Residual errors in visuomotor adaptation persist despite extended motor preparation periods

Authors: Matthew Weightman[1,3,4*], John-Stuart Brittain[2,4], R. Chris Miall[2,3,4], Ned Jenkinson[1,3,4]

Affiliations:

[1] School of Sport, Exercise and Rehabilitation Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

[2] School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

[3] MRC-Versus Arthritis Centre for Musculoskeletal Ageing Research, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

[4] Centre for Human Brain Health, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

*Corresponding Author:

Matthew Weightman
School of Sport, Exercise and Rehabilitation Sciences,
The University of Birmingham
Edgbaston
Birmingham
B15 2TT
Email: mcw423@adf.bham.ac.uk

Running Head: Persistent visuomotor errors despite extended motor preparation

Abstract

A consistent finding in sensorimotor adaptation is a persistent undershoot of full compensation, such that performance asymptotes with residual errors greater than seen at baseline. This behaviour has been attributed to limiting factors within the implicit adaptation system, which reaches a sub-optimal equilibrium between trial-by-trial learning and forgetting. However, recent research has suggested that allowing longer motor planning periods prior to movement eliminates these residual errors. The additional planning time allows required cognitive processes to be completed before movement onset, thus increasing accuracy. Here we looked to extend these findings by investigating the relationship between increased motor preparation time and the size of imposed visuomotor rotation (30°, 45° or 60°), with regards to the final asymptotic level of adaptation. We found that restricting preparation time to 0.35 seconds impaired adaptation for moderate and larger rotations, resulting in larger residual errors compared to groups with additional preparation time. However, we found that even extended preparation time failed to eliminate persistent errors, regardless of magnitude of cursor rotation. Thus, the asymptote of adaptation was significantly less than the degree of imposed rotation, for all experimental groups. Additionally, there was a positive relationship between asymptotic error and implicit retention. These data suggest that a prolonged motor preparation period is insufficient to reliably achieve complete adaptation and therefore our results provide support for the proposal that the balance between error-based learning and forgetting (i.e., incomplete retention) contributes to asymptotic adaptation levels.

Key Words: Sensorimotor Adaptation; Motor Preparation; Mental Rotation; Learning Asymptote

Introduction

Sensorimotor adaptation has been extensively studied using visuomotor rotations (Cunningham, 1989; Krakauer, Ghilardi, & Ghez, 1999; Krakauer, Pine, Ghilardi, & Ghez, 2000). In this task, individuals adapt reaching movements to counter visual feedback that is rotated, for example, 30° or 45° from the hand's position. However, adaptation is typically incomplete, and performance plateaus with errors a few degrees greater than at baseline, regardless of the rotation magnitude imposed (Fernandez-Ruiz, Wong, Armstrong, & Flanagan, 2011; Huberdeau, Haith, & Krakauer, 2015; van der Kooij, Brenner, van Beers, & Smeets, 2015; Vaswani et al., 2015; Weightman, Brittain, Punt, Miall, & Jenkinson, 2020; Langsdorf, Maresch, Hegele, McDougle, & Schween, 2021). State-space models of learning accurately capture this incomplete compensation (Smith, Ghazizadeh, & Shadmehr, 2006; Kording, Tenenbaum, & Shadmehr, 2007). In these models, error-driven learning and forgetting (or a reversion to baseline) work in opposition, and equilibrate below optimal performance, resulting in the commonly observed persistent error.

However, Vaswani and colleagues (2015) demonstrated that under certain conditions, individuals disengage from this limited error-dependent learning to attain greater task success. In one of their experimental conditions, Vaswani et al. (2015) 'clamped' visual feedback after an initial learning block, such that a small, fixed, visual error was presented, regardless of movement accuracy. They found that under these conditions, participants appeared to select an alternative, more exploratory learning policy, which enabled them to close the errors and even to overcompensate for the rotation (which was not predicted by the state-space model). The authors suggested that the altered feedback distribution triggered alternative learning processes (and enabled the elimination of residual errors), which are usually suppressed during naturalistic feedback conditions.

More recently, Langsdorf et al. (2021) presented an alternative theory to explain why under normal, non-clamped environments, the central nervous system fails to eliminate residual errors during motor adaptation. They suggested an intrinsic speed-accuracy trade-off: where time consuming planning processes are interrupted by the imperative onset of movement, resulting in fast, but inaccurate movements. In their study, they showed that when an obligatory 2.5 second wait period was introduced between target presentation and movement initiation, participants were able to fully adapt to a 45° rotation, leaving no persisting errors at the end of learning. However, if this wait period was not enforced or was introduced at the end of the movement, when no planning was assumed to be taking place, participants failed to fully counteract the rotation. The authors highlighted mental rotation as a time-consuming cognitive process potentially involved in the planning of visuomotor adaptation.

For some time now, visuomotor adaptation has been framed as a combination of distinct learning processes (Mazzoni & Krakauer, 2006; Taylor, Krakauer, & Ivry, 2014; Bond & Taylor, 2015; McDougle, Bond, & Taylor, 2015; Voets, Panouilleres, & Jenkinson, 2020). These processes are customarily described as implicit and explicit. The implicit component adapts slowly and is driven by sensory prediction errors (Smith et al., 2006; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). The explicit component is a fast adaptation process and involves, among other processes, strategic re-aiming to counter the detected perturbation (Taylor & Ivry, 2011; Heuer & Hegele, 2008; McDougle et al., 2015). Such strategies are thought to include a form of metal rotation (McDougle & Taylor, 2019). Langsdorf et al. (2021) suggest that under naturalistic feedback conditions, parametric mental rotations from the target to the intended movement goal are prematurely

terminated (despite no time constraints) and result in aimed movement trajectories falling short of the imposed rotation.

Behavioural and neurophysiological research suggests a role of mental rotation in the planning of movements aimed at angles away from visually defined targets (Georgopoulos & Massey, 1987; Bhat & Sanes, 1998; Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989; Lurito, Georgakopoulos, & Georgopoulos, 1991; Pellizzer & Georgopoulos, 1993). Neuronal population vectors recorded in the monkey motor cortex gradually rotate from a stimulus direction to a cued movement direction during the planning of a reach (Georgopoulos et al., 1989; Lurito et al., 1991). Additionally, the completion of mental rotation tasks require long reaction times with larger magnitudes of rotation (Shepard & Metzler, 1971; Georgopoulos & Massey, 1987); a signature of cognitive strategies (Fernandez-Ruiz et al., 2011; Haith, Huberdeau, & Krakauer, 2015; McDougle & Taylor, 2019).

Given this knowledge, we aimed to replicate and extend the findings of Langsdorf et al. (2021), in order to further understand the roles of extended planning periods and mental rotation in attaining full adaptation. We designed an online visuomotor adaptation task, where participants had either long (2.5 seconds), medium (1 second) or short (0.35 seconds) enforced preparation periods between target presentation and movement onset, and were required to adapt to either a small (30°), moderate (45°) or large (60°) visuomotor rotation. Previous studies (Langsdorf et al., 2021) suggest that the 45° rotation would be fully corrected with the longest preparation period; errors for the middle interval would be greater; and a substantial residual error should be found for the shortest preparation interval. This negative relationship between preparation interval and residual error should be most obvious for the 60° rotation; the smallest rotation (30°) might allow full

compensation even at the shortest preparation interval. In other words, the response time could be considered the sum of a mental rotation period linearly related to the rotation magnitude, and a fixed movement initiation period; if the sum exceeds the prescribed preparation interval, then residual errors should be seen.

Materials and Methods

Participants

A total of 180 participants were recruited (aged 18-37 years, mean ± SD = 23 ± 4 years, 82 males); all gave informed consent before participating and received no remuneration for completing the study. The study was approved by the University of Birmingham ethics board (Science, Technology, Engineering and Mathematics Ethical Review Committee). Participants were self-reported as right-handed (161) or left-handed (19) and used their preferred hand to complete the task (all but 5 of the left-handed participants completed the task using their right hand). All participants had normal, or corrected to normal, vision and reported no history of neurological disease. Participants were pseudorandomised into one of nine experimental groups (each n = 20), which differed in the amount of preparation time provided (0.35, 1 or 2.5 seconds) and the magnitude of cursor rotation (30°, 45° or 60°).

Task

We developed a visuomotor adaptation task using the behavioural science experiment platform: PsychoPy (Peirce et al., 2019), which was implemented online via Pavlovia (https://pavlovia.org). Participants were required to have access to a desktop or laptop computer with internet connection and a mouse or trackpad to navigate through and complete the task (117 participants used a trackpad; 63 participants used a mouse).

Participants were sent a link to access the task and entered a unique code which determined which combination of preparation time and rotation angle they would encounter. Participants were asked to sit in a location of their choosing, so that they could easily see their computer screen and comfortably reach and manipulate the mouse or trackpad. They made centre-out movements with either their mouse or on their trackpad from an on-screen central starting position to targets which appeared on an invisible circular array surrounding it (Figure. 1a). They were told to make one fast and straight 'shooting' movement, aiming to get the on-screen cursor as close as possible to the target. Prior to starting the task, all participants completed a brief tutorial, which included the task instructions and aims. At this point, participants were asked to contact a researcher if they were unclear about any part of the task and/or had any questions relating to the instructions.

At the beginning of every trial the cursor (red filled circle) would be located in the centre of the screen (grey background). The cursor was surrounded by two larger red annuli, which formed a bullseye-like formation (Figure. 1b). At a set moment, the outer ring disappeared, followed by the inner ring 0.5 seconds later, and the cursor then changed colour from red to white after a further 0.5 seconds. Participants were told that this sequence of events should be treated as a countdown to movement and that they should aim to time their movement so that it was initiated in synchrony with the cursor changing colour from red to white (Figure. 1b). Depending on the experimental group, the target (green filled circle) would appear either 2.5 seconds, 1 second or 0.35 seconds before the movement cue - thus creating three distinct preparation periods. The target could appear at any one of eight possible locations, equally spaced (separated by 45˚) around an invisible circular array centred on the start position, and pseudorandomised so that the target appeared at each

location once every cycle of eight trials. The position at which the cursor passed the invisible perimeter was displayed for 0.5 seconds as static open white circle, providing feedback of movement accuracy. After an inter-trial interval of 0.5 seconds the cursor would reset to the central position ready for the next trial. Participants were encouraged to move their hand back to a comfortable starting position after each trial. All elements of the visual display were scaled according to the size of the task window and thus were the same relative size for all participants. Consequently, the physical movement size required varied between participants depending on their set up and was not recorded beyond input device. If participants attempted to move 0.15 seconds before or after the go cue, or if movement time exceeded 0.25 seconds, the message "Response too fast/slow" appeared on the screen and the trial was aborted. These measures were to encourage fast movements, initiated correctly with the task instructions.

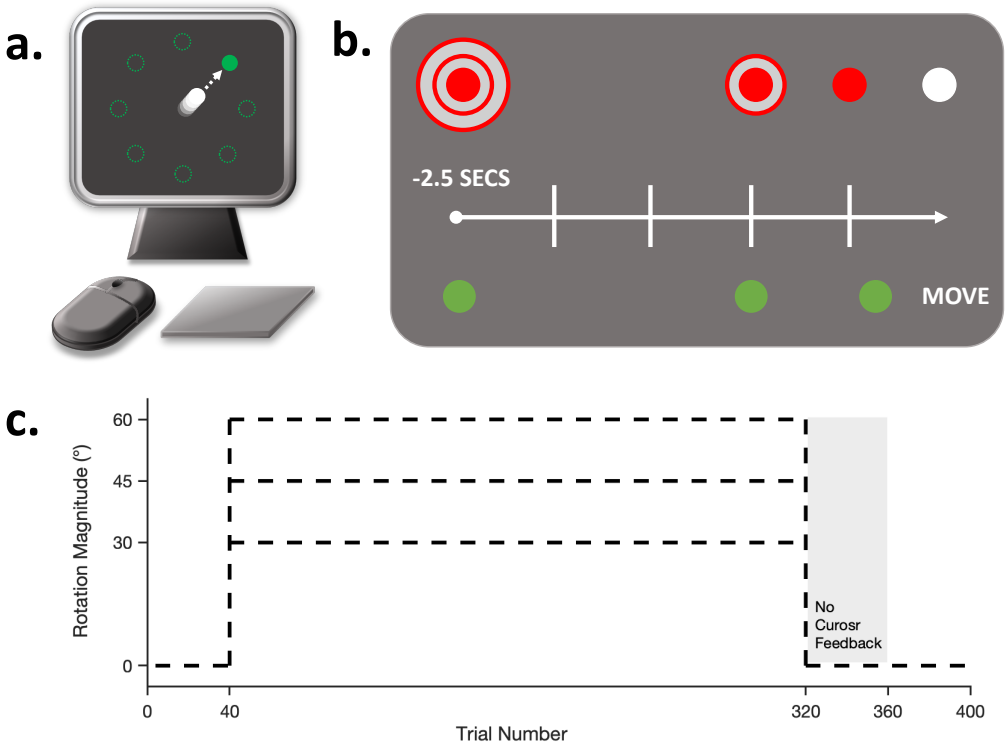

Figure 1: *The experimental design.* ***a*** *Participants used either a mouse or trackpad to direct an on-screen cursor towards targets presented radially around a central starting position.* ***b*** *An example of the cursor countdown sequence and movement cue. At the beginning of each*

trial the (red) cursor would appear in the centre of the screen, flanked by two larger (red) rings (shown here on the top row). During the trial the two rings would disappear in sequence and the cursor would change colour to white. Participants were required to initiate their movement in synchrony with the cursor colour change, using the disappearing rings as a countdown. The target (shown on the bottom row) would appear either 2.5, 1 or 0.35 seconds prior to the movement cue, depending on group assignment. ***c*** *Time course of the study protocol. Participants completed 40 baseline trials, followed by 280 adaptation trials (where either a 30°, 45° or 60° cursor rotation was imposed), then 40 no-feedback trials and finally 40 de-adaptation trials.*

Experimental Design

Participants first performed eight practice trials (one at each target location). These trials were performed with veridical cursor feedback and were used to familiarise the participants with the timing of their version of the task. The main task directly followed the practice trials and included four phases: baseline, adaptation, no-feedback and de-adaptation (Figure. 1c). During baseline trials (n = 40) participants received veridical cursor feedback, such that the on-screen cursor moved in accordance with participants' movements. Adaptation trials immediately followed, in which the cursor feedback was rotated 30°, 45° or 60° (depending on the experimental group, see below) relative to participants' movement. This block lasted 280 trials, selected to ensure learning approached its asymptotic limit, based on pilot data collected prior to the present study. While there is some indication that full asymptotic saturation of learning was not achieved in all conditions, regression analysis of the last 40 trials of adaptation indicated that there was no significant trend remaining (all $p > 0.19$) and thus we use the term 'asymptote' to refer to the final state reached at the end of the 280 adaptation trials. Following adaptation trials, participants performed no-feedback trials (n = 40). During these trials, participants were told to stop using any strategies they might have employed to achieve the task objectives and try to aim directly for the target. The cursor was hidden at all times during the trial,

apart from when located in the central position for the countdown cue. End-point error was not displayed during the no-feedback phase. Veridical cursor feedback and display of end-point error were then restored for the final de-adaptation trials (n = 40).

There were nine participant groups (Table. 1), to cover all combinations of preparation time (long: 2.5 seconds, medium: 1 second, short: 0.35 seconds) and the magnitude of cursor rotation (large: 60°, moderate: 45°, small: 30°). The preparation time was held constant throughout the whole task; the rotation was applied only during the adaptation phase.

	0.35 seconds			1 second			2.5 seconds		
	30°	45°	60°	30°	45°	60°	30°	45°	60°
N (n male)	20 (9)	20 (6)	20 (8)	20 (11)	20 (12)	20 (4)	20 (10)	20 (13)	20 (9)
Age (years) ± SD	23.5 (± 2.0)	25.4 (± 3.4)	25.9 (± 3.4)	21.0 (± 1.1)	21.5 (± 3.7)	22.6 (± 5.0)	20.8 (± 1.3)	21.0 (± 1.6)	22.7 (± 3.7)

Table 1: *Summary of experimental groups.*

Data Analysis

There were three main outcome variables: reach angle, response time and movement duration. Our primary dependent variable - reach angle - was the angular difference between the target location and participants' movement at end-point (i.e., the difference in angle between the vector linking the starting position and the target marker, and the vector linking the starting position and the point at which participants' movement crossed the target circle perimeter). Trials were deemed outliers and removed if they fell 2.5 standard deviations outside the group average on each trial. A total of 1.06% of all trials were removed from further analysis. Data from each participant was then averaged into bins of 4 trials to be used for visual representation and statistical analysis. Response time was defined as the time period between target presentation and movement onset (i.e., cursor movement breaking an invisible line immediately surrounding the starting position) and

movement duration was defined as the time period between movement onset and when movement crossed the target circle. Reach angle data was not recorded for trials where the response or movement time limits were violated.

Statistical Analysis

Asymptotic levels of adaptation were defined as the mean error over the last 40 trials of the adaptation phase and compared between groups in a two-way ANOVA (Rotation Magnitude = 3 levels (30°/45°/60°) x Preparation Time = 3 levels (0.35 seconds/1 second/2.5 seconds)), with any significant main effects or interactions followed up with Bonferrroni-corrected multiple comparisons. Asymptotic differences from the imposed rotation magnitude were compared using a Wilcoxon Signed Rank test, after data from some groups failed normality checks (Shapiro-Wilk test). All statistical analyses were carried out in MATLAB (R2018b) and SPSS (IBM, version 27). All ANOVAs were run as general linear models. The threshold for statistical significance was set at $p < 0.05$ and we report W, F and p-values, as well as effect sizes from ANOVAs (partial eta squared (ηp^2)).

Modelling

To model the adaptation data, we made two assumptions. First, the time required to plan a reach action was linearly proportional to the rotation magnitude M (i.e., mental rotation speed (*rs)* was constant). If preparation time (T) was insufficient, the planned reach angle was to the angle mentally reached. Second, the asymptotic level of adaptation (achieved reach angle, A) would be proportional to the planned reach angle scaled by the learning ratio (*lr)* of learning and forgetting rates (Smith et al., 2006). Thus,

$$A = lr^{*}\min(M,\ rs^{*}T), \qquad (1)$$

with two free parameters, *lr* and *rs*. The mean asymptotic reach angles for the 9 groups were fitted with this equation using the MATLAB '*nlinfit*' function, estimating *lr* and *rs*, and providing 95% confidence intervals for each. The learning ratio *lr* defines the proportion of the rotation magnitude reached at steady state i.e., an angle where learning driven by the remaining error and forgetting back to baseline are in equilibrium; the ratio of *lr*/(1-*lr*).

Results

Baseline performance does not differ between groups

Differences in reach angle during the baseline phase were assessed in a two-way ANOVA (Rotation Magnitude x Preparation Time), which revealed no significant main effects for Rotation Magnitude ($F(2, 172) = 0.71$, $p = 0.93$, $\eta p^2 = 0.001$), Preparation Time ($F(2, 172) = 0.29$, $p = 0.75$, $\eta p^2 = 0.003$), and no significant Rotation Magnitude*Preparation Time interaction ($F(4, 172) = 0.45$, $p = 0.77$, $\eta p^2 = 0.1$). This result suggests that all groups performed similarly during baseline trials (Figure. 2) and thus, group differences are unlikely to influence performance later in the task. We felt this analysis important, given the limited experimenter input associated with online research.

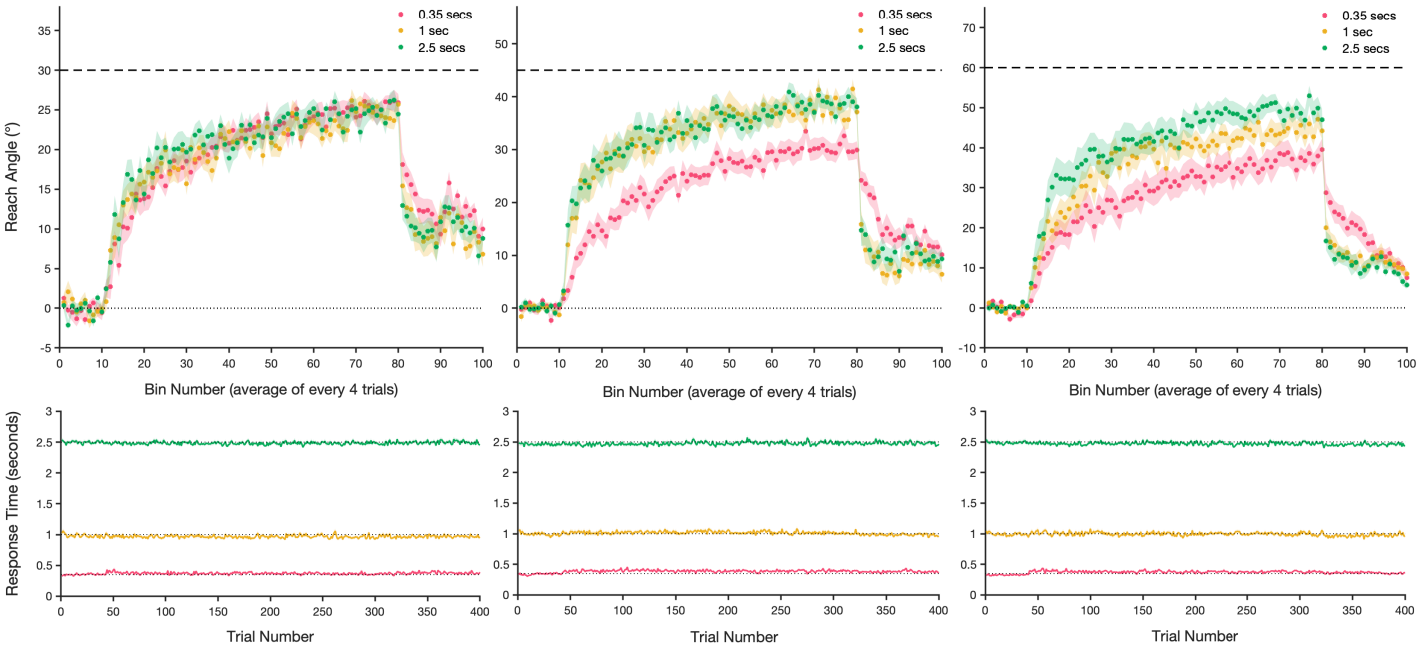

Figure 2: *Mean reach angle and response time for each of the experimental groups. Top panel: Reach error (± standard error, shaded region) is averaged every four trials into bins for (from left to right) the 30°, 45° and 60° groups, with zero degrees and the magnitude of imposed rotation shown as a dotted and dashed line respectively. Bottom panel: Mean response time (time between target presentation and movement initiation), ± standard error (shaded region) for each group. Note, preparation times were predetermined at 0.35, 1 or 2.5 seconds (dotted lines) and were tightly controlled.*

The effect of differing preparation time on asymptotic levels of adaptation

A two-way ANOVA comparing asymptotic levels of adaptation revealed significant main effects for Rotation Magnitude ($F (2, 172) = 121.01$, $p < 0.001$, $\eta p^2 = 0.59$), Preparation Time ($F (2, 172) = 15.17$, $p < 0.001$, $\eta p^2 = 0.15$) and a significant Rotation Magnitude*Preparation Time interaction ($F (4, 172) = 5.24$, $p < 0.001$, $\eta p^2 = 0.11$). Multiple comparisons revealed that in the 45° rotation group, there were some differences between learning asymptotes, with regards to preparation time provided. The 0.35 second preparation time group displayed impaired adaptation compared to the 1 and 2.5 second groups (both $p < 0.001$), with no further differences between the latter two conditions ($p > 0.99$). However, contrary to Langsdorf et al. (2021), all final levels of adaptation significantly differed from 45° (0.35 seconds: $W = -210.0$, $p < 0.001$, 95% CI = [-16.72, -11.32]; 1 second: $W = -200.0$, $p < 0.001$, 95% CI = [-9.71, -2.50]; 2.5 seconds: $W = -210.0$, $p < 0.001$, 95% CI = [-9.33, 3.18]). The 0.35 seconds preparation time group compensated 67.3% for the rotation, with the 1 and 2.5 second groups achieving 85.1% and 86.1% compensation respectively (Figures. 2 & 3), suggesting that additional preparation time allowed for greater compensation but not the elimination of residual errors.

Similarly, for the 60° rotation condition, shortening planning time to 0.35 seconds significantly reduced the final level of adaptation compared to both 1 and 2.5 second preparation periods (0.35 seconds vs 1 second: $p = 0.001$, 0.35 seconds vs 2.5 seconds: $p <$

0.001). However, there was no difference between the 1 and 2.5 second groups with respect to final adaptation levels ($p = 0.17$). Participants averaged 62.4% compensation with 0.35 seconds preparation time, 75.0% with 1 second preparation time and 81.7% with 2.5 seconds preparation time (Figures. 2 & 3). Additionally, all asymptotic levels of adaptation significantly differed from the imposed 60° rotation (0.35 seconds: $W = -210$, $p < 0.001$, 95% CI = [-31.14, -16.02]; 1 second: $W = -210.0$, $p < 0.001$ 95% CI = [-16.27, -10.27]; 2.5 seconds: $W = -206.0$, $p < 0.001$, 95% CI = [-16.76, -6.44]).

In the 30° rotation group, there were no differences in asymptotic error between any of the different preparation time groups (all $p > 0.99$, Figure. 2). Furthermore, all final levels of adaptation differed significantly from 30° (0.35 seconds: $W = -210.0$, $p < 0.001$, 95% CI = [-5.35, -2.39]; 1 second: $W = -204.0$, $p < 0.001$, 95% CI = [-6.87, -2.98]; 2.5 seconds: $W = -210.0$, $p < 0.001$, 95% CI = [-8.09, -3.25]), with adaptation reaching 84.7%, 82.8% and 82.0% of the optimum, respectively (Figure. 3).

In summary, our results support previous work suggesting that mental rotation contributes an interval to the planning process which is proportional to rotation magnitude, and that short periods of preparation interrupt planning, leading the greater residual errors. However, for the smallest rotation, we found no relationship between preparation time and error, suggesting that mental rotation was completed within the allowed time. But even in these circumstances, there were significant residual errors. In fact, in opposition to results reported by Langsdorf et al. (2021), all groups displayed incomplete adaptation regardless of the preparation time provided.

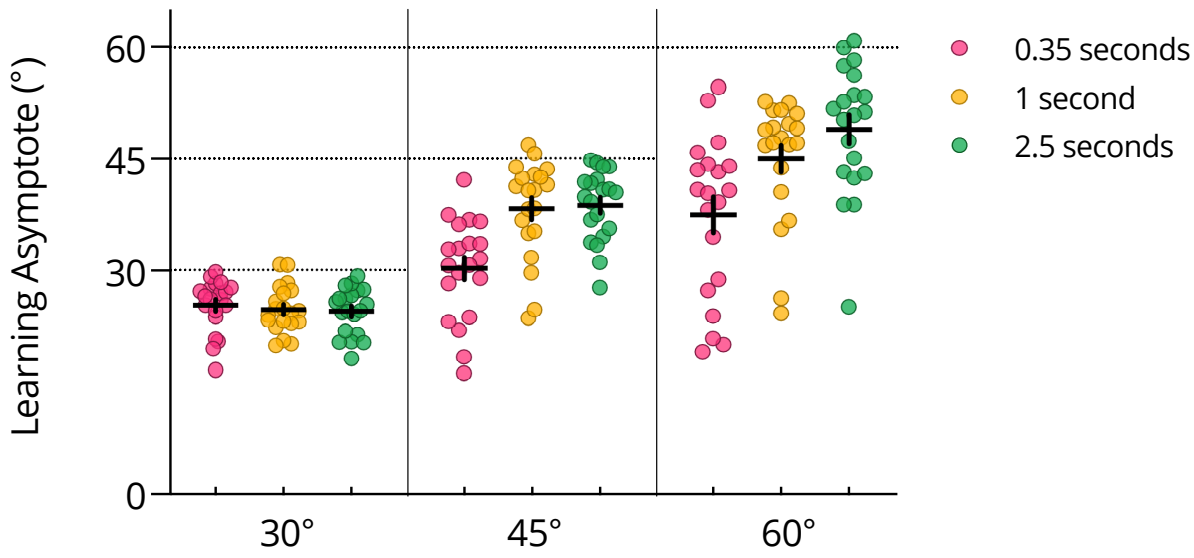

Figure 3: *The asymptotic levels of adaptation for each participant in each of the rotation magnitude and preparation time groups. Filled circles represent the adaptation asymptote for each participant (defined as the average of the last 40 adaptation trials), with mean values and standard error depicted by horizontal and vertical lines respectively. Dashed horizontal lines depict the imposed cursor rotation for each group.*

Modelling asymptotic performance

The nine group mean asymptotic reach angles were well fitted by the model (Figure. 4), with the confidence intervals of the fit overlapping with each group mean. The estimated values of the two free parameters were *lr* = 0.814 (95% CI: 0.761- 0.867) and *rs* =118.9 degrees/sec, (95% CI 101.64 - 136.34). From the learning ratio, *lr*, the learning rate is estimated to be at least 4.4 times the forgetting rate. This is potentially an underestimate, however, as some of adaptation curves may not have fully saturated (Figure. 2), despite regression analysis indicating no significant trend (all $p > 0.19$).

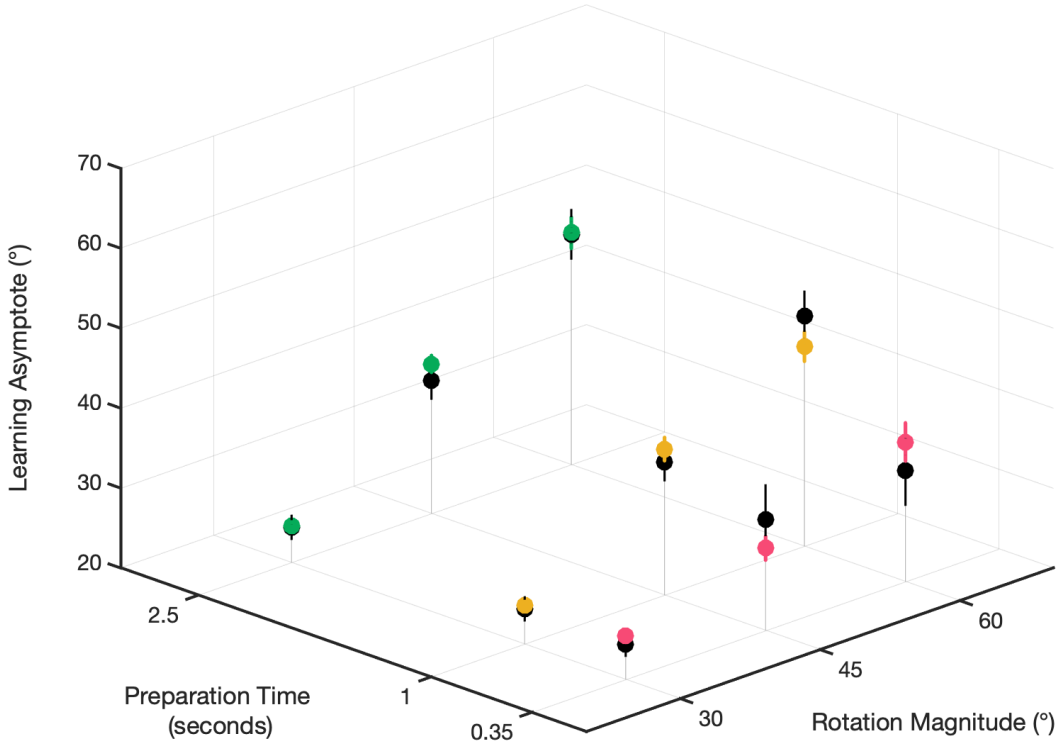

Figure 4. *The group mean asymptotic adaptation angles (coloured dots, ± 1 SEM) are well estimated by the model (see main text). The model (black dots, ± 95% confidence intervals) assumes a fixed mental rotation speed and a fixed ratio between learning and forgetting rates.*

Restricting motor preparation time resulted in a stronger implicit retention

Implicit retention was defined as the mean reach angle in the first 16 no-feedback trials (two cycles of reaches to each target location) and was compared between groups in a two-way ANOVA (Rotation Magnitude x Preparation Time). Results from the ANOVA revealed a significant main effect of Rotation Magnitude ($F(2, 172) = 6.71$, $p = 0.002$, $\eta p^2 = 0.07$) and Preparation Time ($F(2, 172) = 18.33$, $p < 0.001$, $\eta p^2 = 0.18$), but no significant interaction ($F(4, 172) = 1.08$, $p = 0.37$, $\eta p^2 = 0.03$). Multiple comparisons showed that participants in the restricted 0.35 second motor preparation time groups displayed greater retention than both the 1 second ($p < 0.001$) and 2.5 second ($p < 0.001$) groups, with no differences between the latter two ($p > 0.99$).

Input device (trackpad vs mouse) had no effect on late adaptation levels

In order to determine whether the input device used to complete the task affected the extent of adaptation, we compared asymptotic learning levels in each rotation and preparation time group, dependent on whether a mouse or trackpad was used, in a 3x3x2 mixed-design ANOVA (Rotation Magnitude x Preparation Time x Input Device). The ANOVA revealed no significant main effect of Input Device ($F(1, 172) = 1.13$, $p = 0.29$, $\eta p^2 = 0.007$) and no significant three-way interaction ($F(4, 172) = 0.38$, $p = 0.82$, $\eta p^2 = 0.009$). In fact, no interaction that included the term Input Device revealed significance (Rotation Magnitude*Input Device: $F(2, 172) = 0.53$, $p = 0.59$, $\eta p^2 = 0.006$, Preparation Time*Input Device: $F(2, 172) = 0.21$, $p = 0.81$, $\eta p^2 = 0.003$), suggesting that the input device used had little effect on adaptive performance during the task (Supplementary Figure. 1, see https://doi.org/10.6084/m9.figshare.14797926).

Discussion

We aimed to test the assumption that increased motor preparation periods may allow for more complete adaptation during visuomotor rotation tasks. As such, we hypothesised that shorter preparation periods would be sufficient to fully counteract a 30° rotation, as a small rotation would require less (and therefore quicker) mental rotation before motor execution. We then predicted that this effect would scale with an increased cursor rotation, so that 45° and 60° would require greater mental rotation and thus more time to fully compensate. Indeed, we did find that restricting planning time for moderate and larger rotations resulted in impaired final adaptation levels and greater implicit retention compared to those groups with more preparation time. However, contrary to research from Langsdorf et al. (2021), we

found no evidence to suggest that extended motor preparation periods allow for the elimination of residual errors observed during late stages of adaptation, as all groups displayed final adaptation performance significantly lower than the imposed cursor rotation.

Hence, we failed to replicate the results from Langsdorf et al. (2021), who found that enforcing a 2.5 second planning period between target presentation and reach onset allowed individuals to fully counteract a 45° visuomotor rotation, leaving no residual mean error at asymptote. The authors suggested that the extended planning period allowed for time-consuming cognitive processes, such as mental rotation, to be completed prior to the go-signal and resulted in complete compensation. This theory, centred around a speed-accuracy trade-off, seems plausible given that reaction times increase in a linear fashion when subjects are asked to reach at increasing angles from a target - a relationship that mimics the behaviour seen in mental rotation tasks (Shepard & Metzler, 1971; Georgopoulos & Massey, 1987; McDougle & Taylor, 2019). Accordingly, brain regions activated in both visuomotor adaptation and mental rotation tasks have also been shown to overlap (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010), suggesting that mental rotation contributes to visuomotor adaptation. Recent evidence investigating preparatory activity in the motor cortex of non-human primates further suggests the necessity for motor planning time in visuomotor adaptation (Vyas, O'Shea, Ryu, & Shenoy, 2020). In addition, Langsdorf et al. (2021) found that delaying movement initiation resulted in an overcompensation of the imposed rotation, similar to the overshoot in reach estimation shown by Georgopoulos and Massey (1987), suggesting similar cognitive rotation strategies may have been in play.

418 Notwithstanding these studies, we found that on average participants' learning plateaued
419 before eliminating error, with asymptotic learning levels statistically different from the
420 degree of imposed rotation for all rotational groups (30°, 45°, 60°), regardless of the amount
421 of preparation time enforced. These findings are consistent with previous reports which
422 have suggested that sustained errors during visuomotor adaptation are a product of the
423 implicit learning system; either suppressing alternative learning mechanisms which may be
424 able to overcome persisting errors (Shmuelof et al., 2012; Vaswani et al., 2015) and/or
425 modulating the system's sensitivity to errors dependent on their size, variability and history
426 (Albert et al., 2021).
427 One factor that may explain the discrepancy between our results and those of Langsdorf
428 et al. (2021), is the level of experimental control. Our study was conducted online, with
429 participants completing the task unsupervised at home, whereas Langsdorf et al. (2021)
430 conducted a laboratory-based study. The disparities associated with these environments
431 may have contributed to small but significant differences in motivation, attention and
432 behaviour. That said, our data are typical of many previous lab-based visuomotor
433 adaptation studies, with comparable levels of final performance (Huberdeau et al., 2015;
434 Morehead, Qasim, Crossley, & Ivry, 2015; Vaswani et al., 2015; Neville & Cressman, 2018;
435 Weightman et al., 2020; Weightman, Brittain, Miall, & Jenkinson, 2021). Furthermore, initial
436 evidence suggests that kinematic data and results from online motor learning studies are
437 analogous with those collected in a controlled lab environment (Tsay, Lee, Ivry, & Avraham,
438 2021) and that online tasks perform well in terms of accuracy and precision with regards to
439 timing of visual stimuli and response capture (Bridges, Pitiot, MacAskill, & Peirce, 2020).
440 An additional difference between the two studies, which may have had some bearing on
441 the results, is the nature of response cueing used. We used a visual countdown sequence

442 which enabled participants to accurately synchronise their movements with the go-signal
443 and ensured a tight coupling between response times and the preparation time groupings.
444 In contrast, Langsdorf et al. (2021) displayed the target and instructed participants to wait
445 until they heard a tone before responding. This difference in protocol resulted in response
446 times closer to 3 seconds. One may argue that more than 2.5 seconds are required to fully
447 prepare for a 45° rotated reach. This is unlikely however, as we show that even a 30° angle
448 was not fully compensated, and there was no evidence for a relationship with the
449 preparation interval for those groups. Previous research has also shown that mental
450 rotation and aiming towards angles up to 90° can be achieved in ∼1 second (McDougle &
451 Taylor, 2019). The modelling data additionally supports this, as it assumes that mental
452 rotation to the target angle is achieved within the allotted preparation time for most
453 conditions (with the eventual reach angle reduced by the learning ratio). There is perhaps
454 an argument to suggest that attending to the countdown sequence may have interfered
455 with mental rotation and other cognitive planning processes, by, for instance vying for
456 attentional resources and thus contributing to a consistent reach undershoot (Taylor &
457 Thoroughman, 2007; Galea, Sami, Albert, & Miall, 2010). Nevertheless, prior studies using
458 auditory response cueing have not cited attention to the timed-response sequence as a
459 potential confound (Haith et al., 2015; Leow, Gunn, Marinovic, & Carroll, 2017; McDougle &
460 Taylor, 2019).
461 Despite participants failing to eliminate residual errors during late adaptation, our data do
462 include some hallmarks of a speed-accuracy trade-off. We found that motor adaptation was
463 impaired in the 45° and 60° rotational groups, when planning time was restricted to 0.35
464 seconds. This result is in line with previous studies who report reduced error compensation
465 when preparation times are limited (Fernandez-Ruiz et al., 2011; Leow, Gunn, et al., 2017;

466 Leow, Marinovic, Riek, & Carroll, 2017; Albert et al., 2021) and may reflect the suppression
467 of explicit re-aiming/cognitive strategies. Additionally, impaired adaptation associated with
468 restricted preparation times was coupled with an increased retention during no-feedback
469 trials, which is consistent with the idea that learning involved more implicit, procedural
470 processes (Fernandez-Ruiz et al., 2011; Haith et al., 2015). The greatest retention was seen
471 in the 0.35 seconds / 60° group, which implies that the greater residual errors in this group
472 led to stronger implicit learning. This suggestion is reinforced by the equal retention seen
473 for the 2.5 second condition, across all three rotation magnitudes. In this case, the residual
474 errors are approximately equal, because the preparation time exceeded that required for
475 mental rotation. However, these assumptions should be treated with some caution after
476 recent commentary on how the dichotomy of implicit and explicit components of motor
477 adaptation are inferred (Hadjiosif & Krakauer, 2021).
478 Although not statistically evident, a speed-accuracy trade-off may also be apparent in the
479 60° rotational group (Figure. 3). On average, there was a linear increase in learning
480 asymptote as preparation time increased, which may reflect how mental rotation of the
481 intended movement angle increases the accuracy of reaches (McDougle & Taylor, 2019;
482 Langsdorf et al., 2021). Addition of further adaptation trials might exaggerate these
483 asymptotic differences, until statistically significant, yet data from our other rotational
484 groups and previous literature would suggest that errors would still persist. To achieve full
485 compensation, it is possible that explicit information about the nature of rotation ought to
486 be provided (McDougle & Taylor, 2019) or strategies primed using methods such as verbal
487 aiming reports (Bond & Taylor, 2015; Brudner, Kethidi, Graeupner, Ivry, & Taylor, 2016;
488 Wilterson & Taylor, 2019; Albert et al., 2021; Langsdorf et al., 2021), which are inherently
489 coupled with increased reaction/plan times.

In summary, our data suggests that extending motor preparation and planning periods alone is insufficient to eliminate residual errors during visuomotor adaptation, irrespective of the size of imposed cursor rotation. While increased preparation time may help to improve error reduction at larger rotation magnitudes, our results suggest there remains a limit at which learning saturates at asymptote, perhaps only overcome with priming of explicit strategies, further instruction or changes to experimental variables. Understanding why the central nervous system fails to fully adapt movements in response to environmental changes may be key when aiming to optimise rehabilitation protocols following brain injury or disease.

References

Albert, S. T., Jang, J., Sheahan, H. R., Teunissen, L., Vandevoorde, K., Herzfeld, D. J., & Shadmehr, R. (2021). An implicit memory of errors limits human sensorimotor adaptation. *Nature human behaviour*, 1–15. doi: https://doi.org/10.1038/s41562- 020-01036-x

Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2010). Contributions of spatial working memory to visuomotor learning. *Journal of cognitive neuroscience*, *22*(9), 1917–1930. doi: https://doi.org/10.1162/jocn.2009.21351

Bhat, R. B., & Sanes, J. N. (1998). Cognitive channels computing action distance and direction. *Journal of Neuroscience*, *18*(18), 7566–7580. doi: https://doi.org/10.1523/JNEUROSCI.18-18-07566.1998

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of neurophysiology*, *113*(10), 3836–3849. doi: https://doi.org/10.1152/jn.00009.2015

Bridges, D., Pitiot, A., MacAskill, M. R., & Peirce, J. W. (2020). The timing mega-study: comparing a range of experiment generators, both lab-based and online. *PeerJ*, *8*, e9414. doi: 10.7717/peerj.9414

Brudner, S. N., Kethidi, N., Graeupner, D., Ivry, R. B., & Taylor, J. A. (2016). Delayed feedback during sensorimotor learning selectively disrupts adaptation but not strategy use. *Journal of neurophysiology*, *115*(3), 1499–1511. doi: https://doi.org/10.1152/jn.00066.2015

Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *Journal of experimental psychology: Human perception and performance*, *15*(3), 493. doi: https://doi.org/10.1037/0096- 1523.15.3.493

Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behavioural brain research*, *219*(1), 8–14. doi: https://doi.org/10.1016/j.bbr.2010.11.060

Galea, J., Sami, S., Albert, N., & Miall, R. C. (2010). Secondary tasks impair adaptation to step-and gradual-visual displacements. *Experimental brain research*, *202*(2), 473– 484. doi: 10.1007/s00221-010-2158-x

Georgopoulos, A. P., Lurito, J. T., Petrides, M., Schwartz, A. B., & Massey, J. T. (1989). Mental rotation of the neuronal population vector. *Science*, *243*(4888), 234–236. doi: https://doi.org/10.1126/science.2911737

Georgopoulos, A. P., & Massey, J. (1987). Cognitive spatial-motor processes. *Experimental brain research*, *65*(2), 361–370. doi: https://doi.org/10.1007/BF00236309

Hadjiosif, A. M., & Krakauer, J. W. (2021). The explicit/implicit distinction in studies of visuomotor learning: Conceptual and methodological pitfalls. *European Journal of Neuroscience*, *53*(2), 499–503. doi: https://doi.org/10.1111/ejn.14984

Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The influence of movement preparation time on the expression of visuomotor learning and savings. *Journal of neuroscience*, *35*(13), 5109–5117. doi: https://doi.org/10.1523/JNEUROSCI.3869- 14.2015

Heuer, H., & Hegele, M. (2008). Adaptation to visuomotor rotations in younger and older adults. *Psychology and aging*, *23*(1), 190. doi: https://doi.org/10.1037/0882- 7974.23.1.190

Huberdeau, D. M., Haith, A. M., & Krakauer, J. W. (2015). Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *Journal of neurophysiology*, *114*(2), 969–977. doi: https://doi.org/10.1152/jn.00369.2015

Kording, K. P., Tenenbaum, J. B., & Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature neuroscience*, *10*(6), 779–786. doi: https://doi.org/10.1038/nn1901

Krakauer, J. W., Ghilardi, M.-F., & Ghez, C. (1999). Independent learning of internal models for kinematic and dynamic control of reaching. *Nature neuroscience*, *2*(11), 1026. doi: https://doi.org/10.1038/14826

Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience*, *20*(23), 8916–8924. doi: https://doi.org/10.1523/JNEUROSCI.20- 23-08916.2000

Langsdorf, L., Maresch, J., Hegele, M., McDougle, S. D., & Schween, R. (2021). Prolonged response time helps eliminate residual errors in visuomotor adaptation. *Psychonomic Bulletin & Review*, 1–11. doi: https://doi.org/10.3758/s13423-020-01865-x

Leow, L.-A., Gunn, R., Marinovic, W., & Carroll, T. J. (2017). Estimating the implicit component of visuomotor rotation learning by constraining movement preparation time. *Journal of neurophysiology*, *118*(2), 666–676. doi: https://doi.org/10.1152/jn.00834.2016

Leow, L.-A., Marinovic, W., Riek, S., & Carroll, T. J. (2017). Cerebellar anodal tdcs increases implicit learning when strategic re-aiming is suppressed in sensorimotor adaptation. *PLoS One*, *12*(7), e0179977. doi: https://doi.org/10.1371/journal.pone.0179977

Lurito, J., Georgakopoulos, T., & Georgopoulos, A. (1991). Cognitive spatial- motor processes. *Experimental Brain Research*, *87*(3), 562–580. doi: https://doi.org/10.1007/BF00227082

Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *Journal of neuroscience*, *26*(14), 3642–3645. doi: https://doi.org/10.1523/JNEUROSCI.5317-05.2006

McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. *Journal of Neuroscience*, *35*(26), 9568–9579. doi: https://doi.org/10.1523/JNEUROSCI.5061- 14.2015

McDougle, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor learning. *Nature communications*, *10*(1), 1–13. doi: https://doi.org/10.1038/s41467-018-07941-0

Morehead, J. R., Qasim, S. E., Crossley, M. J., & Ivry, R. (2015). Savings upon re-aiming in visuomotor adaptation. *Journal of neuroscience*, *35*(42), 14386–14396.

Neville, K.-M., & Cressman, E. K. (2018). The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Experimental brain research*, *236*(7), 2047–2059. doi: https://doi.org/10.1007/s00221-018-5282-7

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., Lindeløv, J. K. (2019). Psychopy2: Experiments in behavior made easy. Behavior Research Methods, 51(1), 195–203. doi: https://doi.org/10.3758/s13428-018-01193-y

Pellizzer, G., & Georgopoulos, A. P. (1993). Common processing constraints for visuomotor and visual mental rotations. *Experimental Brain Research*, *93*(1), 165–172. doi: https://doi.org/10.1007/BF00227791

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*(3972), 701–703. doi: https://doi.org/10.1126/science.171.3972.701

Shmuelof, L., Huang, V. S., Haith, A. M., Delnicki, R. J., Mazzoni, P., & Krakauer, J. W. (2012). Overcoming motor "forgetting" through reinforcement of learned actions. *Journal of Neuroscience*, *32*(42), 14617–14621a. doi: https://doi.org/10.1523/JNEUROSCI.2184-12.2012

Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS biology*, *4*(6). doi: 10.1371/journal.pbio.0040179

Taylor, J. A., & Ivry, R. B. (2011). Flexible cognitive strategies during motor learning. *PLoS computational biology*, *7*(3). doi: 10.1371/journal.pcbi.1001096

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *Journal of Neuroscience*, *34*(8), 3023– 3032. doi: https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Taylor, J. A., & Thoroughman, K. A. (2007). Divided attention impairs human motor adaptation but not feedback control. *Journal of neurophysiology*, *98*(1), 317–326. doi: https://doi.org/10.1152/jn.01070.2006

Tsay, J. S., Lee, A. S., Ivry, R. B., & Avraham, G. (2021). Moving outside the lab: The viability of conducting sensorimotor learning studies online. *bioRxiv*. doi: https://doi.org/10.1101/2021.01.30.181370

Tseng, Y.-w., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of neurophysiology*, *98*(1), 54–62. doi: https://doi.org/10.1152/jn.00545.2007

van der Kooij, K., Brenner, E., van Beers, R. J., & Smeets, J. B. (2015). Visuomotor adaptation: how forgetting keeps us conservative. *PLoS One*, *10*(2), e0117901. doi: https://doi.org/10.1371/journal.pone.0117901

Vaswani, P. A., Shmuelof, L., Haith, A. M., Delnicki, R. J., Huang, V. S., Mazzoni, P., Shadmehr, R., Krakauer, J. W. (2015). Persistent residual errors in motor adaptation tasks: reversion to baseline and exploratory escape. *Journal of Neuroscience*, *35*(17), 6969– 6977. doi: https://doi.org/10.1523/JNEUROSCI.2656-14.2015

Voets, S. H., Panouilleres, M. T., & Jenkinson, N. (2020). An implicit plan still overrides an explicit strategy during visuomotor adaptation following repetitive transcranial magnetic stimulation of the cerebellum. *Experimental Results*, *1*. doi: https://doi.org/10.1017/exp.2020.16

Vyas, S., O'Shea, D. J., Ryu, S. I., & Shenoy, K. V. (2020). Causal role of motor preparation during error-driven learning. *Neuron*, *106*(2), 329–339. doi: https://doi.org/10.1016/j.neuron.2020.01.019

Weightman, M., Brittain, J.-S., Miall, R. C., & Jenkinson, N. (2021). Direct and indirect effects of cathodal cerebellar tdcs on visuomotor adaptation of hand and arm movements. *Scientific Reports*, *11*(1), 1–10. doi: https://doi.org/10.1038/s41598- 021-83656-5

Weightman, M., Brittain, J.-S., Punt, D., Miall, R. C., & Jenkinson, N. (2020). Targeted tdcs selectively improves motor adaptation with the proximal and distal upper limb. *Brain Stimulation*, *13*(3), 707–716. doi: https://doi.org/10.1016/j.brs.2020.02.013

Wilterson, S. A., & Taylor, J. A. (2019). Implicit visuomotor adaptation remains limited after several days of training. *BioRxiv*, 711598. doi: https://doi.org/10.1101/711598

Acknowledgements

This work was funded by the MRC-Versus Arthritis Centre for Musculoskeletal Ageing Research (CMAR). RCM was also partly funded by the Royal Society, Leverhulme and Wellcome Trust.

Author Contributions

MW, JSB and NJ conceived and designed the study with input from RCM. MW collected the data. MW, JSB, RCM and NJ analysed and interpreted the data. MW wrote the first draft of the paper. JSB, RCM and NJ reviewed and edited the paper and all authors agreed with the final submitted version.

The authors declare no competing interests.