

# 1 Prolonged reaction times eliminate residual errors in visuomotor adaptation

2 Lisa Langsdorf<sup>\*1,2</sup>, Jana Maresch<sup>3</sup>, Mathias Hegele<sup>1,2</sup>, Samuel D. McDougle<sup>II,4</sup> & Raphael  
3 Schween<sup>II,1</sup>

4 <sup>1</sup> NemoLab - Neuromotor Behavior Laboratory, Section Experimental Sensomotorics,  
5 Justus Liebig University Giessen, Germany

6 <sup>2</sup> Center for Mind, Brain and Behavior (CMBB), Universities of Marburg and Giessen,  
7 Germany

8 <sup>3</sup> Department of Brain and Cognitive Sciences, Ben-Gurion University of the Negev,  
9 Beersheva, Israel

10 <sup>4</sup> Department of Psychology, University of California, Berkeley, USA

11

12 <sup>II</sup> shared senior authorship

13 <sup>\*</sup>Lisa Langsdorf

14 Justus Liebig University Giessen, Germany

15 Department of Psychology and Sport Science

16 Kugelberg 62

17 D-35394 Giessen, Germany

18 Lisa.Langsdorf@sport.uni-giessen.de

19

## 20 Abstract

21 One persistent curiosity in visuomotor adaptation tasks is the fact that participants often  
22 reach a learning asymptote well below full compensation. This incomplete asymptote has been  
23 explained as a consequence of obligatory computations in the implicit adaptation system, such  
24 as an equilibrium between learning and forgetting. A body of recent work has shown that in  
25 standard adaptation tasks, cognitive strategies operate alongside implicit learning. We reasoned  
26 that incomplete learning in adaptation tasks may primarily reflect a speed-accuracy tradeoff on  
27 time-consuming motor planning. Across three experiments, we find evidence supporting this  
28 hypothesis, and demonstrate that the incomplete asymptote of adaptation appears to be  
29 primarily a consequence of hastened motor planning. When an obligatory waiting period was  
30 administered before participants executed their movements, they were able to fully counteract  
31 imposed perturbations (experiment 1). Inserting the same delay between trials - rather than  
32 during movement planning - did not induce full compensation, suggesting that motor planning  
33 time predicts the learning asymptote (experiment 2). In the last experiment, instead of directly

34 manipulating the planning time, we asked participants to continuously report their movement  
35 aim. We show that emphasizing explicit re-aiming strategies also leads to full asymptotic  
36 learning, supporting the idea that prolonged motor planning may involve a parametric rotation  
37 of aiming direction whose premature termination yields incomplete asymptotic learning  
38 (experiment 3). Findings from all experiments support the hypothesis that incomplete  
39 adaptation is, in part, the result of an intrinsic speed-accuracy tradeoff, perhaps related to  
40 cognitive strategies that require parametric attentional reorienting from the visual target to the  
41 goal.

42

43       Keywords: sensorimotor adaptation; reaction time; motor planning; asymptote; explicit  
44 strategies;

45

## 46 **Introduction**

47       When the relation between motor commands and their consequences is changed by  
48 physical or visual perturbations, the sensorimotor system adapts to restore accurate motor  
49 performance (Cunningham, 1989; Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994).  
50 One common observation in this context is an incomplete learning asymptote. That is, if  
51 participants are required to make reaching movements and counteract, say, a 30° visuomotor  
52 rotation, their adaptation curve tends to asymptote below full compensation, for instance around  
53 ~25° (Holland, Codol, & Galea, 2018; Huberdeau, Haith, & Krakauer, 2015; van der Kooij,  
54 Brenner, van Beers, & Smeets, 2015; van der Kooij, Overvliet, & Smeets, 2016). Indeed,  
55 previous studies have pointed out that this residual asymptotic error is typically significantly  
56 different from zero (Hinder, Riek, Tresilian, Rugby, & Carson, 2010; Shmuelof et al., 2012;

57 Spang, Wischhusen, & Fahle, 2017; van der Kooij et al., 2015; van der Kooij et al., 2016;  
58 Vaswani et al., 2015).

59         One explanation for this phenomenon is derived from state-space models of adaptation,  
60 which are incremental Markovian learning algorithms that balance both learning and forgetting  
61 during adaptation (Cheng & Sabes, 2006; Smith, Ghazizadeh, & Shadmehr, 2006;  
62 Thoroughman & Shadmehr, 2000). When fit to human learning data, many different values of  
63 learning and forgetting parameters can produce a steady-state equilibrium at an arbitrary  
64 asymptotic level. State-space models provide a natural explanation of the commonly observed  
65 undershoot via an assumption that some amount of forgetting (i.e., reversion to baseline) is  
66 inevitable on each trial of the task. This interpretation suggests that incomplete compensation  
67 during motor adaptation is simply a built-in feature of the implicit adaptation mechanism.

68         A recent study has pointed out that human subjects in principle possess the capacity to  
69 overcome the incomplete asymptote (Vaswani et al., 2015): The researchers found under-  
70 compensation in normal adaptation circumstances where visual feedback contained naturalistic  
71 motor noise, an effect that was easily captured by the state-space model. However, when visual  
72 feedback was “clamped” after learning (i.e., it moved in a fixed trajectory toward the target or  
73 in a nearby direction), participants appeared to adopt a new learning strategy that allowed them  
74 to break free of their residual errors and fully compensate for the perturbation. Given this  
75 apparent capacity for full compensation, why does the central nervous system not use it under  
76 normal, non-error-clamped, circumstances? To explain this, the authors of the study suggested  
77 that one specific learning process obeys the dynamics of the state-space model and suppresses  
78 other processes. The suppressed processes then only make a relevant contribution when the  
79 former process is disengaged (Shmuelof et al., 2012; Vaswani et al., 2015; Vaswani &  
80 Shadmehr, 2013; Wong, Haith, & Krakauer, 2015). In the present study, we propose and  
81 evaluate an alternative account of why the motor system does not overcome incomplete

82 asymptotic learning, namely that it primarily reflects an intrinsic speed-accuracy tradeoff based  
83 on time-consuming movement planning.

84         The inverse relation between the accuracy of a response and the time taken to produce  
85 it has been shown to be a pervasive principle of information processing across task domains  
86 (Heitz, 2014; Plamondon & Alimi, 1997). For instance, research in perceptual decision-making  
87 tasks has established that freely chosen reaction times reflect a tradeoff between waiting for  
88 more information and moving early in order to speed up the accrual of (uncertain) reward on  
89 future trials (Churchland, Kiani, & Shadlen, 2008; Cisek, Puskas, & El-Murr, 2009; Thura,  
90 Beauregard-Racine, Fradet, & Cisek, 2012; Thura & Cisek, 2017). While visuomotor  
91 adaptation tasks traditionally are not studied in the framework of decision-making, recent  
92 research has highlighted an important role for volitional decision-making strategies in  
93 adaptation tasks (i.e., the explicit re-aiming of movements to counteract perturbations during  
94 learning; (Bond & Taylor, 2015; Heuer & Hegele, 2015; McDougle, Bond, & Taylor, 2015;  
95 Schween & Hegele, 2017; Taylor, Krakauer, & Ivry, 2014)). Further evidence suggests that in  
96 the context of adaptation to a novel visuomotor rotation such strategies may take the form of  
97 mentally rotating the aiming direction of the reaching movement (McDougle & Taylor, 2019),  
98 which has been known to require long preparation times (Fernandez-Ruiz, Wong, Armstrong,  
99 & Flanagan, 2011; Haith, Huberdeau, & Krakauer, 2015; McDougle & Taylor, 2019). Thus, an  
100 incomplete learning asymptote could simply arise from hurried movement initiation leading to  
101 prematurely terminating the mental rotation of the aiming vector during movement planning.

102         We tested this hypothesis over three behavioral experiments where we artificially  
103 extended planning time and predicted that this would alleviate incomplete asymptotic behavior.  
104 In the first experiment (experiment 1), we introduced a mandatory waiting period between  
105 target presentation and movement onset. In experiment 2, we sought to exclude effects of the  
106 total experiment duration by emphasizing the role of within-trial movement planning time.

107 Finally, in experiment 3, we used aiming reports (Taylor et al., 2014) to emphasize the  
108 application of explicit strategies before movement execution during training and elucidate its  
109 impact on learning asymptote.

## 110 **Methods**

### 111 **Participants**

112 Ninety neurologically healthy and right-handed students from the Justus Liebig  
113 University Giessen were recruited as participants (Experiment 1: N = 36, Experiment 2: N = 36,  
114 Experiment 3: N = 18) and received monetary compensation or course credit for their  
115 participation. Written, informed consent was obtained from all participants before testing. The  
116 experimental protocol was approved by the local ethics committee of the Department of  
117 Psychology and Sport Science. All participants were self-declared right-handers. Data of one  
118 participant (experiment 2) was excluded due to a large number of irregular trials (i.e. premature  
119 movement initiation, moving too fast or too slow).

### 120 **Apparatus**

121 Participants sat on a height-adjustable chair facing a 22'' widescreen LCD monitor  
122 (Samsung 2233RZ; display size: 47,3 cm x 29,6 cm; resolution: 1680 x 1050 pixels; frame rate  
123 120 Hz), which was placed on eye level 100 cm in front of them. Their right hand held a  
124 digitizing stylus, which they could move across a graphics tablet (Wacom Intuos 4XL). Their  
125 hand position recorded from the tip of the stylus was sampled at 130 Hz. Stimulus presentation  
126 and movement recording were controlled by a custom build MATLAB script (R2017b) using  
127 the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). An occluder, which was placed 20 cm  
128 above the table platform, prevented direct vision of the hand (left panel Figure 1A).

129 Task

130 Participants performed center-out reaching movements from a common start location to  
131 targets in different directions. They were instructed to move the cursor as quickly as possible  
132 from the start location in the direction of a target location, and “shoot through it”. On the  
133 monitor, the start location was in the center of the screen, marked by the outline of a circle of  
134 7 mm in diameter. On the table surface, the start location was 20 - 25 cm in front of the  
135 participant on the body midline. The target location, marked by a filled green circle of 4 mm in  
136 diameter, varied from trial to trial. Targets were placed on an invisible circle with a radius of  
137 100 mm around the start location; target locations were 0, 45, 90, 135, 180, 225, 270, and 315°  
138 (0° is from the start location to the right, 90° is forward, 270° is backward; right panel Figure  
139 1A). On baseline and adaptation trials, visual feedback was given by a filled white circle (radius  
140 2.5 mm).

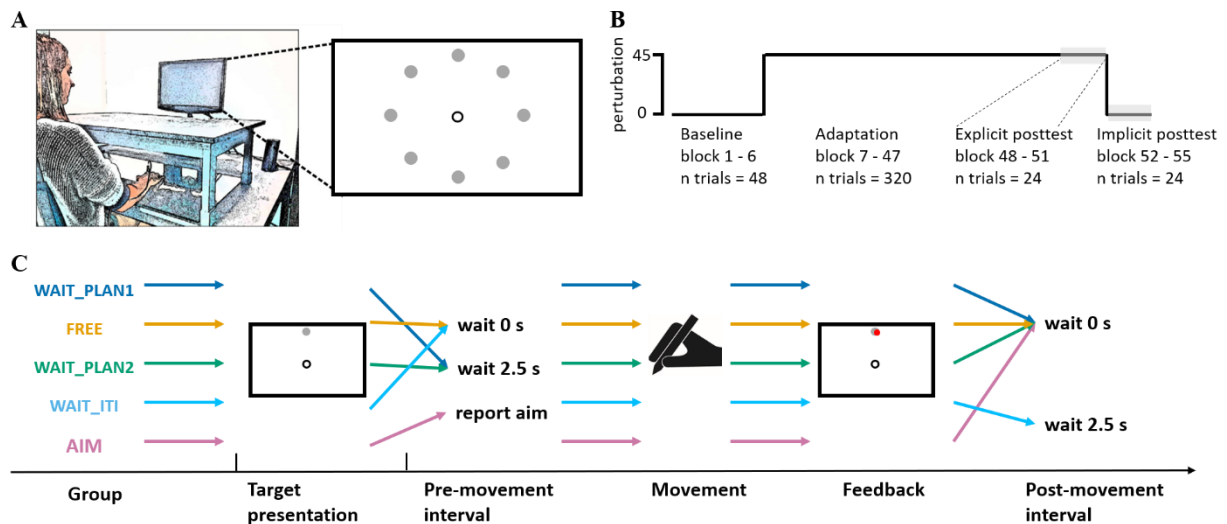


Figure 1 schematic display of the experimental setup (A), overall protocol (B) and sequence of one trial (C). Each participant performed center-out reaching movements with a stylus on the tablet. Visual stimuli and the cursor were presented on a monitor. The visual cursor was displaced according to the protocol (B). During baseline, cursor and stylus position were veridical, during adaptation, the cursor was rotated 45° clockwise relative to the stylus position. Within-trial timing differed between groups (C). Group dependent differences within one trial occurred either during the pre- or post-movement interval. Whereas the FREE and WAIT\_ITI groups had no specific task during the pre-movement interval, WAIT\_PLAN1 and WAIT\_PLAN2 groups were required to wait 2.5 s and the AIM group reported their movement aim. During post-movement interval, only the participants in the WAIT\_ITI group were required to wait 2.5 s, whereas all other group continued with the next trial immediately. Panel A adapted from (Schween, Taylor, & Hegele, 2018) under CC-BY-4.0 license.

## 141 Design and procedure

142 The experiment comprised three phases: baseline training, training with a 45° clockwise  
 143 (CW) visuomotor rotation, and posttests (Figure 1B). Baseline training had veridical hand-  
 144 cursor mapping and was organized into three blocks of eight trials each. In experiment 3,  
 145 baseline training included three additional blocks in which participants had to report their  
 146 aiming direction prior to movement onset. Each block consisted of a random permutation of the  
 147 eight target directions without any direction being repeated in successive trials. Training of the  
 148 visuomotor rotation of 45° CW consisted of 40 blocks of eight trials each.

149 The posttest phase consisted of two types of trials: an explicit test (see below)  
 150 comprising three blocks of eight trials each, with each target location occurring once per block,  
 151 and three blocks of eight test trials without visual feedback, and with the instruction that the  
 152 cursor rotation was absent.

153 Each single-movement trial started with the presentation of a white circle in the center  
 154 of the screen, serving as the starting position for the subsequent reaching movement. The cursor

155 was displayed when it was within 3 mm of the start location, a tone (440Hz, 0.05 ms) was  
156 presented, followed by a green target (radius 4 mm) appearing in one of the eight target  
157 positions and the start circle disappeared. Depending on the assigned group, participants were  
158 either instructed to move freely after the target appeared (experiment 1: FREE; experiment 2:  
159 WAIT\_ITI), to wait 2.5 s for a second tone serving as a go signal for the reaching movement  
160 (experiment 1: WAIT\_PLAN1; experiment 2: WAIT\_PLAN2) or to report their movement aim  
161 and then initiate the movement (experiment 3: AIM).

162 The white cursor was visible until it exceeded a movement amplitude of 3 mm, where  
163 it disappeared. When the participant's hand crossed an invisible circle that contained the target,  
164 the cursor froze and turned red, providing terminal endpoint feedback for 1.25 s. Movements  
165 that fell outside the range of instructed movement time criteria ( $MT < 100$  ms or  $> 300$  ms)  
166 were followed by an error message on the screen and the trial was aborted. Those trials were  
167 neither repeated nor used for subsequent analyses. If participants moved too soon in one of the  
168 waiting groups (before the target appearance or the go cue, see below), they were reminded to  
169 wait, and the trial was repeated.

170 The return movement back to the start location was performed without vision of the  
171 cursor, except when the hand was  $< 3$  mm from start location. In order to help guide  
172 participants' movements back to the start, a white concentric circle appeared after feedback  
173 presentation, scaling its radius based on the cursor's distance from the starting circle.

174 In explicit test trials (Hegele & Heuer, 2010; Heuer & Hegele, 2008), start and target  
175 locations were presented together with a white line, centered in the start location with its length  
176 corresponding to target distance. Initially, the line was presented at an angle of  $180^\circ$  CCW of  
177 the respective target's direction. Participants instructed the experimenter to adjust the  
178 orientation of the line to match the direction of the movement they judged to be correct for the  
179 particular target presented.



## 180 Groups

181           The three experiments included five different groups: Two groups of participants took  
182 part in experiment 1. One group was instructed to move straight to the target after it appeared  
183 with no additional time constraints before moving (FREE). The other group (WAIT\_PLAN1)  
184 was instructed to wait until they heard a high-pitched tone (1000 Hz, 0.05 ms) that served as a  
185 go-signal. Inspired by previous work indicating that participants are able to mentally rotate and  
186 move 90° off target within ~1 s (McDougle & Taylor, 2019), we chose a 2.5 s wait interval to  
187 provide ample planning time for the task at hand. The high-pitched tone was presented after  
188 this wait interval.

189           Experiment 2 consisted of two groups: the WAIT\_PLAN2 group was designed as a  
190 replication of the WAIT\_PLAN1 group in experiment 1. Participants in the WAIT\_ITI group  
191 could initiate movements as soon as the target had appeared on the screen replicating the FREE  
192 group from experiment 1, but they experienced an additional 2.5 s waiting period after the  
193 presentation of the endpoint feedback. Thus, the two groups, WAIT\_PLAN2 and WAIT\_ITI,  
194 had matched trial lengths. During the 2.5 s delay in the WAIT\_ITI group, only the target was  
195 visible on the screen and participants were told to maintain their final hand position.

196           Experiment 3 included a single group of participants who were asked to report their  
197 aiming direction prior to movement initiation (AIM group; (Bond & Taylor, 2015; McDougle  
198 et al., 2015; Taylor et al., 2014). The participants of this group saw a numbered ring of  
199 landmarks. The numbers were arranged at 5.6-degree intervals and included the target at the  
200 “0” position. Clockwise, the numbers became larger, and counterclockwise the numbers  
201 became smaller (up to 32, -32, respectively), forming a circle 20 cm in diameter. Participants  
202 were instructed to verbally report the number they aimed at before moving (see (Taylor et al.,  
203 2014) for further information). Verbal reports were manually registered by the experimenter on  
204 each reporting trial.

## 205 Data Analysis

206 Position of the stylus on the tablet surface was sampled at 130 Hz and each trial was  
207 separately low-pass filtered (fourth-order Butterworth, 10 Hz) using Matlab's *filtfilt* command,  
208 and numerically differentiated. Tangential velocity was calculated as the Euclidean of x- and  
209 y-velocity vectors. Movements were analyzed in terms of two parameters: reaction time and  
210 endpoint error. Endpoint error was calculated as the angular difference between the vector  
211 connecting the start circle and the target, and the vector connecting the start circle and the  
212 terminal hand position. Endpoint errors were calculated for both training trials and the  
213 aftereffect trials. The outcome variable of the perceptual judgement test was calculated as the  
214 angular difference between the participant-specified line orientation on the screen and the  
215 vector connecting the start and target positions.

216 Reaction time (RT) was calculated as the interval between target presentation and  
217 movement onset, which was defined when tangential velocity exceeded 30 mm/s for at least  
218 38 ms.

219 For each block of training trials and for the posttest, medians were computed for each  
220 participant following a screening for outliers. Movements whose endpoint error fell outside  
221 three standard deviations of the participants' individual mean endpoint error in that phase were  
222 considered outliers and removed (1.4% of all trials). To compare different levels of asymptote,  
223 the last five blocks of the training phase were median averaged and compared between groups  
224 using a two-sample Wilcoxon's rank-sum test. Statistical analyses were done in Matlab  
225 (R2017b) and R (version 3.5.1, <http://www.R-project.org/>). All results are based on median  
226 averaged data, which did not qualitatively change outcomes compared to corresponding  
227 parametric tests (data not shown).

## 228 Results

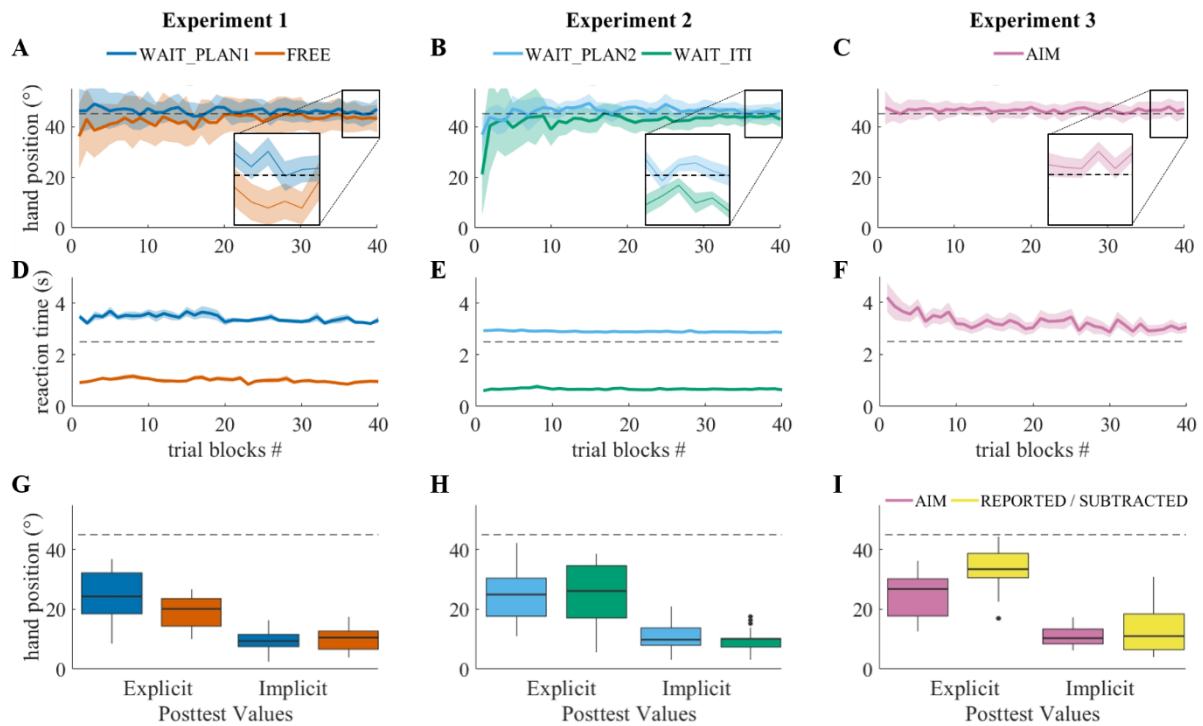


Figure 2. Median hand direction (panels A-C) and mean reaction times (panels D-F) during practice plotted separately by experiments and groups. Panel G-I show the median hand direction during explicit and implicit posttests, separately. Panel I additionally shows the verbally reported aim (yellow boxplot in Explicit) and the difference between actual hand position and reported aim (yellow boxplot in Implicit). The horizontal dashed lines in panels A-C and H-I indicate ideal compensation for the 45° cursor rotation. In panels D-F, they indicate the forced waiting times of 2.5 seconds in the WAIT\_PLAN groups. Shaded error bands represent median absolute deviation (MADs).

### 229 Experiment 1

230 Experiment 1 tested the speed-accuracy hypothesis by artificially prolonging movement  
 231 planning time. To do so, we compared two groups. The FREE group could freely initiate their  
 232 movement, representing a “standard” adaptation experiment. The WAIT\_PLAN1 group was  
 233 required to withhold movement initiation until hearing a “go”-signal 2.5 s after target onset. As  
 234 shown in Figure 2A, the FREE group displayed the typical incomplete asymptote, whereas the  
 235 WAIT\_PLAN1 group achieved a greater asymptote ( $\text{mean}_{\text{WAIT\_PLAN1}} = 46.66$ ,  
 236  $\text{sd}_{\text{WAIT\_Plan1}} = 5.85$ ,  $\text{mean}_{\text{FREE}} = 41.15$ ,  $\text{sd}_{\text{FREE}} = 8.28$ ;  $V = 244$ ,  $p = 0.001$ ). Hand directions late  
 237 during practice were significantly less than 45° in the FREE group ( $V = 32.5$ ,  $p = 0.018$ ), while  
 238 the WAIT\_PLAN1 group did not differ significantly from 45° ( $V = 108$ ,  $p = 0.62$ ).

239 In the explicit judgment test (Figure 2G), the FREE group estimated the rotation to be  
 240 significantly smaller relative to the WAIT\_PLAN1 group ( $\text{mean}_{\text{FREE}} = 24.78^\circ$ ,  $\text{sd}_{\text{FREE}} = 5.45^\circ$ ,

241  $\text{mean}_{\text{WAIT\_PLAN1}} = 30.65^\circ$ ,  $\text{sd}_{\text{WAIT\_PLAN1}} = 8.33^\circ$ ;  $V = 81.5$ ,  $p = 0.036$ ). Implicit aftereffects  
242 (Figure 2G) did not differ significantly between the groups ( $\text{mean}_{\text{FREE}} = 9.99^\circ$ ,  $\text{sd}_{\text{FREE}} = 3.81^\circ$ ,  
243  $\text{mean}_{\text{WAIT\_PLAN1}} = 9.35^\circ$ ,  $\text{sd}_{\text{WAIT\_PLAN1}} = 3.67^\circ$ ;  $V = 179$ ,  $p = 0.59$ ).

## 244 Experiment 2

245 Experiment 1 showed that forcing participants to prolong their planning time before  
246 movement onset on each trial led to an increase in asymptotic learning. While this observation  
247 is consistent with our speed-accuracy tradeoff hypothesis, the WAIT\_PLAN1 group also  
248 exhibited significantly larger amounts of explicit knowledge of the rotation, raising the  
249 possibility that this group shows complete asymptote simply because of larger amounts of  
250 accumulated explicit knowledge during training. To test this, in experiment 2 we manipulated  
251 when the additional waiting time occurred within a trial. If it was a matter of simply building a  
252 more elaborate representation of the perturbation by raising awareness and thus accumulating  
253 more explicit knowledge of the rotation, then additional processing time between movements  
254 should suffice to facilitate complete asymptotic learning. If, on the other hand, the pre-  
255 movement planning period was crucial, one would expect that adding time to the interval  
256 between the appearance of the target and the signal to initiate the movement would lead to better  
257 performance than adding time to the post-feedback interval, i.e. the time interval between the  
258 disappearance of terminal endpoint feedback and the onset of the next target. Experiment 2  
259 tested this by contrasting asymptotic learning in a second group that had to wait for 2.5 s during  
260 movement planning (WAIT\_PLAN2; replication of WAIT\_PLAN1) with a group that had to  
261 wait for 2.5 s after feedback presentation before the next trial started (WAIT\_ITI). In line with  
262 our speed-accuracy-hypothesis, inserting waiting time into the planning phase led to an  
263 asymptote not significantly different from  $45^\circ$  ( $V = 235$ ,  $p = 0.28$ ) whereas inserting the waiting  
264 time into the intertrial interval lead to an asymptote significantly less than  $45^\circ$  ( $V = 63$ ,  
265  $p = 0.019$ ). Those two asymptotes were significantly different from each other

266 (mean<sub>WAIT\_PLAN2</sub> = 46.33, sd<sub>WAIT\_PLAN2</sub> = 3.99; mean<sub>WAIT\_ITI</sub> = 43.96, sd<sub>WAIT\_ITI</sub> = 3.01;  
267 W = 311, p = 0.011) (Figure 2B).

268 Importantly, for explicit knowledge (Figure 2H), the temporal locus of the additional  
269 waiting time did not have a significant effect: Both groups appeared to accumulate equivalent  
270 amounts of explicit knowledge (mean<sub>WAIT\_ITI</sub> = 30.53°, sd<sub>WAIT\_ITI</sub> = 8.57°,  
271 mean<sub>WAIT\_PLAN2</sub> = 30.88°, sd<sub>WAIT\_PLAN2</sub> = 10.21°; W = 209, p = 0.79), but showed greater  
272 explicit estimations than the FREE group in experiment 1, whose trial structure did not contain  
273 any additional waiting interval (FREE ~ WAIT\_PLAN2: W = 85, p = 0.031; FREE ~  
274 WAIT\_ITI: W = 93, p = 0.027). As for implicit aftereffects, both groups in experiment 2  
275 achieved similar results (mean<sub>WAIT\_ITI</sub> = 8.45°, sd<sub>WAIT\_ITI</sub> = 4.77°, mean<sub>WAIT\_PLAN2</sub> = 7.63°,  
276 sd<sub>WAIT\_PLAN2</sub> = 3.87°; W = 214, p = 0.89).

### 277 Experiment 3

278 In the last experiment, we sought to account for the possibility that it is not time per se,  
279 but the increased participation of explicit processes that raises the level of asymptote. We thus  
280 instructed participants to verbally report their movement aim prior to movement execution trial-  
281 by-trial (Taylor et al., 2014), potentially priming the explicit component of adaptation. We  
282 reasoned that this procedure serves as an opportunity to replicate our findings in a procedure  
283 that requires active explicit engagement during the planning interval. Compensation for the  
284 rotation asymptoted around 46.63° (sd = 4.12°), which was significantly larger than 45°  
285 (V = 125, p = 0.045), suggesting that adaptation at asymptote was complete and, in fact,  
286 overcompensated for the rotation (Figure 2C).

287 Explicit judgements of required compensation (mean = 28.32, sd = 10.95) (Figure 2I)  
288 were significantly less than 45° (V = 0, p < 0.0002) but significantly greater than 0° (V = 170,  
289 p < 0.0002). Implicit aftereffects (mean = 9.38, sd = 3.4) were also significantly different from  
290 both 0° and 45° (V = 171, p < 0.0001, V = 0, p < 0.0001, respectively). If we assume that the

291 explicit and implicit components are the two main elements in a fully additive model that  
292 generates adaptive behavior, the implicit component can be calculated by subtracting the hand  
293 position from the aim report (Figure 2L). Comparing those values to the posttest values, we do  
294 not find a significant difference, neither in explicit nor in the implicit component ( $W = 123$ ,  
295  $p = 0.22$ ;  $W = 129$ ,  $p = 0.31$ , respectively).

296 To test whether the reporting task influenced the outcome of the explicit judgement  
297 tests, we compared the posttest values between the AIM group and those of the other groups in  
298 experiments 1 and 2. There was a significant difference in the explicit judgements between the  
299 AIM group and the FREE group from experiment 1 ( $W = 197.5$ ,  $p = 0.025$ ) but none between  
300 the WAIT\_PLAN and AIM ( $W = 160.5$ ,  $p = 0.76$ ). Across the AIM group and WAIT\_PLAN2  
301 and WAIT\_ITI groups in experiment 2, there were no differences in the explicit judgement tests  
302 ( $W = 160$ ,  $p = 0.57$ ;  $W = 190.5$ ,  $p = 0.85$ ). Similar results were observed for the implicit  
303 aftereffects: Neither the FREE group, the WAIT\_PLAN1 group from experiment 1, nor the  
304 WAIT\_PLAN2 and WAIT\_ITI groups had significantly different aftereffects relative to the  
305 AIM group ( $W = 140.5$ ,  $p = 0.69$ ;  $W = 167.5$ ,  $p = 0.93$ ;  $W = 227.5$ ,  $p = 0.08$ ;  $W = 265.5$ ,  
306  $p = 0.05$ , respectively). These results suggest that experimentally querying the explicit process  
307 of adaptation does not qualitatively alter the explicit/implicit learning balance but does act to  
308 improve the adaptation asymptote by slowing down planning.

## 309 **Discussion**

310 This study aimed to investigate whether previously reported findings of incomplete  
311 asymptotic learning in visuomotor adaptation tasks may be reframed as a consequence of a  
312 ubiquitous computational principle in human information processing: the tradeoff between the  
313 accuracy of a response and the speed with which it is generated. In line with this hypothesis,  
314 artificially prolonging the waiting period prior to movement onset facilitated asymptotic  
315 learning and appeared to eliminate residual errors. This benefit was specific to prolonging motor

316 planning; that is, the time interval between the appearance of the visual target and the go-signal.  
317 Prolonging the interval between the disappearance of visual feedback and the start of the next  
318 trial did not provide the same benefit to learning. Our results provide support for a parsimonious  
319 explanation that time-consuming planning processes are primarily responsible for incomplete  
320 asymptotic adaptation.

321 Initially, the incomplete asymptote phenomenon was explained by state-space models  
322 of adaptation (Cheng & Sabes, 2006; Smith et al., 2006; Thoroughman & Shadmehr, 2000),  
323 according to which the adapted state reaches an equilibrium between learning from error and  
324 decaying towards baseline. As subsequent studies indicated that this model alone is insufficient  
325 for explaining incomplete asymptotic behavior, alternatives were proposed: For example,  
326 Vaswani and colleagues (Vaswani et al., 2015) showed that in a nonzero error clamp with zero  
327 feedback deviation, participants can be triggered to overcome the residual error. This led the  
328 authors to suggest that the contextual change elicited by the absence of motor variability  
329 triggered a change in the learning policy from error-based learning to exploration. They further  
330 suggested that a learning process driven by spatial error information suppresses exploration, in  
331 line with their previous reasoning that the presence of spatial error feedback suppressed  
332 reinforcement-based contributions to learning (Shmuelof et al., 2012). In our study, participants  
333 in all groups received spatial error feedback; thus, a potential suppression should have affected  
334 all groups equally. Our results therefore suggest that positional error feedback suppressing other  
335 learning mechanisms is not sufficient to explain the modulations in asymptote we observed.

336 Recent accounts have framed motor planning as a time-consuming optimization process  
337 from which a reduction in movement accuracy arises naturally when constraints are imposed  
338 (Al Borno, Vyas, V. Shenoy, & Delp, 2019). Our findings suggest that similar principles apply  
339 when one is intentionally choosing to perform a movement in another direction than the one

340 implied by the target presented, and that learners naturally constrain their planning time even  
341 in seemingly unconstrained conditions.

342         Furthermore, Haith and colleagues (Haith, Pakpoor, & Krakauer, 2016) recently showed  
343 that movement preparation and initiation are independent i.e. that, instead of complete  
344 preparation triggering movement initiation, humans appear to determine a time for movement  
345 initiation based on when it expects planning to be completed. This view naturally implies the  
346 possibility to initiate a movement that has not been sufficiently prepared. The planning time  
347 chosen may therefore trade off the accuracy it expects planning to achieve within a given time  
348 and an urgency to move on (e.g. fueled by a desire to increase reward rate (Churchland et al.,  
349 2008; Cisek et al., 2009; Thura et al., 2012; Thura & Cisek, 2017)). In the wait conditions of  
350 our study, we delay movement initiation and enable planning to proceed further and arrive at a  
351 more accurate solution.

352         But why does incomplete planning result in consistent undershooting rather than  
353 overshooting, or merely in greater movement variability? We propose that parametric mental  
354 computations in visuomotor rotation tasks could explain the undershooting phenomenon: In  
355 visuomotor rotation tasks, participants' reaction times increase linearly with the magnitude of  
356 the imposed rotation (Georgopoulos & Massey, 1987; McDougle & Taylor, 2019), reflecting a  
357 putative mental rotation process. Thus, in our hypothesis, under-compensation is the  
358 consequence of participants not fully completing a mental rotation of their planned reach  
359 trajectory. This view is further supported by the results of our third experiment, in which  
360 emphasizing the application of explicit aiming strategies prior to movement initiation led to  
361 qualitatively similar asymptotic learning as in the groups with prolonged planning intervals.  
362 Interestingly, delaying movement initiation not only caused full compensation, but typically  
363 induced overcompensation. We suggest that implicit processes superimposed onto an accurate



364 explicit strategy caused drift, gradually moving the hand further in the direction of  
365 compensation (Mazzoni & Krakauer, 2006)

366         A new approach to the state-space model is that residual errors in adaptation paradigms  
367 are caused by implicit processes that tune the sensitivity to errors until it reaches the equilibrium  
368 with constant forgetting (Albert et al., 2019). The authors in this recent study manipulated the  
369 variability of the perturbation and found that residual errors increase with the perturbations'  
370 variance. We note that, whereas our hypothesis could potentially be adapted to account for these  
371 variations in asymptote (e.g. experiencing perturbation variability could affect the benefit that  
372 learners expect from planning, and thus the time they spend on it), we did not consider this  
373 possibility *a priori* in hypothesis generation. However, we note that in one experiment, this  
374 study also showed a speed-accuracy tradeoff by obtaining larger residual errors when the  
375 reaction time is artificially shortened compared to free reaction times, regardless of the variance  
376 of perturbation. Thus, we argue, that additional planning time is an essential element in  
377 eliminating residual errors to achieve full compensation, though it need not be the only thing  
378 determining the exact asymptotic value.

379         Many of the canonical explanations for incomplete asymptote outlined above imply that  
380 it is a fundamental property of learning. Psychology and kinesiology traditionally distinguish  
381 learning effects from performance effects, where underlying knowledge can be identical in  
382 different cases, but retrieval processes in specific test conditions can lead to different  
383 performance profiles (Magill & Anderson, 2017; Schmidt & Lee, 2011). Whereas our  
384 experiments were not specifically designed to distinguish learning from performance effects,  
385 our findings suggest that both may contribute to incomplete asymptote in adaptation.  
386 Specifically, explicit knowledge as a measure of underlying learning was increased in the  
387 WAIT\_PLAN1 group (experiment 1), suggesting that some of the benefit of longer planning  
388 times may come about by learners honing their explicit knowledge. However, the observation

389 that explicit knowledge was similarly increased in both groups of experiment 2 indicates that  
390 this learning effect may be a non-specific consequence of longer ITIs. Future research can  
391 address these issues more specifically.

392 Lastly, we do not claim that other mechanisms affecting learning do not contribute to  
393 asymptotic behavior (Albert et al., 2019), or that a state-space model with gradual decay  
394 towards zero is generally invalid. For example, Brennan and Smith (Brennan & Smith, 2015)  
395 report results that support gradual decay when learning is followed by an error clamp; the  
396 mechanism we propose does not explain their results. What we suggest is that the eventual key  
397 for why the sensorimotor system does not overcome these asymptotic errors under “standard  
398 conditions” is the speed accuracy tradeoff. A key realization here is that the brain sets its motor  
399 planning time short of maximal task performance even when it is not pressed to react quickly.  
400 This combines common findings in perceptual and value-based decision-making, highlighting  
401 an important parallel between these two fields. We speculate that simple interventions, like  
402 explicitly prolonging reaction times, could improve performance in motor skill learning tasks  
403 in general.

404

## 405 **Conclusion**

406 In conclusion, we found that prolonging reaction times raised the level of asymptote in  
407 visuomotor adaptation tasks. Moreover, we propose that the under-compensation often  
408 observed in adaptation tasks may result from a hastened mental rotation process during the re-  
409 aiming of movements away from visual targets. Further research may investigate how planning  
410 time influences both explicit and implicit learning processes.

## 411 Reference List

- 412 Al Borno, M., Vyas, S., V. Shenoy, K., & Delp, S. L. (2019). *High-fidelity Musculoskeletal*  
413 *Modeling Reveals a Motor Planning Contribution to the Speed-Accuracy Tradeoff: bioRxiv*  
414 *doi: 10.1101/804088*. Unpublished manuscript.
- 415 Albert, S. T., Jang, J., Sheahan, H., Teunissen, L., Vandevoorde, K., & Shadmehr, R. (2019).  
416 *Asymptotic limits of sensorimotor adaptation: bioRxiv doi: 10.1101/868406*. Unpublished  
417 manuscript.
- 418 Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor  
419 adaptation task. *Journal of neurophysiology*, *113*(10), 3836–3849.
- 420 Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- 421 Brennan, A. E., & Smith, M. A. (2015). The Decay of Motor Memories Is Independent of  
422 Context Change Detection. *PLoS computational biology*, *11*(6), e1004278.
- 423 Cheng, S., & Sabes, P. N. (2006). Modeling Sensorimotor Learning with Linear Dynamical  
424 Systems. *Neural Computation*, *18*(4), 760–793.
- 425 Churchland, A. K., Kiani, R., & Shadlen, M. N. (2008). Decision-making with multiple  
426 alternatives. *Nature neuroscience*, *11*(6), 693–702.
- 427 Cisek, P., Puskas, G. A., & El-Murr, S. (2009). Decisions in changing conditions: The urgency-  
428 gating model. *The Journal of neuroscience : the official journal of the Society for*  
429 *Neuroscience*, *29*(37), 11560–11571.
- 430 Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a  
431 structure for visual-motor maps. *Journal of Experimental Psychology: Human Perception*  
432 *and Performance*, *15*(3), 493–506.
- 433 Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between  
434 reaction time and reach errors during visuomotor adaptation. *Behavioural brain research*,  
435 *219*(1), 8–14.

- 436 Georgopoulos, A. P., & Massey, J. T. (1987). Cognitive spatial-motor processes. 1. The making  
437 of movements at various angles from a stimulus direction. *Experimental brain research*,  
438 65(2), 361–370.
- 439 Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The influence of movement  
440 preparation time on the expression of visuomotor learning and savings. *The Journal of*  
441 *neuroscience : the official journal of the Society for Neuroscience*, 35(13), 5109–5117.
- 442 Haith, A. M., Pakpoor, J., & Krakauer, J. W. (2016). Independence of Movement Preparation  
443 and Movement Initiation. *The Journal of neuroscience : the official journal of the Society*  
444 *for Neuroscience*, 36(10), 3007–3015.
- 445 Hegele, M., & Heuer, H. (2010). Implicit and explicit components of dual adaptation to  
446 visuomotor rotations. *Consciousness and cognition*, 19(4), 906–917.
- 447 Heitz, R. P. (2014). The speed-accuracy tradeoff: History, physiology, methodology, and  
448 behavior. *Frontiers in neuroscience*, 8, 150.
- 449 Heuer, H., & Hegele, M. (2008). Adaptation to visuomotor rotations in younger and older  
450 adults. *Psychology and aging*, 23(1), 190–202.
- 451 Heuer, H., & Hegele, M. (2015). Explicit and implicit components of visuo-motor adaptation:  
452 An analysis of individual differences. *Consciousness and cognition*, 33, 156–169.
- 453 Hinder, M. R., Riek, S., Tresilian, J. R., Rugey, A. de, & Carson, R. G. (2010). Real-time error  
454 detection but not error correction drives automatic visuomotor adaptation. *Experimental*  
455 *brain research*, 201(2), 191–207.
- 456 Holland, P., Codol, O., & Galea, J. M. (2018). Contribution of explicit processes to  
457 reinforcement-based motor learning. *Journal of neurophysiology*, 119(6), 2241–2255.
- 458 Huberdeau, D. M., Haith, A. M., & Krakauer, J. W. (2015). Formation of a long-term memory  
459 for visuomotor adaptation following only a few trials of practice. *Journal of*  
460 *neurophysiology*, 114(2), 969–977.

- 461 Lackner, J. R., & Dizio, P. (1994). Rapid adaptation to Coriolis force perturbations of arm  
462 trajectory. *Journal of neurophysiology*, 72(1), 299–313.
- 463 Magill, R., & Anderson, D. I. (2017). *Motor learning and control: Concepts and applications*  
464 (Eleventh edition, [McGraw-Hill Education International edition]). New York: McGraw-  
465 Hill.
- 466 Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during  
467 visuomotor adaptation. *The Journal of neuroscience : the official journal of the Society for*  
468 *Neuroscience*, 26(14), 3642–3645.
- 469 McDougale, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and Implicit Processes  
470 Constitute the Fast and Slow Processes of Sensorimotor Learning. *The Journal of*  
471 *neuroscience : the official journal of the Society for Neuroscience*, 35(26), 9568–9579.
- 472 McDougale, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor  
473 learning. *Nature communications*, 10(1), 40.
- 474 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming  
475 numbers into movies. *Spatial Vision*, 10(4), 437–442.
- 476 Plamondon, R., & Alimi, A. M. (1997). Speed/accuracy trade-offs in target-directed  
477 movements. *The Behavioral and brain sciences*, 20(2), 279-303; discussion 303-49.
- 478 Schmidt, R. A., & Lee, T. D. (2011). *Motor control and learning: A behavioral emphasis* (Fifth  
479 edition). Champaign, Ill.: Human Kinetics.
- 480 Schween, R., & Hegele, M. (2017). Feedback delay attenuates implicit but facilitates explicit  
481 adjustments to a visuomotor rotation. *Neurobiology of learning and memory*, 140, 124–133.
- 482 Shadmehr, R., & Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during  
483 learning of a motor task. *The Journal of Neuroscience*, 14(5), 3208–3224.
- 484 Shmuelof, L., Huang, V. S., Haith, A. M., Delnicki, R. J., Mazzoni, P., & Krakauer, J. W.  
485 (2012). Overcoming motor "forgetting" through reinforcement of learned actions. *The*

- 486 *Journal of neuroscience : the official journal of the Society for Neuroscience*, 32(42), 14617–  
487 14621.
- 488 Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with  
489 different timescales underlie short-term motor learning. *PLoS biology*, 4(6), e179.
- 490 Spang, K., Wischhusen, S., & Fahle, M. (2017). Limited Plasticity of Prismatic Visuomotor  
491 Adaptation. *i-Perception*, 8(2), 2041669517701458.
- 492 Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to  
493 learning in a sensorimotor adaptation task. *The Journal of neuroscience : the official journal*  
494 *of the Society for Neuroscience*, 34(8), 3023–3032.
- 495 Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination  
496 of motor primitives. *Nature*, 407(6805), 742–747.
- 497 Thura, D., Beauregard-Racine, J., Fradet, C.-W., & Cisek, P. (2012). Decision making by  
498 urgency gating: Theory and experimental support. *Journal of neurophysiology*, 108(11),  
499 2912–2930.
- 500 Thura, D., & Cisek, P. (2017). The Basal Ganglia Do Not Select Reach Targets but Control the  
501 Urgency of Commitment. *Neuron*, 95(5), 1160-1170.e5.
- 502 van der Kooij, K., Brenner, E., van Beers, R. J., & Smeets, J. B. J. (2015). Visuomotor  
503 adaptation: How forgetting keeps us conservative. *PloS one*, 10(2), e0117901.
- 504 van der Kooij, K., Overvliet, K. E., & Smeets, J. B. J. (2016). Temporally stable adaptation is  
505 robust, incomplete and specific. *The European journal of neuroscience*, 44(9), 2708–2715.
- 506 Vaswani, P. A., & Shadmehr, R. (2013). Decay of motor memories in the absence of error. *The*  
507 *Journal of neuroscience : the official journal of the Society for Neuroscience*, 33(18), 7700–  
508 7709.
- 509 Vaswani, P. A., Shmuelof, L., Haith, A. M., Delnicki, R. J., Huang, V. S., Mazzoni, P., et al.  
510 (2015). Persistent residual errors in motor adaptation tasks: Reversion to baseline and

- 511 exploratory escape. *The Journal of neuroscience : the official journal of the Society for*  
512 *Neuroscience*, 35(17), 6969–6977.
- 513 Wong, A. L., Haith, A. M., & Krakauer, J. W. (2015). Motor Planning. *The Neuroscientist : a*  
514 *review journal bringing neurobiology, neurology and psychiatry*, 21(4), 385–398.