. 20, 82152 Planegg, Martinsried, Germany

[3] Department of Neurology, LMU University Hospital LMU, Munich, Marchioninistr. 15, 81377 Munich, Germany

[4] School of Kinesiology and Health Science, Centre for Vision Research, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada

et al. 2019), and in cerebellar patients (Hulst et al. 2020), and here we probe these questions further.

Rebound and the two-rate model of motor learning

The rebound phenomenon is where after adapting to one perturbation and then having a washout or a reversal phase, behavior does not return to baseline, but is consistent with the first learnt adaptation. Since the rebound occurs with zero-clamped error feedback, it is highly unlikely to reflect any strategic or explicit adaptation components. Instead, it should only reflect implicit components of adaptation. To exclude explicit adaptation and focus on implicit adaptation, here we use the rebound magnitude as our primary measure.

The presence of a rebound, which proves that there is some retention of an initial perturbation that persists even after adapting to a second perturbation, demonstrates the contribution of at least two processes, a fast and slow process (Smith et al. 2006). 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. The fast and slow process of the two-rate model (Smith et al. 2006) have been suggested to map onto the explicit and implicit processes of learning, respectively (McDougle et al. 2015). If there is a greater contribution of implicit learning when a perturbation is introduced gradually, then we should see a greater contribution of the slow process as well.

Motor learning in older adults and people with cerebellar ataxia

The cerebellum plays a crucial role in our implicit motor learning (Hull 2020). Although the functional deficits for people with cerebellar damage are still unclear, people with cerebellar ataxia can use an explicit strategy to compensate in making adaptive movements (Taylor et al. 2010). Previous research has found greater aftereffects when using a gradual perturbation schedule in people with severe cerebellar ataxia (Criscimagna-Hemminger et al. 2010). However, these findings were not always replicated in later studies (Gibo et al. 2013; Schlerf et al. 2013). Other work has found that aging has an analogous pattern of degeneration to that of people with cerebellar degenerative disease, and in some cases has been used as a model system of cerebellar disease (Hulst et al. 2015). Although there is evidence to show that the cognitive processes that decline with aging affect explicit learning processes, this deficit can be compensated with implicit learning (Vandevoorde and Orban de Xivry 2019; Vachon et al. 2020).

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 ramped. We originally hypothesized that these different perturbation schedules would result in different levels of adaptation, and thus two-rate model fits. This hypothesis was based on two assumptions: (1) the fast and slow processes of the two-rate model map onto explicit and implicit motor learning, respectively, and (2) abruptly and gradually introduced perturbations elicit different amounts of explicit and implicit learning. We also predicted that performance and model fits could be further modulated by age, which may increase implicit adaptation, and by mild cerebellar ataxia, which may increase explicit adaptation.

Methods

Experiment 1: rotation size

Participants

Fifty-nine students from York University participated in this experiment. There were thirty subjects who participated in the ‘30-degree’ group, and twenty-nine participants who participated in the ‘60-degree’. Of this, 7 participants were removed from the 30-degree group, and 5 participants were removed from the 60-degree group, as they did not adapt to at least one of the perturbations. The 30-degree group consisted of subjects ages 20 ± 4 years old, and the 60-degree group were ages 20 ± 2 years old. 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

The equipment used in this experiment was a laptop (Dell Inc.), computer monitor (Dell Inc. 20″, 30 Hz refresh rate, 1680 × 1050 resolution), mirror, tablet (Wacom Intuos Pro, 311 × 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 (Fig. 1).

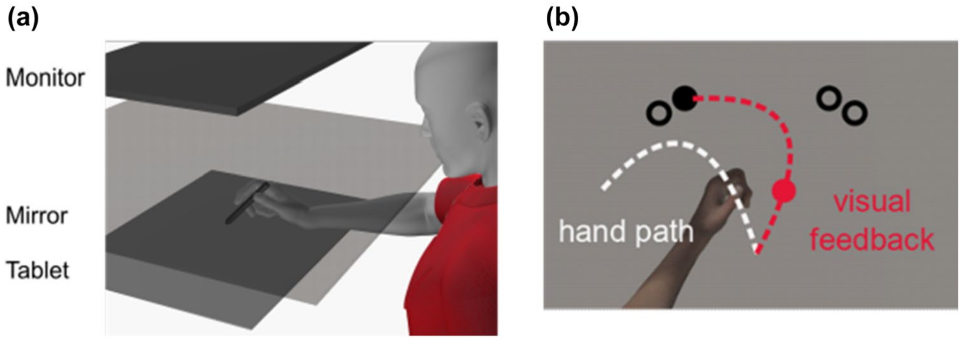


Fig. 1 **a** Experimental setup. The monitor was located 28 cm above the reflective surface, and the reflective surface was located 26 cm above the tablet. **b** Hand-cursor reach. The cursor representing the hand is rotated by 30°. Visual targets here are presented either 40 or 50 degrees from the midline 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 30º clockwise. Once adapted, this is corrected such that the white hand path is moving 30º in the opposite direction and the cursor is moving straight to the target

Procedure

Visuomotor rotation task 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, and was located 10.4 cm away from the home position. The visual targets were presented either 40° or 50° from the midline on either the left or right side of the workspace (Fig. 1B). 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 had four different phases: aligned, training, reversal, error-clamp (Fig. 2). Both conditions started with the aligned phase, where the cursor represented the true location of the participant's unseen right

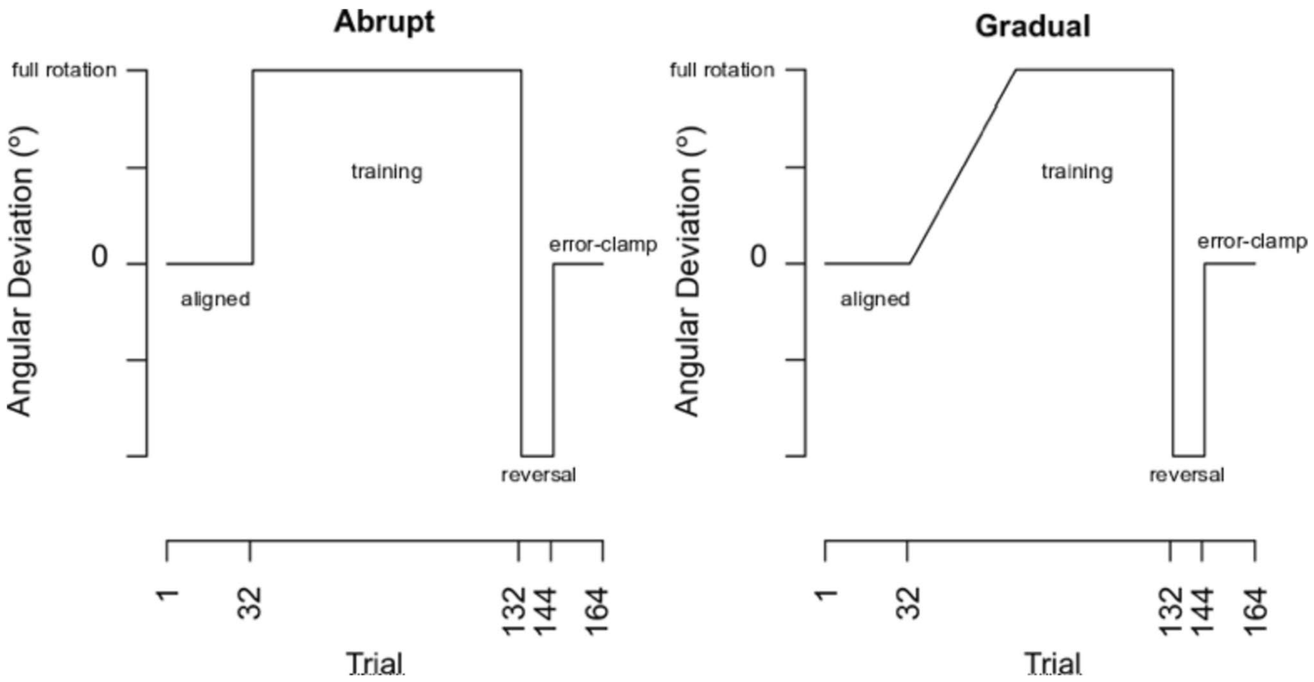


Fig. 2 Procedure. Overview of a counterclockwise perturbation schedule introduced abruptly and gradually. A full rotation during the training phase could be either 30° or 60°, and the reversal phase would be of equal magnitude (30° or 60°) and in the opposite direction of the training phase

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 (in both cases: 2.5% of the rotation per trial), and continued at the full rotation for the remaining 60 trials of the training phase (Fig. 2). 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. The movement of the cursor along this straight trajectory was still under control of the participant insofar as the distance of the cursor from the home position was kept the same as the distance between the actual hand and the home position. 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, 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. 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 (Fig. 2).

Design

For both groups (30-degree, 60-degree), the experiment was a within-subjects design, such that all participants completed both abrupt and ramped conditions. The experiment began with a familiarization phase, which comprised eight aligned trials and eight 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. ramp). The following variables were counterbalanced across participants: the order of the conditions (abrupt or ramp), the side of the workspace that the targets appeared (left or right), 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

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 scaled the angular reach deviation to a percentage of adaptation by dividing it by the rotation size.

Order effects Before addressing the main objectives, we first checked for any order effects from the within-subjects design. We fitted a simple asymptotic decay model to each individual participant's data from the first rotation of the abrupt condition. This model had two parameters: an asymptotic level of adaptation (N0) and a learning rate (lambda), which expresses how quickly the asymptotic level of adaptation is achieved. Since these learning rates can only be evaluated from the abrupt conditions, we compared learning for participants who did this condition first, to those who did it second (after the ramped condition). Reach deviations for each 30-degree and 60-degree groups were divided by their respective visuomotor rotation of 30 and 60 degrees. The models were fit to the scaled reach deviations, so that the asymptotic levels of adaptation (N0) are all scaled between 0 and 1. An ANOVA was performed with group (30-degree, 60-degree) and first condition (abrupt, ramp) as between-subjects factors.

Asymptotic level of adaptation and rebounds To assess any reach adaptation differences between the abrupt and ramped conditions, we performed a repeated measures ANOVA on normal reach deviation, averaged across the last ten trials of each block. We used block (rotated or clamp) and condition (abrupt and ramped) as within-subject factors and rotation size (30-degree, 60-degree) as between-subjects factor. If we found no significant differences, we took it one step further to evaluate the equivalence of these conditions by running a simple Bayes Factor Analysis.

Model fits In the two-rate model (Smith et al. 2006), the motor output X on trial t (X_t) is simply the sum of the output of the slow and fast processes on the same trial. Both processes learn from the error on the previous trial (e_{t-1}), and retain part of the previous adaptation ($X_{s,t-1}$, $X_{f,t-1}$). The four crucial parameters that are being tested are the error sensitivities (L_s, L_f), and the retention rates (R_s, R_f) for each of the two processes. The two-rate model integrated the learning and retention factors for each process as follows:

$$X_t = X_{s,t} + X_{f,t}$$

$$X_{s,t} = L_s * e_{t-1} + R_s * X_{s,t-1}$$

$$X_{f,t} = L_f * e_{t-1} + R_f * X_{f,t-1}.$$

The values for all four parameters (L_s, L_f, R_s, R_f) should fall in the range [0, 1]. To ensure that the fast process learns quicker than the slow process, we add the constraint that $L_f > L_s$, and to ensure the slow process retains more than the fast process, we add the constraint that $R_f < R_s$.

The model was fitted to the behavioural data for each abrupt and gradual condition of every participant using a mean square error (MSE) minimization method. To find optimal starting positions for MSE minimization, a grid search was performed to evaluate the least means square error for all of the model fits. The grid contained 14^4 points, and was reduced to the parameter combinations in the grid complying with the constraints. From the grid search, the ten best fitting parameter combinations were used as starting points for a least mean squared error fitting algorithm. The four parameters (L_s, L_f, R_s, R_f) from the fit with the lowest mean squared error were used. The differences between the model parameters of the different conditions were assessed by means of bootstrapping. The 95% confidence intervals for the differences in parameter values were compared to the 95% confidence interval of recovered parameters in both groups, for all four parameters.

All data was processed and analyzed using R version 4.0.5. The data can be found on the OSF repository: https://osf.io/c5ezv/. Data processing and analysis can be found at https://github.com/thartbm/GradualTwoRate.

Experiment 2: mild cerebellar ataxia and age

Participants

Seventy-seven subjects participated in this experiment (30 younger adults, 25 older adults, 22 mild cerebellar ataxic patients). The younger adult group consisted of subjects ages 20 ± 2 years old, the older adult group were ages 60 ± 9 years old, and the mild cerebellar ataxic patients were ages 61 ± 15 years old. Subjects were tested partly at the Centre for Vision Research, York University, Toronto, CA, and partly at the University Hospital LMU, Munich, GE. To minimize the effects of extra-cerebellar impairments, recruitment was focused primarily on cerebellar infarcts. Only 7 of the 22 patients (Table 1) had degenerative diseases most likely affecting extra-cerebellar regions. The experimental setup, the protocol, and the task were identical at both locations. The used hardware differed in only minor details. All participants reported having normal or corrected-to-normal vision. All participants gave prior informed written consent, and were naive to the purpose of the study.

Apparatus

The equipment used in this experiment was a computer monitor (HPL2245wg, 22″, 60 Hz), mirror, tablet (WACOM Cintiq 21UX, 432 mm × 324 mm), and stylus. Similar to experiment 1, 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.

Procedure

The visuomotor rotation task was similar to Experiment 1, with the main differences being in the perturbation schedule. There were minor differences in the reach amplitude and the target locations were slightly closer to the midline. In this experiment, the rotation size of the perturbation was 45°, each abrupt and gradual condition consisted of 220 trials, and instead of a reversal phase, there was a washout phase. A washout phase is similar to the aligned phase, where there is no rotation of the cursor. This was used to make the experiment doable for patients who would otherwise have had to adapt to a 90° change in rotation between the first and second rotated phases of the task. Both abrupt and gradual conditions had an aligned phase of 40 trials, a training phase of 120 trials, a washout phase of 20 trials, and an error-clamp phase of 40 trials. The training phase of the gradual condition ramped up in increments of 0.75° (or $1\frac{2}{3}$% of the rotation per trial), such that it took 60 trials to get to the full 45° rotation, and then continued at the full rotation for the last 60 trials of the phase. The target was located 12 cm away, and presented either 25° or 35° from the midline on either the left or right side of the workspace.

Design

This experiment was a within-subjects design, such that all participants completed both abrupt and gradual conditions. After the familiarization phase, participants completed 80 baseline trials: 40 aligned trials and 40 error-clamp trials (10 trials to each target per phase). 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 order of the conditions (abrupt or gradual), and the side of the workspace that the targets appeared (left or right) were counterbalanced. The two targets on the left side were presented during tasks with a

Table 1 Mild cerebellar ataxic patients

Years since diagnosis	Diagnosis	SARA	Laterality
34	Infarct superior cerebellar artery	0.5	Left-sided lesion
14	Infarct superior cerebellar artery	3.5	Left-sided lesion
0	Infarct superior cerebellar artery	8	Left-sided lesion
9	Infarct posterior inferior cerebellar artery	0	Right-sided lesions
10	Infarct posterior inferior cerebellar artery	0	Left-sided lesion
14	Infarct posterior inferior cerebellar artery	2.5	Left-sided lesion
11	Infarct posterior inferior cerebellar artery	3	Bilateral lesions
0	Infarct posterior inferior cerebellar artery	5.5	Left-sided lesion
14	Not further specified cerebellar infarct	0	Left-sided lesion
9	Not further specified cerebellar infarct	0	Right-sided lesions
12	Not further specified cerebellar infarct	3.5	Right-sided lesions
14	Not further specified cerebellar infarct	4	Right-sided lesions
0	Not further specified cerebellar infarct	5	Left-sided lesion
14	Not further specified cerebellar infarct	7	Left-sided lesion
12	Not further specified cerebellar infarct	9	Right-sided lesions
37	Cerebellar atrophy	6.5	Bilateral lesions
0	Cerebellar atrophy	19.5	Left-sided lesion
5	Autosomal-dominant cerebellar ataxia	8	Bilateral lesions
16	Autosomal-dominant cerebellar ataxia	10	Bilateral lesions
17	Spino-cerebellar ataxia	5	Bilateral lesions
16	Episodic cerebellar ataxia type II	8	Bilateral lesions
49	Autosomal-dominant cerebellar ataxia	11	Bilateral lesions

Information on the years since diagnosis, diagnosis, SARA score, and side of lesion. SARA is the scale of the assessment and rating of ataxia, an 8-item performance based scale resulting in a score between 0 and 40, where 0 is almost no ataxia and 40 is severe ataxia

clockwise rotation, and the two on the right were presented during a counterclockwise rotation. Therefore, participants received one of four possible variations of the experiment.

Data analysis

Same as Experiment 1.

Results

Experiment 1: rotation size

Order effects

Before we could address our main question of whether there were learning differences between the conditions, we first had to rule out any effects of order with our within-subjects design. We found no effect of first condition on learning rate across the two rotation sizes (F (1, 41) = 0.496, $p = 0.523$).

Asymptotic level of adaptation and rebounds

Once the order effects had been ruled out, we proceeded to check the asymptotic level of adaptation, and the absolute size of the rebounds in the error-clamp phases. As expected, there was an effect of block (rotated or clamped) showing larger deviations at the end of the rotated block compared to the rebound at the end of clamped block (Fig. 3) (F (1, 43) = 810.707, $p < 0.001$). There was also an effect of rotation size (F (1, 43) = 18.125, $p = 0.0001$) that interacts with block (F (1, 43) = 13.781, $p < 0.001$) due to a larger rebound in the 30-degree group. However, the main take-away was that there was no main effect of condition (F (1, 43) = 0.00, $p = 0.999$), nor does condition interact with any of the other variables. This would mean that the way the rotation was introduced (abrupt or ramped) had no effect on the asymptotic level of adaptation here, nor did it affect the size of the spontaneous rebound. A simple

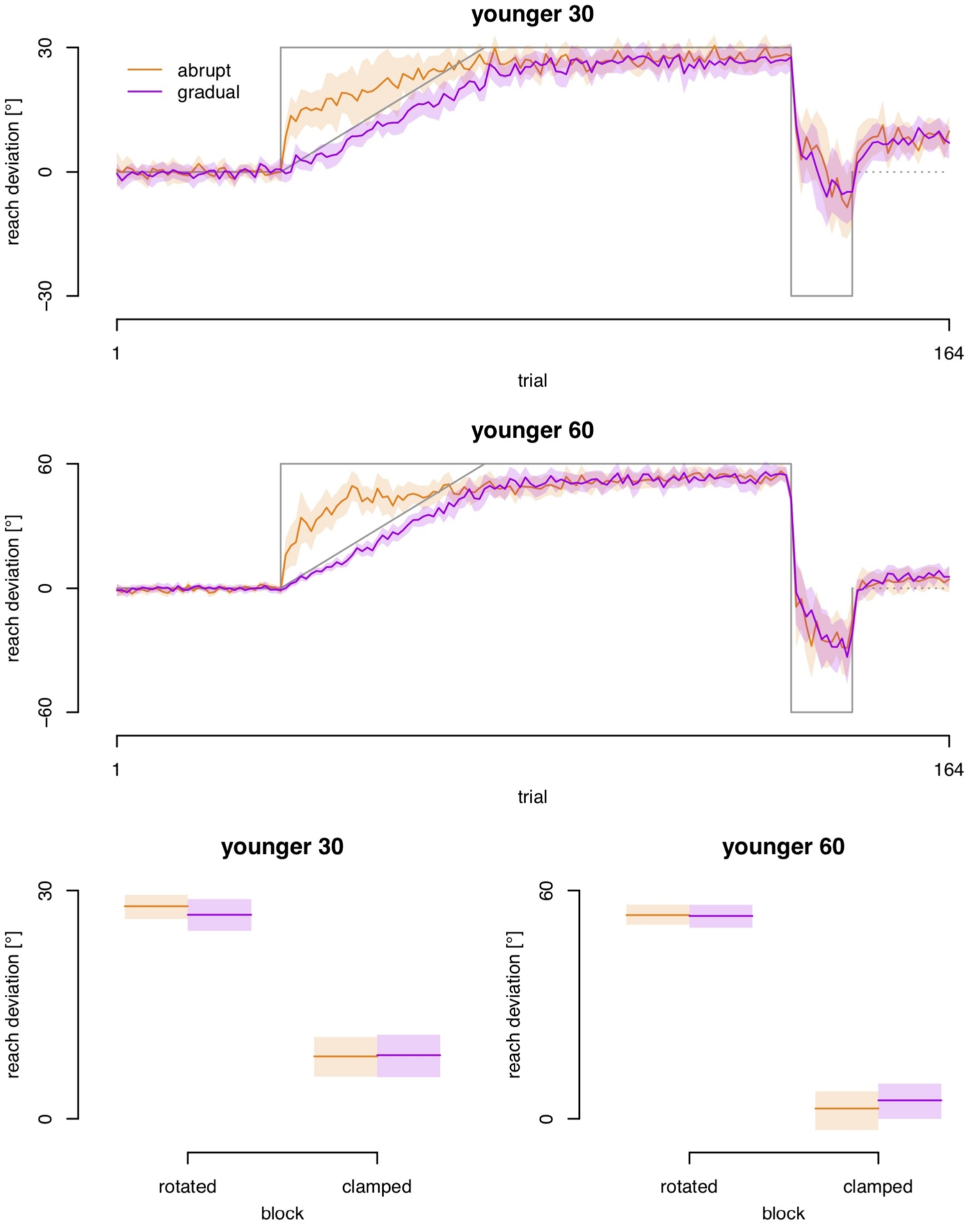


Fig. 3 Reach deviations for each of the abrupt and ramped conditions. Top two rows: The data in orange here represents the mean angular reach deviations of the abrupt condition, whereas the data in purple represents the mean angular reach deviations of the ramped condition for groups adapting to the 30-degree rotation (top) and 60-degree rotation (middle row). The lightly shaded area in each graph represents the 95% confidence interval. The bottom graphs are the mean reach deviations for the last 10 trials of the rotated and error-clamped blocks for the 30-degree rotation group on the left and 60-degree rotation group on the right

Bayesian analysis also provided moderate support for this null hypothesis (Fig. 4).

Two-rate model fits

Lastly, we wanted to see if the two-rate model would be different between the abrupt and ramped conditions. Looking at Fig. 5, the distributions of parameter values clearly overlap. We looked at the confidence intervals for the difference between the parameter values obtained from the two conditions, separately for the two groups, and found that zero was included in all of the confidence intervals. This suggests that the parameters for the two conditions were not significantly different.

Experiment 2: mild cerebellar ataxia and age

Order effects

As before, we first tested for an effect of order, by comparing the learning rate in the abrupt condition, as assessed by an exponential decay model with an asymptote,

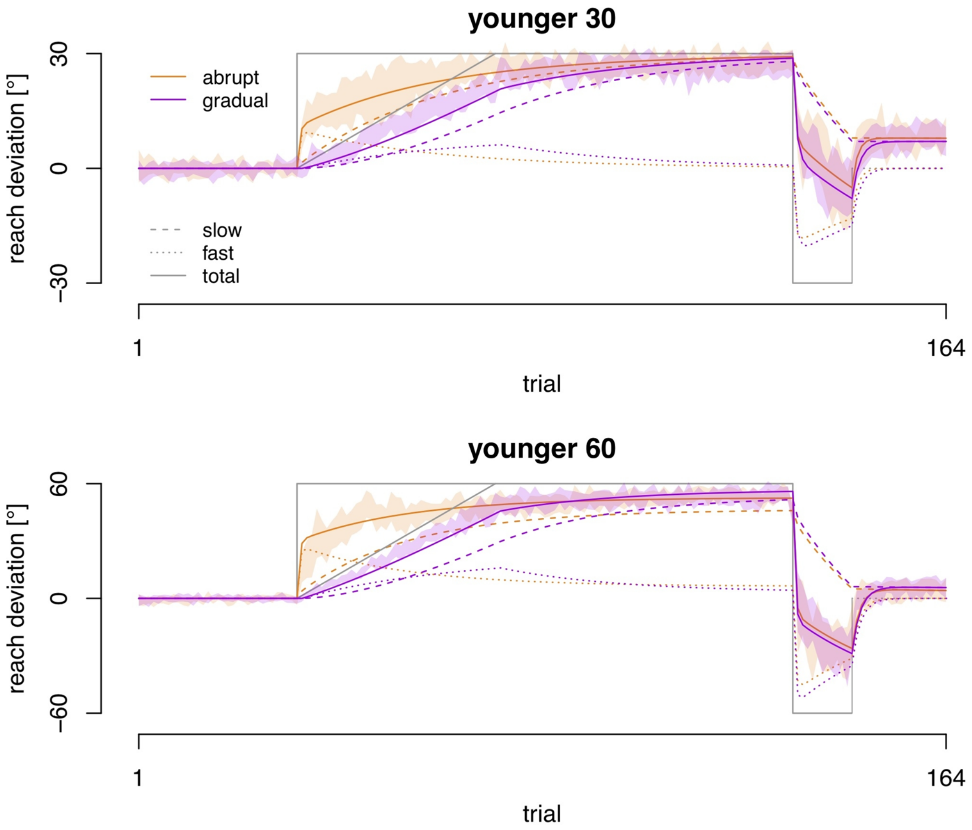


Fig. 4 Two-rate model fits. The solid line in orange here represents the mean angular reach deviations of the abrupt condition, whereas the solid line in purple represents the mean angular reach deviations of the ramped condition. The lightly shaded area in each graph represents the 95% confidence intervals. The dotted lines represent the slow processes, whereas the dashed lines represent the fast processes. This data was fit for groups adapting to the 30-degree rotation (top) and 60-degree rotation (bottom row)

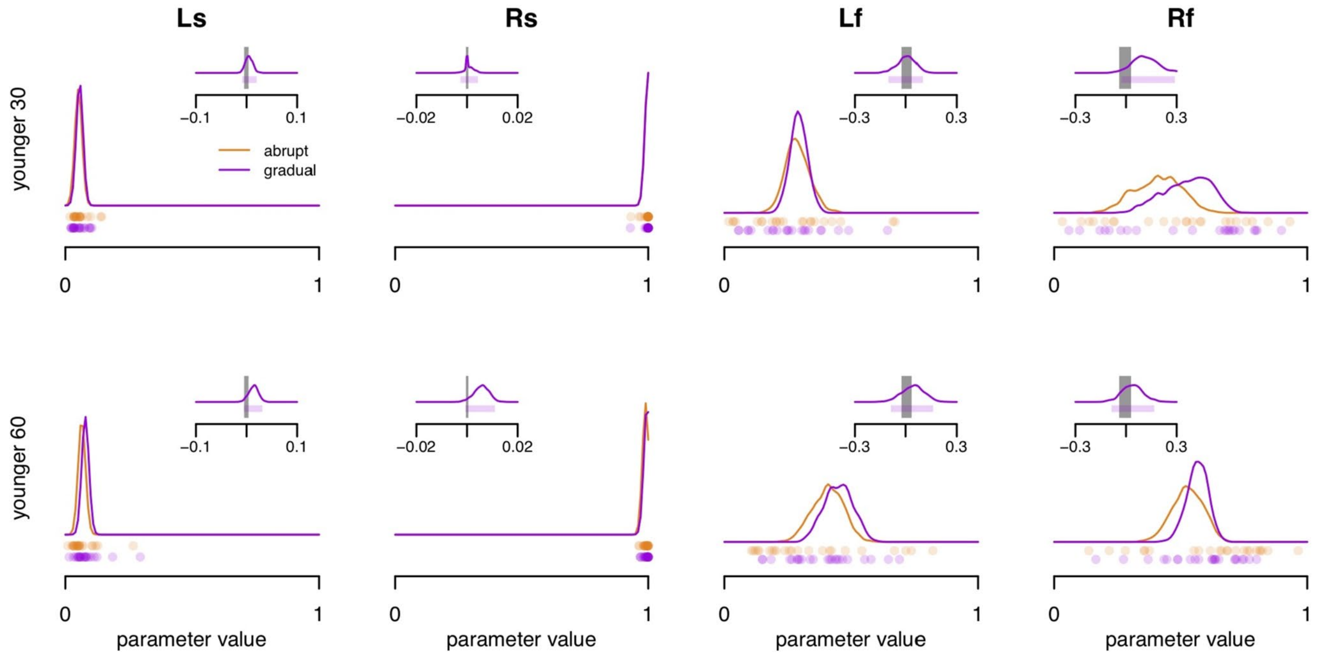


Fig. 5 Two-rate model parameter differences. The orange and purple lines represent the distribution of bootstrapped parameters and the dots are the parameter values for individual participants. The orange is the abrupt condition, and the purple is the ramped. In the small inset, we see a distribution of differences (purple density curve) and 95% confidence interval (purple shaded area). This can be compared to the 95% confidence interval of recovered parameters (gray shaded area)

between participants who did the abrupt condition first and who did it second. There was no effect of rotation size (F (2, 64) = 1.252, p = 0.292), no effect of order (F (1, 64) = 0.763, p = 0.385), and no interaction between the two (F (2, 64) = 0.923, p = 0.402). This means there are no order effects, and we will use all data as is.

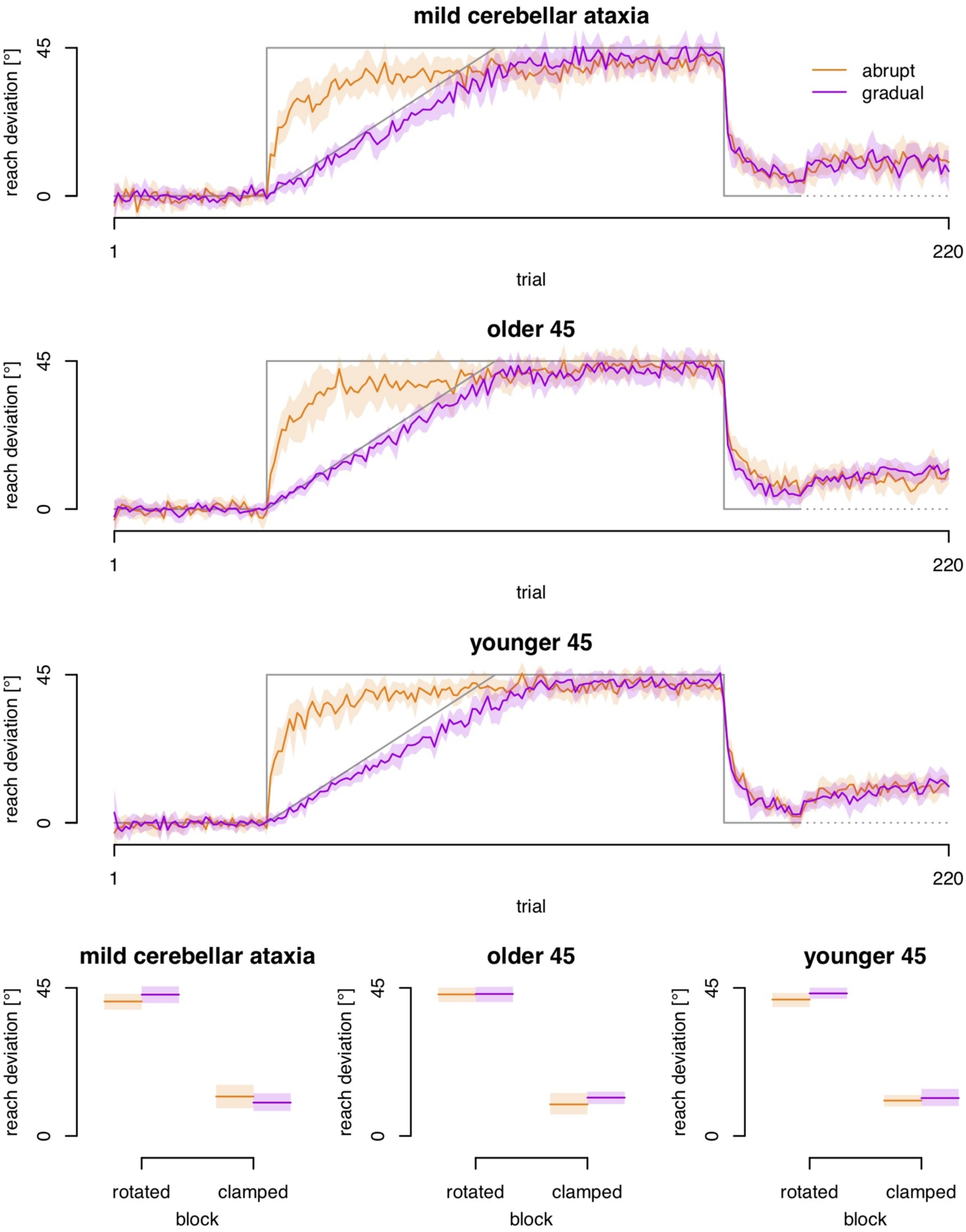
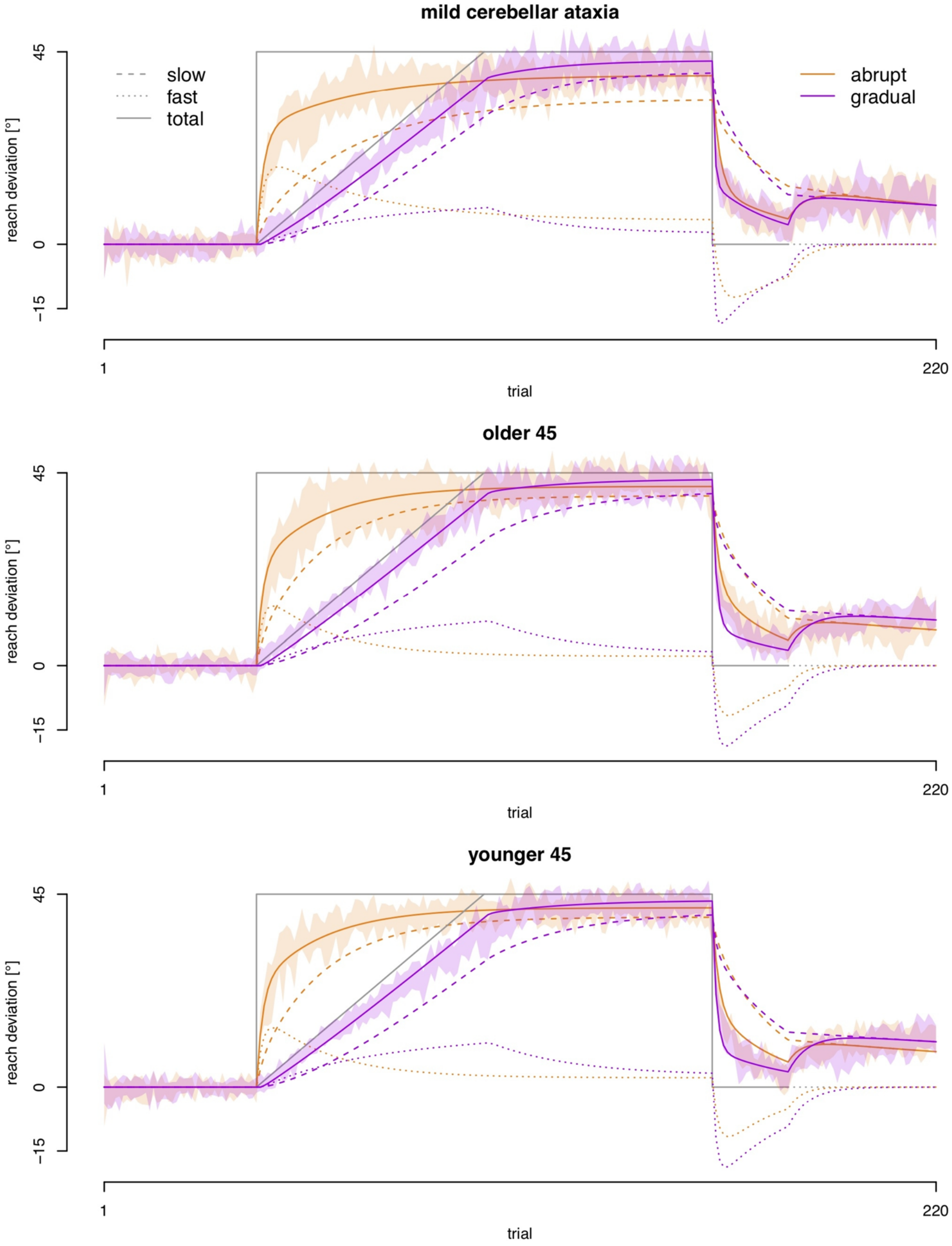


Fig. 6 Reach deviations for each of the abrupt and ramped conditions. Top three rows: The data in orange here represents the mean angular reach deviations of the abrupt condition, whereas the data in purple represents the mean angular reach deviations of the ramped condition for the groups adapting to the 45-degree rotation in the cerebellar ataxic population (top row), the older adult population (second row), and younger adult population (third row). The lightly shaded area in each graph represents the 95% confidence intervals. The bottom graphs are the mean reach deviations for the last 10 trials of the rotated and error-clamped blocks

Fig. 7 Two-rate model fits. The solid line in orange here represents the mean angular reach deviations of the abrupt condition, whereas the solid line in purple represents the mean angular reach deviations of the ramped condition. The lightly shaded area in each graph represents the 95% confidence intervals. The dotted lines represent the slow processes, whereas the dashed lines represent the fast processes. This data was fit for the groups adapting to the 45-degree rotation in the cerebellar ataxic population (top row), the older adult population (middle row), and younger adult population (last row)



Asymptotic level of adaptation and rebounds

Similar to Experiment 1, there was no effect of group (F (2, 67) = 0.069, p = 0.933), or condition (F (1, 67) = 1.222, p = 0.273) on either the asymptotic level of adaptation in the first rotated phase, or error-clamped phase (F (2, 67) = 1.530, p = 0.224). Again as expected, there was an effect of block (F (1, 67) = 1902.528, p < 0.001). Bayesian analysis also provides moderate support for the null hypothesis that there is no effect of how the rotation is introduced on reach deviations (Figs. 6 and 7).

Two-rate model fits

We looked at the confidence intervals for each of the parameter differences for all the groups and found that for the two older groups (mild cerebellar ataxia, and their age-matched

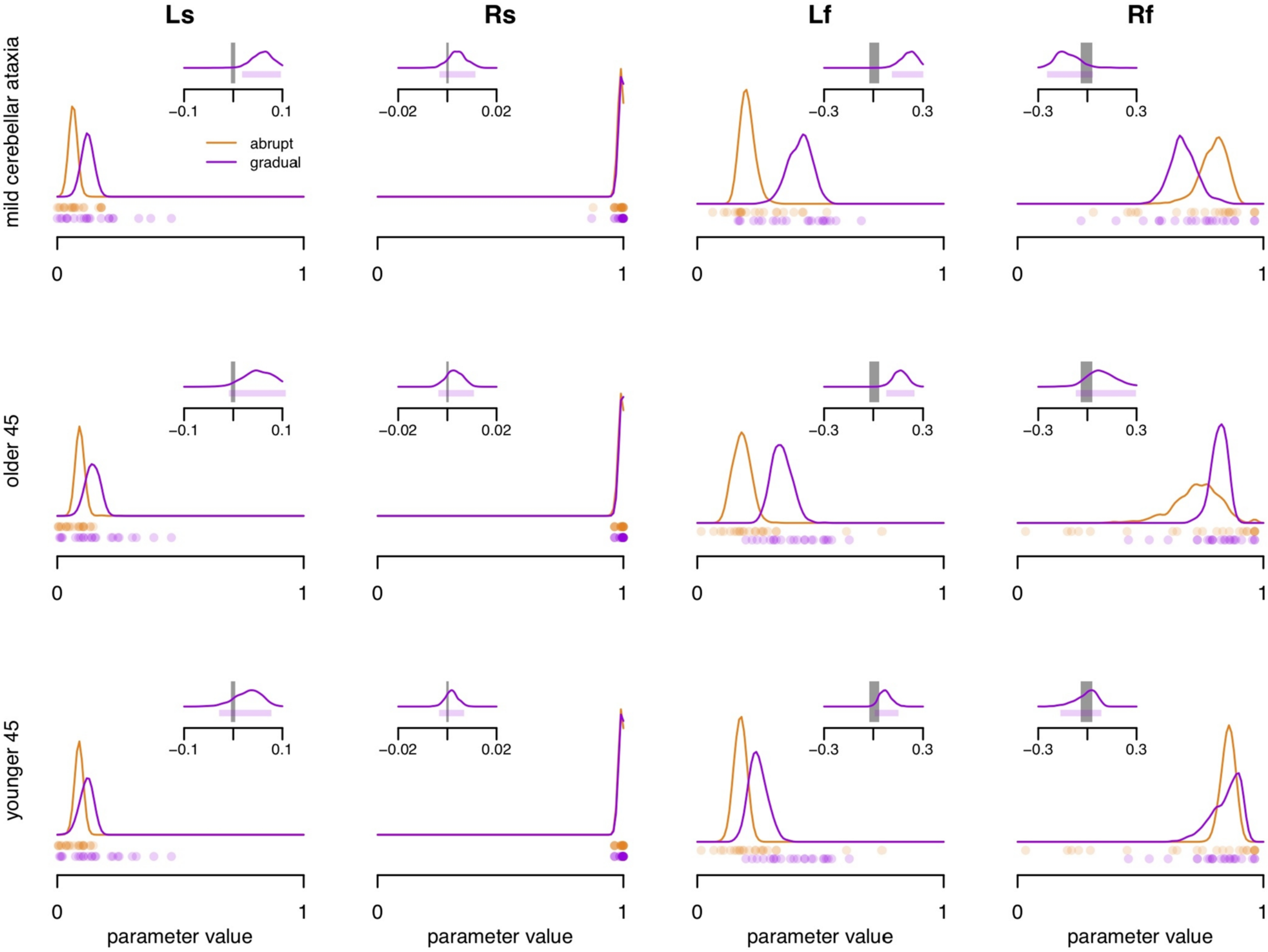


Fig. 8 Two-rate model parameter differences. The lines represent the distribution of bootstrapped parameters and the dots are the parameter values for individual participants. The orange is the abrupt condition, and the purple is the ramped. The insets show distributions of differences as a purple density curve, and the corresponding 95% confidence interval as a shaded purple area. Again, the gray bars are the 95% confidence intervals from the parameter recovery simulation

controls), the 95% confidence interval of differences in values of parameter Lf between abrupt and ramped conditions does not include zero, nor do they overlap with the expected interval of differences based on the parameter recovery simulation (Fig. 8). This shows that in the ramped condition, these groups have a higher error sensitivity for the fast process, although the slow process shows no differences. In the younger group, the fast error sensitivities do show a small difference between the abrupt and ramped conditions, but the 95% confidence interval for this difference overlaps with the 95% confidence interval for the parameter from the parameter recovery simulation, so it is likely due to chance.

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 motor adaptation between the abrupt and gradual conditions. This was true in both experiments: (1) when adapting to a 30-degree and 60-degree perturbation for younger adults, as well as (2) when adapting to a 45-degree rotation for younger adults, older adults, and for people with mild cerebellar ataxia. 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 and 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. This was true for all the 30-degree, 45-degree, and 60-degree rotation sizes. The implicit component of motor learning, that is reach aftereffects, is thought to cap at ~ 15°, regardless of the rotation magnitude (Kim et al. 2018; Morehead et al. 2017; Modchalingam et al. 2019, 2023). The fact that our results show no significant differences in the rebound between rotation sizes, provides further evidence that the size of the rotation likely does not affect the extent of implicit learning. Given there is no effect of rotation size on implicit learning, a larger rotation likely just recruits more explicit learning (Bond and Taylor 2015; Heuer and Hegele 2008; Neville and 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.

In reviewing the literature, 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 and 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 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 in young adults (Buch et al. 2003; Alhussein et al. 2019), or in typically developed children (Kagerer et al. 2006). 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 (Coltman et al. 2021; Modchalingam et al. 2023) 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.

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.

Motor learning in older adults and people with cerebellar ataxia

Similar to the rest of the literature, research in aging and in people with cerebellar ataxia has been mixed. There is evidence to support that there are greater aftereffects with using a gradual compared to abrupt perturbation schedule in people with severe cerebellar ataxia (Criscimagna-Hemminger et al. 2010). Originally, the thought was that aging and cerebellar ataxia may have different contributions of implicit and explicit learning, and therefore modulate the fast and slow processes differently as well. However, a recent paper looking at abrupt and gradual motor learning in cerebellar ataxia had contradicting results (Hulst et al. 2020). Many have also found a lack of support for the fact that error-sensitivity is modulated differently for abrupt and gradual perturbation schedules in healthy subjects (Eggert et al. 2021), as well as in cerebellar patients (Gibo et al. 2013; Schlerf et al. 2013; Butcher et al. 2017), and here we find the same. The lack of differences between our patients and the elderly controls also indicates that cerebellar lesions, even if they are accompanied by mild but marked signs of cerebellar ataxia, do not necessarily lead to adaptation deficits. This may also be related to fact that most of our 15 patients with cerebellar infarcts were in a stable condition long after the first diagnosis (11±8 years; Table 1) and may have had sufficient time to develop compensatory mechanisms.

Limitations and future studies

Admittedly, there are difficulties with interpreting null results. One way we enhanced the statistical power in this study was using a within-subjects design to increase the number of participants in each condition, and use paired or repeated measures analyses. Kagerer et al. (1997) had five subjects for each abrupt and gradual condition, Buch et al. (2003) had five subjects per condition, Klassen et al. (2005) had eight subjects per condition, and Kagerer et al. (2006) had ten subjects perform both conditions. In our study we had about 26 subjects perform both abrupt and gradual conditions, and this was true for all of the groups. Although there are always struggles with understanding null findings, our within-subjects design and large sample size give some additional strength to the interpretation of our results.

In this study, we did not directly test the explicit and implicit components of motor learning, but rather relied on the rebound magnitude as a measure of residual implicit contributions. While this provides a different perspective on contributions of implicit adaptation after abruptly and gradually introduced rotation, it also likely shows only more stable components of implicit adaptation, that have been decreased by an unknown degree during the reversal or washout phase. Nevertheless, the results here are in line with several previous studies, including one from our own lab, that use different measures and paradigms. In future studies, it might be beneficial to add a direct test of explicit and implicit learning during these experiments as well (eg. aiming reports or exclude strategy reaches). Getting this information on the relative contribution of explicit learning could 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 contributions from both implicit and explicit learning.

Conclusions

Our main finding here was that there were no significant differences in adaptation between a perturbation that was introduced abruptly or gradually. This was true across rotation sizes (30, 45, and 60 degrees), as well as between younger adults, older adults, and people with mild cerebellar ataxia. One major take-away from this study is that maybe we should not equate the fast and slow processes of the two-rate model to the explicit and implicit components of motor learning. As a secondary take-away, the lack of difference in the rebound provides further support for the idea that the size of the rotation may not affect the extent of the slow process that could be reflect implicit learning. Although it is not fully settled, our study provides a significant contribution to the conversation about whether error-sensitivity is modulated by the way a perturbation is introduced.

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Author contributions DYPH, BM’t, TE, and AS contributed to the study conception and design. Data collection was performed primarily by AB, UC, BM’t, and TE. Data analysis was completed by BM’t. The manuscript was primarily written by AB, and approved by all authors.

Data availability The datasets generated during and/or analysed during the current study are available in the Open Science Framework repository, https://osf.io/c5ezv/.

Code availability All data can be found on the OSF repository: https://osf.io/c5ezv/. Data processing and analysis scripts can be found at https://github.com/thartbm/GradualTwoRate.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval The protocols used in this study were approved by the York Human Participants Review Sub-committee and by the Ethics Committee of the Ludwig-Maximilians University, Munich (559–15).

Consent to participate Informed consent was obtained from all individual participants included in the study.

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