

35 suggesting that the motor planning interval predicts the learning asymptote (experiment 2). In
36 the last experiment, we asked participants to continuously report their movement intent. We
37 show that emphasizing explicit re-aiming strategies (and concomitantly increasing planning
38 time) also lead to complete asymptotic learning. Findings from all experiments support the
39 hypothesis that incomplete adaptation is, in part, the result of an intrinsic speed-accuracy trade-
40 off, perhaps related to cognitive strategies that require parametric attentional reorienting from
41 the visual target to the goal.

42

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

45

46 **Introduction**

47 One of the persistent curiosities in studying the human mind is the idea of canonical
48 computations, i.e. that the brain applies similar computations to perform a wide range of
49 different tasks (e.g. Miller, 2016; Pack & Bensmaia, 2015). While most examples for such
50 canonical computations, e.g. linear receptive fields (Movshon et al., 1978, DiCarlo & Johnson,
51 2000), divisive gain control and normalization (e.g. Carandini & Heeger, 2011) or soft-
52 thresholding of noisy signals (e.g. Ringach & Malone, 2007) have been identified in the fields
53 of neuroscience and artificial intelligence, they have largely eluded scientists in psychology.
54 However, there have been a few but famous instances when psychologists have discovered
55 law-like descriptions of human behavior suggesting the application of similar behavioral
56 algorithms across a wide range of tasks.

57 One example of such a canonical computation in behavior is the speed-accuracy
58 tradeoff, that is the inverse relation between the accuracy of an action and the time taken to
59 produce it (for a recent review, see Heitz, 2014). The speed-accuracy tradeoff has been shown
60 to shape behavior (a) across domains from motor control (Fitts, 1954; Plamondon & Alimi,
61 1997) and perception (Grosjean et al., 2007; Ratcliff, 2002) to memory (Hacker, 1980) and
62 mental imagery (Cerritelli et al., 2000; Decety & Jeannerod, 1996), and (b) across species from
63 insects (e.g. Chittka et al., 2003; Ings & Chittka, 2008) and rodents (e.g. Rinberg et al., 2006)
64 to monkeys (Heitz & Schall, 2012) and humans (Wickelgren, 1977).

65 Another example is the law of practice, according to which performance improvements
66 are generally larger early during practice before they become systematically smaller as practice
67 progresses giving rise to a negatively accelerated relationship between performance and the
68 number of practice trials (Snoddy, 1926, Crossman, 1959, Chen et al., 2005). Regardless of its
69 actual parameters, all versions of the law of practice postulate that performance improvements
70 asymptote, at some point, to a specific performance plateau. For complex skills such as

71 swimming or track and field, it is almost impossible to determine *a priori* the absolute
72 maximum level of performance (but see Berthelot et al., 2015). This is not the case in many
73 experimental paradigms, for instance, in novel visuomotor transformation tasks (e.g., force
74 field adaptation or rotations of visual feedback), where individuals have to adapt an existing
75 movement. These simple manipulations allow for the evaluation of performance improvements
76 relative to an absolute maximum, i.e. an ideal, complete compensation of the transformation
77 (Cunningham, , Lackner & Dizio, 1994, Shadmehr et al.,).

78 Interestingly, one common observation in this context is that of an incomplete learning
79 asymptote. That is, if individuals are required to make reaching movements and counteract a
80 30° visuomotor rotation, their performance curve tends to asymptote below full compensation,
81 for instance around ~25° (Holland et al., 2018, Huberdeau et al., 2015, Haith et al., 2015, Kooij
82 et al., 2016, van der Kooij et al., 2015). This under-compensation leaves a residual performance
83 error significantly different from zero (Hinder et al., 2010, Shmuelof et al., 2012, Spang et al.,
84 2017, Kooij et al., 2016, van der Kooij et al., 2015, Vaswani et al., 2015).

85 One accepted approach to explain this phenomenon is to leverage state-space models
86 of adaptation, which are incremental Markovian learning algorithms that balance both learning
87 and forgetting during adaptation (Cheng & Sabes, 2006, Smith et al., 2006, Thoroughman &
88 Shadmehr, 2000). When fit to human learning data, most values of learning and forgetting
89 parameters can produce a steady-state equilibrium at an arbitrary asymptote. Consequently,
90 these models provide a natural explanation of the commonly observed undershoot, via an
91 assumption that some amount of forgetting (i.e., reversion to baseline) is inevitable on each
92 trial of the task. This interpretation suggests that incomplete compensation during motor
93 learning is simply a built-in feature of the underlying learning mechanism.

94 However, Vaswani and colleagues (2015) demonstrated that humans, in principle,
95 possess the capacity to overcome this incomplete asymptote. In their study, visual feedback of

96 their movement was “clamped” after learning; that is the cursor controlled by the participant
97 moved in a fixed trajectory toward the target or to a nearby location with participants only
98 controlling the amplitude. When visual feedback was clamped to a slight deviation from the
99 target with no variability, individuals appeared to adopt a new learning strategy that allowed
100 them to fully compensate a novel visuomotor transformation. To explain this, Vaswani and
101 colleagues (2015) postulated an exploratory learning mechanism that is suppressed by error-
102 based learning. The putative suppressed process only contributes to performance when error-
103 based learning is disengaged, which in their study was caused by a persistent residual error in
104 combination with a contextual change (i.e., the introduction of a lack of natural movement
105 variability) (Shmuelof et al., 2012, Vaswani et al., 2015, Vaswani & Shadmehr, 2013, Wong
106 et al., 2015).

107 In the present study, we propose and evaluate one alternative, perhaps more
108 parsimonious account of how humans might overcome incomplete asymptotic learning:
109 namely, the level of performance achieved at the later stages of visuomotor adaptation may
110 primarily reflect an intrinsic speed-accuracy tradeoff driven by time-consuming movement
111 planning.

112 In line with this, research in perceptual decision-making has established that choice
113 reaction time reflects a trade-off between waiting for more information and acting early in order
114 to speed up the accumulation of (uncertain) rewards on future trials (Churchland et al., 2008,
115 Cisek et al., 2009, Thura et al., ; Thura & Cisek, 2017). While visuomotor adaptation tasks
116 traditionally are not studied in the framework of decision-making, recent research has
117 highlighted an important role for volitional decision-making strategies in adaptation tasks (i.e.,
118 the explicit re-aiming of movements to counteract perturbations; Bond & Taylor, 2015, Heuer
119 & Hegele, 2015, McDougle et al., 2015, Schween & Hegele, 2017, Taylor et al., 2014). Further
120 evidence suggests that in the context of adaptation to a novel visuomotor rotation such

121 strategies may take the form of mentally rotating the aiming direction of the reaching
122 movement (McDougle & Taylor, 2019), which has been known to require long preparation
123 times (Fernandez-Ruiz et al., 2011, Haith et al., 2015, McDougle & Taylor, 2019). Thus, an
124 incomplete learning asymptote could simply arise from hurried movement initiation leading to
125 prematurely terminating mental rotation of an abstract aiming trajectory during movement
126 planning.

127 We tested our hypothesis over three behavioral experiments where we artificially
128 extended planning time. We predicted that this simple manipulation would alleviate incomplete
129 asymptotic learning. In the first experiment (experiment 1), we introduced a mandatory waiting
130 period between target presentation and movement onset. In experiment 2, we sought to exclude
131 effects of the total experiment duration by emphasizing the role of within-trial movement
132 planning time versus between-trial consolidation. Finally, in experiment 3, we used an aiming
133 report method (Taylor et al., 2014) to promote the application of explicit motor learning
134 strategies before movement execution and elucidate their influence on the learning asymptote.

135

136 **Methods**

137 **Participants**

138 Ninety neurologically healthy and right-handed students from the Justus Liebig
139 University Giessen were recruited as participants (Experiment 1: N = 36, Experiment 2:
140 N = 36, Experiment 3: N = 18) and received monetary compensation or course credit for their
141 participation. Written, informed consent was obtained from all participants before testing. The
142 experimental protocol was approved by the local ethics committee of the Department of
143 Psychology and Sport Science. All participants were self-declared right-handers. Data from
144 one participant (experiment 2) were excluded due to a large number of irregular trials (i.e.

145 premature movement initiation, and moving too fast or too slow).

146

147 Apparatus

148 Participants sat on a height-adjustable chair facing a 22'' widescreen LCD monitor
149 (Samsung 2233RZ; display size: 47,3 cm x 29,6 cm; resolution: 1680 x 1050 pixels; frame rate
150 120 Hz), which was placed on eye level 100 cm in front of them. Their right hand held a
151 digitizing stylus, which they could move across a graphics tablet (Wacom Intuos 4XL). Their
152 hand position recorded from the tip of the stylus was sampled at 130 Hz. Stimulus presentation
153 and movement recording were controlled by a custom build MATLAB script (R2017b),
154 displayed above the table platform, thus preventing direct vision of the hand (left panel Figure
155 1A).

156

157 Task

158 Participants performed center-out reaching movements from a common start location
159 to targets in different directions. They were instructed to move the cursor as quickly as possible
160 from the start location in the direction of the displayed target and “shoot through it”. On the
161 monitor, the start location was in the center of the screen, marked by the outline of a circle of
162 7 mm in diameter. On the table surface, the start location was 20 – 25 cm in front of the
163 participant on the body midline. The target location, marked by a filled green circle of 4 mm
164 in diameter, varied from trial to trial. Targets were placed on an invisible circle with a radius
165 of 100 mm around the start location; target locations were 0, 45, 90, 135, 180, 225, 270, and
166 315° (0° is from the start location to the right, 90° is forward, 270° is backward; right panel
167 Figure 1A). On baseline and adaptation trials, visual feedback was given by a filled white circle
168 (radius 2.5 mm).

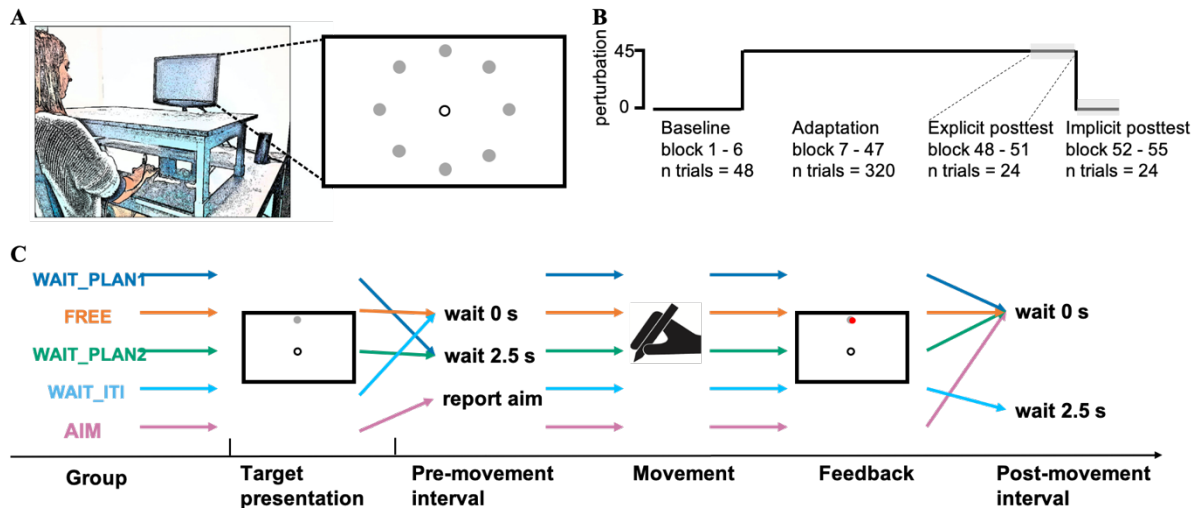


Figure 1 schematic display of the experimental setup (A), overall protocol (B) and sequence of one trial (C). Each participant performed center-out reaching movements with a stylus on the tablet. Visual stimuli and the cursor were presented on a monitor. The visual cursor was displaced according to the 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.

169

170 Design and Procedure

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

178 The posttest phase consisted of two types of trials: an explicit test (see below)
 179 comprising three blocks of eight trials each with each target location occurring once per block,
 180 and three blocks of eight aftereffect test trials without visual feedback, with the instruction that
 181 the cursor rotation would be absent. In the explicit test trials (Hegele & Heuer, 2010, Heuer &
 182 Hegele, 2008), start and target locations were presented together with a white line, centered in

183 the start location with its length corresponding to target distance. Initially, the line was
184 presented at an angle of 180° CCW of the respective target's direction. Participants instructed
185 the experimenter to adjust the orientation of the line to match the direction of the movement
186 they judged to be correct for the particular target presented.

187 Each single-movement trial started with the presentation of a white circle in the center
188 of the screen, serving as the starting position for the subsequent reaching movement. In order
189 to help guide participants' movements back to the start, a white concentric circle appeared after
190 feedback presentation, scaling its radius based on the cursor's distance from the starting circle.
191 The cursor was displayed when it was within 3 mm of the start location. Once the start position
192 was held for 300 ms, a tone (440Hz, 0.05 ms duration) was presented, followed by a green
193 target (radius 4 mm) appearing in one of the eight target positions and the start circle
194 disappeared. Depending on the assigned group, participants were either instructed to move
195 freely after the target appeared (experiment 1: FREE; experiment 2: WAIT_ITI), to wait 2.5 s
196 for a second tone serving as an imperative ("go" signal) for the movement (experiment 1:
197 WAIT_PLAN1; experiment 2: WAIT_PLAN2), or to report their movement direction and
198 subsequently initiate the reach (experiment 3: AIM).

199 The white cursor was visible until it exceeded a movement amplitude of 3 mm, after
200 which it disappeared. When the participant's hand crossed an invisible circle that contained the
201 target, the cursor froze and turned red, providing terminal endpoint feedback for 1.25 s.
202 Movements that fell outside the range of instructed movement time criteria ($MT < 100$ ms or
203 > 300 ms) were followed by an error message on the screen and the trial was aborted. Those
204 trials were neither repeated nor used in subsequent analyses. If participants moved too soon in
205 one of the waiting groups (before the target appearance or the go cue, see below), they were
206 reminded to wait, and the trial was repeated.

207

208 Groups

209 The three experiments included five different groups: Two groups of participants took
210 part in experiment 1. One group (N = 19) was instructed to move straight to the target after it
211 appeared with no additional time constraints before moving (FREE). The other group
212 (WAIT_PLAN1, N = 17) was instructed to wait until they heard a high-pitched tone (1000 Hz,
213 0.05 ms duration) that served as a go-signal. Inspired by previous work indicating that
214 participants are able to mentally rotate their aim 90° off-target within ~1 s (McDougle
215 & Taylor, 2019), we chose a 2.5 s wait interval to provide ample planning time for the 45°
216 rotation task at hand. The go-signal was presented after this wait interval.

217 Experiment 2 consisted of two groups: the WAIT_PLAN2 group (N = 22) was a
218 replication of the WAIT_PLAN1 group in experiment 1. Participants in the WAIT_ITI group
219 (N = 20) could initiate movements as soon as the target had appeared on the screen replicating
220 the planning interval of the FREE group from experiment 1. Critically, the WAIT_ITI
221 experienced an additional 2.5 s waiting period after the presentation of the endpoint feedback.
222 Thus, the two groups, WAIT_PLAN2 and WAIT_ITI, had matched trial lengths but disparate
223 planning intervals. During the 2.5 s inter-trial delay in the WAIT_ITI group, only the target
224 was visible on the screen and participants were told to maintain their final hand position.

225 Experiment 3 included a single group of participants who were asked to report their
226 aiming direction prior to movement initiation (AIM group, N = 18); (Bond & Taylor, 2015,
227 McDougle et al., 2015, Taylor et al., 2014). The participants in this group saw a numbered ring
228 of visual landmarks. The numbers were arranged at 5.63-degree intervals, with the current
229 target positioned at the “0” position. Clockwise, the numbers became larger, and
230 counterclockwise the numbers became smaller (up to 32, -32, respectively), forming a circle
231 20 cm in diameter. Participants were instructed to verbally report the number they were aiming
232 their reach at before moving (see (Taylor et al., 2014) for further information on this task).

233 Verbal reports were manually registered by the experimenter on each reporting trial.

234

235 **Data Analysis**

236 Position of the stylus on the tablet surface was sampled at 130 Hz and each trial was
237 separately low-pass filtered (fourth-order Butterworth, 10 Hz) using Matlab's *filtfilt* command,
238 and then numerically differentiated. Tangential velocity was calculated as the Euclidean of x-
239 and y-velocity vectors. Behavior was analyzed in terms of two parameters: reaction time and
240 endpoint error. Reaction time (RT) was calculated as the interval between target presentation
241 and movement onset, which was defined when tangential velocity exceeded 30 mm/s for at
242 least 5 frames (38.5 ms). Endpoint error was calculated as the angular difference between the
243 vector connecting the start circle and the target, and the vector connecting the start circle and
244 the terminal hand position. Endpoint errors were calculated for both training trials and the
245 aftereffect trials. The outcome variable of the explicit perceptual judgement test was calculated
246 as the angular difference between the participant-specified line orientation on the screen and
247 the vector connecting the start and target positions.

248 For each block of training trials and for the posttest, medians were computed for each
249 participant following screening for outliers. Movements whose endpoint error fell outside three
250 standard deviations of the participants' individual mean endpoint error in that phase were
251 considered outliers and removed (1.4% of all trials). To compare different levels of asymptote,
252 the last five blocks of the training phase were median averaged and compared between groups
253 using a two-sample Wilcoxon's rank-sum test. To interpret the effect size, Pearson's rho and
254 its 95-percent confidence interval was calculated. Statistical analyses were done in Matlab
255 (R2017b) and R (version 3.5.1, <http://www.R-project.org/>). All results are based on median
256 parametric tests

257 Results

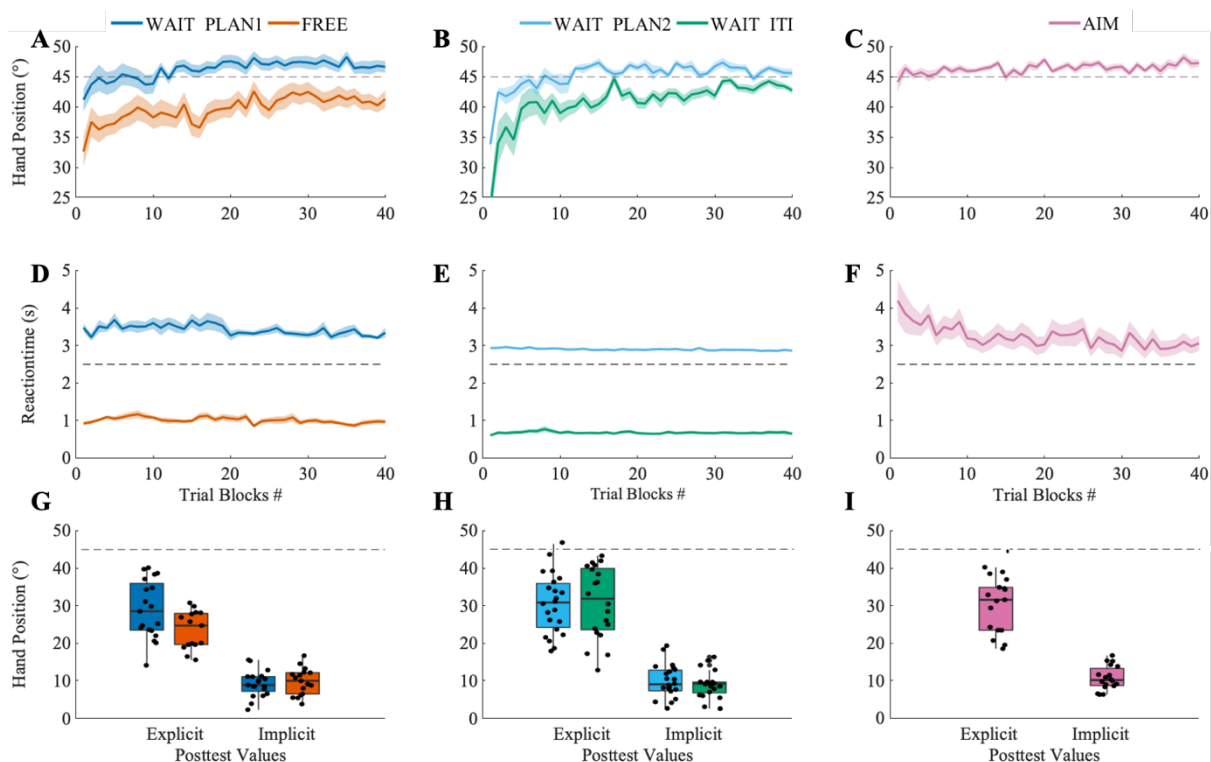


Figure 2 Mean hand direction (panels A-C) and mean reaction times (panels D-F) during practice plotted separately by experiments and groups. Panel G-I show the median hand direction during explicit and implicit posttests, separately and the individual data from single participants. The horizontal dashed 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 standard deviation of the mean.

258 Experiment 1

259 Experiment 1 tested the speed-accuracy hypothesis by artificially prolonging
 260 movement planning time. To do so, we compared two groups. The FREE group could freely
 261 initiate their movement, representing a “standard” adaptation experiment. The WAIT_PLAN1
 262 group was required to withhold movement initiation until hearing a “go”-signal 2.5 s after
 263 target onset. As shown in Figure 2A, the FREE group displayed the typical incomplete
 264 asymptote, whereas the WAIT_PLAN1 group achieved a greater asymptote
 265 ($\text{mean}_{\text{WAIT_PLAN1}} = 46.66$, $\text{sd}_{\text{WAIT_Plan1}} = 5.85$, $\text{mean}_{\text{FREE}} = 41.15$, $\text{sd}_{\text{FREE}} = 8.28$; $V = 244$, $p =$
 266 0.001). Hand directions late during practice were significantly less than 45° in the FREE group
 267 ($V = 32.5$, $p = 0.018$, $r = -0.61$, $95\% \text{ CI} = [-0.84, -0.21]$), while the WAIT_PLAN1 group did
 268 not differ significantly from 45° ($V = 108$, $p = 0.62$, $r = 0.12$, $95\% \text{ CI} = [-0.33, 0.53]$).

269 In the explicit judgment test (Figure 2G), the FREE group estimated the rotation to be
270 significantly smaller relative to the WAIT_PLAN1 group ($\text{mean}_{\text{FREE}} = 24.78^\circ$, $\text{sd}_{\text{FREE}} = 5.45^\circ$,
271 $\text{mean}_{\text{WAIT_PLAN1}} = 30.65^\circ$, $\text{sd}_{\text{WAIT_PLAN1}} = 8.33^\circ$; $V = 81.5$, $p = 0.036$, $r = -0.36$, 95% CI = [-
272 0.62, -0.01]). Implicit aftereffects (Figure 2G) did not differ significantly between the groups
273 ($\text{mean}_{\text{FREE}} = 9.99^\circ$, $\text{sd}_{\text{FREE}} = 3.81^\circ$, $\text{mean}_{\text{WAIT_PLAN1}} = 9.35^\circ$, $\text{sd}_{\text{WAIT_PLAN1}} = 3.67^\circ$; $V = 179$,
274 $p = 0.59$, $r = 0.09$, 95% CI = [-0.24, 0.39]).

275

276 Experiment 2

277 Experiment 1 showed that forcing participants to prolong their planning time before
278 movement onset on each trial led to an increase in asymptotic learning. While this observation
279 is consistent with our speed-accuracy trade-off hypothesis, the WAIT_PLAN1 group also
280 exhibited significantly larger amounts of explicit knowledge of the rotation, raising the
281 possibility that this group shows complete asymptote simply because of larger amounts of
282 accumulated explicit knowledge during training. To test this, in experiment 2 we manipulated
283 when the additional waiting time occurred within a trial. If it was a matter of simply building
284 a more elaborate representation of the perturbation by raising awareness and thus accumulating
285 more explicit knowledge of the rotation, then additional processing time between movements
286 should suffice to facilitate complete asymptotic learning. If, on the other hand, the pre-
287 movement planning period was crucial, one would expect that adding time to the interval
288 between the appearance of the target and the signal to initiate the movement would lead to
289 better performance than adding time to the post-feedback interval, i.e. the time interval between
290 the disappearance of terminal endpoint feedback and the onset of the next target. Experiment
291 2 tested this by contrasting asymptotic learning in a second group that had to wait for 2.5 s
292 during movement planning (WAIT_PLAN2; replication of WAIT_PLAN1) with a group that
293 had to wait for 2.5 s after feedback presentation before the next trial started (WAIT_ITI). In

294 line with our speed-accuracy-hypothesis, inserting waiting time into the planning phase led to
295 an asymptote not significantly different from 45° ($V = 235$, $p = 0.28$, $r = 0.25$, 95% CI = [-0.18,
296 0.66]) whereas inserting the waiting time into the intertrial interval lead to an asymptote
297 significantly less than 45° ($V = 63$, $p = 0.019$, $r = -0.44$, 95% CI = [-0.75, -0.05]). Those two
298 asymptotes were significantly different from each other ($\text{mean}_{\text{WAIT_PLAN2}} = 46.33$,
299 $\text{sd}_{\text{WAIT_PLAN2}} = 3.99$; $\text{mean}_{\text{WAIT_ITI}} = 43.96$, $\text{sd}_{\text{WAIT_ITI}} = 3.01$; $W = 311$, $p = 0.011$, $r = -0.34$,
300 95% CI = [-0.59, -0.05]) (Figure 2B).

301 Importantly, for explicit knowledge (Figure 2H), the temporal locus of the additional
302 waiting time did not have a significant effect: Both groups appeared to accumulate equivalent
303 amounts of explicit knowledge ($\text{mean}_{\text{WAIT_ITI}} = 30.53^\circ$, $\text{sd}_{\text{WAIT_ITI}} = 8.57^\circ$,
304 $\text{mean}_{\text{WAIT_PLAN2}} = 30.88^\circ$, $\text{sd}_{\text{WAIT_PLAN2}} = 10.21^\circ$; $W = 209$, $p = 0.79$, $r = -0.04$, 95% CI = [-
305 0.36, 0.25]), but showed greater explicit estimations than the FREE group in experiment 1,
306 whose trial structure did not contain any additional waiting interval (FREE ~ WAIT_PLAN2:
307 $W = 85$, $p = 0.031$, $r = -0.37$, 95% CI = [-0.63, -0.06]; FREE ~ WAIT_ITI: $W = 93$, $p = 0.027$,
308 $r = -0.37$, 95% CI = [-0.63, -0.08]). As for implicit aftereffects, both groups in experiment 2
309 achieved similar results ($\text{mean}_{\text{WAIT_ITI}} = 8.45^\circ$, $\text{sd}_{\text{WAIT_ITI}} = 4.77^\circ$, $\text{mean}_{\text{WAIT_PLAN2}} = 7.63^\circ$,
310 $\text{sd}_{\text{WAIT_PLAN2}} = 3.87^\circ$; $W = 214$, $p = 0.89$, $r = -0.02$, 95% CI = [-0.34, 0.36]).

311

312 Experiment 3

313 In the last experiment, we sought to account for the possibility that it is not time per se,
314 but the increased participation of explicit processes that raises the level of asymptote. We thus
315 instructed participants to verbally report their movement aim prior to movement execution
316 trial-by-trial (Taylor et al., 2014), potentially priming the explicit component of adaptation. We
317 reasoned that this procedure serves as an opportunity to replicate our findings in a procedure
318 that requires active explicit engagement during the planning interval. Compensation for the

319 rotation reached asymptote around 46.63° ($sd = 4.12^\circ$), which was significantly larger than 45°
320 ($V = 125$, $p = 0.045$, $r = 0.41$, $95\% CI = [-0.08, 0.75]$), suggesting that adaptation at asymptote
321 was complete and, in fact, overcompensated for the rotation (Figure 2C).

322 Explicit judgements of required compensation (mean = 28.32, $sd = 10.95$) (Figure 2I)
323 were significantly less than 45° ($V = 0$, $p < 0.0002$, $r = -0.88$, $95\% CI = [-0.88, -0.87]$) but
324 significantly greater than 0° ($V = 170$, $p < 0.0002$, $r = 0.87$, $95\% CI = [0.82, 0.88]$). Implicit
325 aftereffects (mean = 9.38, $sd = 3.4$) were also significantly different from both 0° and 45°
326 ($V = 171$, $p < 0.0001$, $V = 0$, $p < 0.0001$, $r = -0.87$, $95\% CI = [-0.88, -0.88]$, $r = 0.87$,
327 $95\% CI = [0.87, 0.87]$, respectively). If we assume that the explicit and implicit components
328 are the two main elements in a fully additive model that generates adaptive behavior, the
329 implicit component can be calculated by subtracting the hand position from the aim report
330 (Figure 2L). Comparing those values to the posttest values, we do not find a significant
331 difference, neither in explicit nor in the implicit component ($W = 123$, $p = 0.22$; $W = 129$,
332 $p = 0.31$, respectively).

333 To test whether the reporting task influenced the outcome of the explicit judgement
334 tests, we compared the posttest values between the AIM group and those of the other groups
335 in experiments 1 and 2. There was a significant difference in the explicit judgements between
336 the AIM group and the FREE group from experiment 1 ($W = 197.5$, $p = 0.025$, $r = 0.39$,
337 $95\% CI = [0.05, 0.6]$) but none between the WAIT_PLAN and AIM ($W = 160.5$, $p = 0.76$, $r = -$
338 0.05 , $95\% CI = [-0.36, 0.27]$). Across the AIM group and WAIT_PLAN2 and WAIT_ITI
339 groups in experiment 2, there were no differences in the explicit judgement tests ($W = 160$,
340 $p = 0.57$, $r = -0.09$, $95\% CI = [-0.39, 0.22]$; $W = 190.5$, $p = 0.85$, $r = -0.03$, $95\% CI = [-0.34$,
341 $0.28]$). Similar results were observed for the implicit aftereffects: Neither the FREE group, the
342 WAIT_PLAN1 group from experiment 1, nor the WAIT_PLAN2 and WAIT_ITI groups had
343 significantly different aftereffects relative to the AIM group ($W = 140.5$, $p = 0.69$, $r = -0.07$,

344 95% CI = [-0.38, 0.28]; $W = 167.5$, $p = 0.93$, $r = -0.01$, 95% CI = [-0.35, 0.29]; $W = 227.5$,
345 $p = 0.08$, $r = 0.19$, 95% CI = [-0.13, 0.45]; $W = 265.5$, $p = 0.05$, $r = 0.25$, 95% CI = [-0.07,
346 0.54], respectively). These results suggest that experimentally querying the explicit process of
347 adaptation does not qualitatively alter the explicit/implicit learning balance but does act to
348 improve the adaptation asymptote by slowing down planning.

349

350 Discussion

351 This study was designed to investigate whether previously reported findings of
352 incomplete asymptotic visuomotor learning may be reframed, at least in part, as an instantiation
353 of a ubiquitous canonical computation in human information processing: the tradeoff between
354 the speed and accuracy of actions. In line with this hypothesis, artificially prolonging the
355 waiting period prior to the onset of a goal-directed movement elevated asymptotic learning and
356 appeared to eliminate residual errors. This benefit was specific to prolonging motor planning,
357 the time interval between the appearance of the visual target and the go-signal. Prolonging the
358 interval between visual feedback and the start of the next trial (the intertrial interval) did not
359 provide the same benefit to learning. Our results provide support for a parsimonious
360 explanation that time-consuming planning processes are potentially the main driver of
361 incomplete asymptotic learning.

362 Why did hasty planning result in consistent undershooting rather than both
363 undershooting and overshooting (i.e., greater movement variability)? We propose that
364 parametric mental computations in visuomotor rotation tasks could explain the undershooting
365 phenomenon: In visuomotor rotation tasks, participants' reaction times increase linearly with
366 the magnitude of the imposed rotation (Georgopoulos & Massey, 1987, McDougle & Taylor,
367 2019), reflecting a putative mental rotation process (Shepard & Metzler, 1971). Thus, in our
368 framework, undershooting is the consequence of participants not taking the time needed to

369 fully complete a mental rotation of their planned reach trajectory. This view is further supported
370 by the results of our third experiment, in which emphasizing the application of explicit aiming
371 strategies prior to movement initiation led to qualitatively similar asymptotic learning as in the
372 groups with prolonged planning intervals. Note that delaying movement initiation did not only
373 cause full compensation, but induced overcompensation suggesting that implicit processes
374 superimposed onto an accurate explicit rotation strategy may have caused reach angles to drift,
375 gradually adapting the hand further in the direction of compensation (cf. Mazzoni, 2006).

376 The idea of a speed accuracy tradeoff prematurely interrupting putative mental rotation
377 processes during motor planning also provides an explanation for previously observed age-
378 related differences in visuomotor learning. Hegele & Heuer (2013) used explicit instructions
379 and cognitive pretraining prior to learning a novel visuomotor rotation to boost explicit
380 knowledge of the transformation. Older adults with full explicit knowledge of the
381 transformation turned out to be less efficient in applying it for strategic corrections of their
382 aiming movements. This age-related difference with respect to the behavioral exploitation of
383 explicit knowledge became manifest only when participants had almost perfect explicit
384 knowledge, but not when they had only poor explicit knowledge and thus a small range of
385 associated strategic adjustments at different levels of exploitation. Given the present results,
386 one could speculate that the reduced exploitation of explicit knowledge for strategic corrections
387 in older participants is due to a combination of age-related slowing in mental rotation and the
388 premature termination of (slowed) mentally rotating their aiming direction during motor
389 planning.

390 Traditionally, the incomplete asymptote phenomenon was explained by state-space
391 models of adaptation (Cheng & Sabes, 2006, Smith et al., 2006, Thoroughman & Shadmehr,
392 2000), according to which the adapted state reaches an equilibrium between learning from error
393 and decaying towards baseline in each trial. As subsequent studies indicated that this model

394 alone is insufficient for explaining incomplete asymptotic behavior, alternatives were
395 proposed: For example, Vaswani and colleagues (Vaswani et al., 2015) suggested that a process
396 that learns from spatial error feedback suppresses other mechanisms that could drive full
397 compensation (Shmuelof et al., 2012). In our study, participants in all groups received similar
398 spatial error feedback. Thus, a potential suppression should have affected all groups equally,
399 suggesting that spatial error feedback suppressing other learning mechanisms would not be
400 sufficient to explain the modulations in asymptote we observed.

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

414 Moreover, we also note that consistent undershooting relative to the perturbation, as
415 observed here and in previous studies, is critically not seen in experimental paradigms designed
416 to isolate the implicit component of visuomotor adaptation (Morehead et al., 2017)– indeed,
417 even when rotational perturbation are as small as $\sim 1.75^\circ$, implicit adaptation appears to
418 asymptote around $\sim 15^\circ$ (Kim et al., 2018). These results suggest that claims of an incomplete

419 asymptote within, specifically, the implicit adaptation mechanism must define the asymptote
420 relative to an intrinsic capacity of the system, rather than the size of the visual error. Thus, it
421 may be that incomplete compensation relative to the visual error (i.e., task error) mainly
422 involves cognitive processes like speed-accuracy tradeoffs, as argued here, but incomplete
423 asymptotic performance of the implicit system relative to its own capacity (i.e., responses to
424 sensory prediction error) requires a separate explanation.

425 Recent accounts have framed motor planning as a time-consuming optimization process
426 from which a reduction in movement accuracy arises naturally when constraints are imposed
427 (Al Borno et al., 2019). Our findings suggest that similar principles apply when one is
428 intentionally choosing to perform a movement in another direction than the one implied by the
429 target presented, and that learners naturally constrain their planning time even in seemingly
430 unconstrained conditions. Haith and colleagues (Haith et al., 2016) recently showed that
431 movement preparation and initiation are independent i.e. that, instead of complete preparation
432 triggering movement initiation, humans appear to determine a time for movement initiation
433 based on when it expects planning to be completed. This view naturally implies the possibility
434 to initiate a movement that has not been sufficiently prepared. The planning time chosen may
435 therefore trade off the accuracy it expects planning to achieve within a given time and an
436 urgency to move on (e.g. fueled by a desire to increase reward rate; Churchland et al., 2008,
437 Cisek et al., 2009, Thura et al., , Thura & Cisek, 2017).

438 Many of the common explanations for incomplete asymptote outlined above imply that
439 it is a fundamental property of learning. Psychology and kinesiology traditionally distinguish
440 learning effects from performance effects, where underlying knowledge can be identical in
441 different cases, but retrieval processes in specific test conditions can lead to different
442 performance profiles (Magill & Anderson, 2017, Schmidt & Lee, 2011). Whereas our
443 experiments were not specifically designed to distinguish learning from performance effects,

444 our findings suggest that both may contribute to incomplete asymptote in adaptation.
445 Specifically, explicit knowledge of the rotation magnitude was increased with added planning
446 time in experiment 1, suggesting that some of the benefit of longer planning times may come
447 about by learners honing their explicit knowledge. However, the observation that explicit
448 knowledge was similarly increased regardless of whether additional time was added at the
449 beginning or end of a trial in experiment 2 indicates that this learning effect may be a non-
450 specific consequence of longer ITIs, and that the remaining increase in asymptote is a
451 performance effect. A recent paper analyzing preparatory neural states in rhesus monkeys
452 performing visuomotor learning tasks also found that longer preparation times not only yielded
453 smaller variance on the current trial, but also smaller errors on the subsequent trial, supporting
454 a learning effect (Vyas et al., 2020). Future research could attempt to better delineate learning
455 from performance effects in human motor adaptation.

456 Lastly, we do not claim that other mechanisms affecting learning do not contribute to
457 asymptotic behavior (Albert et al., 2019), or that a state-space model with gradual decay
458 towards zero is generally invalid (Brennan & Smith, 2015). What we suggest is that one
459 potentially major aspect determining the magnitude of asymptotic errors is a speed accuracy
460 trade-off. Since this decision process is likely to be relevant across a broader range of motor
461 tasks, we speculate that our results extend beyond motor adaptation and that simple
462 interventions, like explicitly prolonging reaction times to allow for complete planning, could
463 improve asymptotic performance in a range of motor learning tasks.

464

465 **Author Contribution**

466 LL, JM, MH, SDM and RS conceived and designed research; LL collected data; LL,
467 JM, MH, SDM and RS analyzed data; LL, JM, MH, SDM and RS interpreted results of
468 experiments; LL prepared figures; LL drafted manuscript; LL, JM, MH, SDM and RS edited

469 and revised manuscript; LL, JM, MH, SDM and RS approved final version of manuscript

470 References

- 471 Al Borno, M., Vyas, S., Shenoy, K. V., & Delp, S. L. (2019). High-fidelity Musculoskeletal
472 Modeling Reveals a Motor Planning Contribution to the Speed-Accuracy Tradeoff.
473 <http://biorxiv.org/lookup/doi/10.1101/804088>
- 474 Albert, S. T., Jang, J., Sheahan, H., Teunissen, L., Vandevoorde, K., & Shadmehr, R. (2019).
475 An implicit memory of errors limits human sensorimotor adaptation.
476 <http://biorxiv.org/lookup/doi/10.1101/868406>
- 477 Berthelot, G., Sedeaud, A., Marck, A., Antero-Jacquemin, J., Schipman, J., Saulière, G.,
478 Marc, A., Desgorces, F.-D., & Toussaint, J.-F. (2015). Has Athletic Performance
479 Reached its Peak. *Sports Medicine*
480 *Sports Med*, 45(9), 1263-1271. <https://doi.org/10.1007/s40279-015-0347-2>
- 481 Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a
482 visuomotor adaptation task. *J Neurophysiol*, 113(10), 3836-3849.
483 <https://doi.org/10.1152/jn.00009.2015>
- 484 Brennan, A. E., & Smith, M. A. (2015). The Decay of Motor Memories Is Independent of
485 Context Change Detection. *PLOS Computational Biology*
486 *PLoS Comput Biol*, 11(6), e1004278. <https://doi.org/10.1371/journal.pcbi.1004278>
- 487 Carandini, M., & Heeger, D. J. (2011). Normalization as a canonical neural computation.
488 *Nature reviews. Neuroscience*
489 *Nat Rev Neurosci*, 13(1), 51-62. <https://doi.org/10.1038/nrn3136>
- 490 Cerritelli, B., Maruff, P., Wilson, P., & Currie, J. (2000). The effect of an external load on the
491 force and timing components of mentally represented actions. *Behavioural Brain*
492 *Research*, 108(1), 91-96. [https://doi.org/10.1016/S0166-4328\(99\)00138-2](https://doi.org/10.1016/S0166-4328(99)00138-2)
- 493 Chen, H.-H., Liu, Y.-T., Mayer-Kress, G., & Newell, K. M. (2005). Learning the pedalo
494 locomotion task. *Journal of Motor Behavior*
495 *J Mot Behav*, 37(3), 247-256. <https://doi.org/10.3200/JMBR.37.3.247-256>
- 496 Cheng, S., & Sabes, P. N. (2006). Modeling Sensorimotor Learning with Linear Dynamical
497 Systems. *Neural computation*
498 *Neural Comput*, 18(4), 760-793. <https://doi.org/10.1162/089976606775774651>
- 499 Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for
500 accuracy. *Nature*, 424(6947), 388. <https://doi.org/10.1038/424388a>
- 501 Churchland, A. K., Kiani, R., & Shadlen, M. N. (2008). Decision-making with multiple
502 alternatives. *Nature Neuroscience*
503 *Nat Neurosci*, 11(6), 693-702. <https://doi.org/10.1038/nn.2123>
- 504 Cisek, P., Puskas, G. A., & El-Murr, S. (2009). Decisions in Changing Conditions: The
505 Urgency-Gating Model. *Journal of Neuroscience*, 29(37), 11560-11571.
506 <https://doi.org/10.1523/JNEUROSCI.1844-09.2009>
- 507 Crossman, E. R. F. W. (1959). A theory of the acquisition of speed-skill. *Ergonomics*, 2, 153-
508 166. <https://doi.org/10.1080/00140135908930419>
- 509 Cunningham, H. A. Aiming Error Under Transformed Spatial Mappings Suggests a Structure
510 for Visual-Motor Maps., 14.
- 511 Decety, J., & Jeannerod, M. (1996). Mentally simulated movements in virtual reality: does
512 Fitts's law hold in motor imagery. *Behavioural Brain Research*, 8.
- 513 DiCarlo, J. J., & Johnson, K. O. (2000). Spatial and Temporal Structure of Receptive Fields
514 in Primate Somatosensory Area 3b: Effects of Stimulus Scanning Direction and
515 Orientation. *The Journal of Neuroscience*

- 516 *J. Neurosci.*, 20(1), 495-510. <https://doi.org/10.1523/JNEUROSCI.20-01-00495.2000>
- 517 Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between
518 reaction time and reach errors during visuomotor adaptation. *Behavioural Brain*
519 *Research*, 219(1), 8-14. <https://doi.org/10.1016/j.bbr.2010.11.060>
- 520 Georgopoulos, A. P., & Massey, J. T. (1987). Cognitive spatial-motor processes. 1. The
521 making of movements at various angles from a stimulus direction. *Experimental Brain*
522 *Research*
523 *Exp Brain Res*, 65(2), 361-370. <https://doi.org/10.1007/BF00236309>
- 524 Grosjean, M., Shiffrar, M., & Knoblich, G. (2007). Fitts's Law Holds for Action Perception.
525 *Psychological Science*
526 *Psychol Sci*, 18(2), 95-99. <https://doi.org/10.1111/j.1467-9280.2007.01854.x>
- 527 Hacker, M. J. (1980). Speed and accuracy of recency judgments for events in short-term
528 memory. *Journal of Experimental Psychology: Human Learning & Memory*, 6, 651-
529 675. <https://doi.org/10.1037/0278-7393.6.6.651>
- 530 Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The Influence of Movement
531 Preparation Time on the Expression of Visuomotor Learning and Savings. *Journal of*
532 *Neuroscience*, 35(13), 5109-5117. <https://doi.org/10.1523/JNEUROSCI.3869-14.2015>
- 533 Haith, A. M., Pakpoor, J., & Krakauer, J. W. (2016). Independence of Movement Preparation
534 and Movement Initiation. *Journal of Neuroscience*, 36(10), 3007-3015.
535 <https://doi.org/10.1523/JNEUROSCI.3245-15.2016>
- 536 Hegele, M., & Heuer, H. (2010). Implicit and explicit components of dual adaptation to
537 visuomotor rotations. *Consciousness and Cognition*, 19(4), 906-917.
538 <https://doi.org/10.1016/j.concog.2010.05.005>
- 539 Heitz, R. P. (2014). The speed-accuracy tradeoff: history, physiology, methodology, and
540 behavior. *Frontiers in Neuroscience*
541 *Front Neurosci*, 8. <https://doi.org/10.3389/fnins.2014.00150>
- 542 Heitz, R. P., & Schall, J. D. (2012). Neural mechanisms of speed-accuracy tradeoff. *Neuron*,
543 76(3), 616-628. <https://doi.org/10.1016/j.neuron.2012.08.030>
- 544 Heuer, H., & Hegele, M. (2008). Adaptation to visuomotor rotations in younger and older
545 adults. *Psychology and Aging*, 23(1), 190-202. <https://doi.org/10.1037/0882-7974.23.1.190>
- 546
547 Heuer, H., & Hegele, M. (2015). Explicit and implicit components of visuo-motor adaptation:
548 An analysis of individual differences. *Consciousness and Cognition*, 33, 156-169.
549 <https://doi.org/10.1016/j.concog.2014.12.013>
- 550 Hinder, M. R., Riek, S., Tresilian, J. R., de Rugy, A., & Carson, R. G. (2010). Real-time error
551 detection but not error correction drives automatic visuomotor adaptation. *Experimental*
552 *Brain Research*
553 *Exp Brain Res*, 201(2), 191-207. <https://doi.org/10.1007/s00221-009-2025-9>
- 554 Holland, P., Codol, O., & Galea, J. M. (2018). Contribution of explicit processes to
555 reinforcement-based motor learning. *Journal of Neurophysiology*, 119(6), 2241-2255.
556 <https://doi.org/10.1152/jn.00901.2017>
- 557 Huberdeau, D. M., Haith, A. M., & Krakauer, J. W. (2015). Formation of a long-term
558 memory for visuomotor adaptation following only a few trials of practice. *Journal of*
559 *Neurophysiology*, 114(2), 969-977. <https://doi.org/10.1152/jn.00369.2015>
- 560 Ings, T. C., & Chittka, L. (2008). Speed-accuracy tradeoffs and false alarms in bee responses
561 to cryptic predators. *Current biology: CB*
562 *Curr. Biol.*, 18(19), 1520-1524. <https://doi.org/10.1016/j.cub.2008.07.074>
- 563 Kim, H. E., Morehead, J. R., Parvin, D. E., Moazzezi, R., & Ivry, R. B. (2018). Invariant
564 errors reveal limitations in motor correction rather than constraints on error sensitivity.
565 *Commun Biol*, 1, 19. <https://doi.org/10.1038/s42003-018-0021-y>

- 566 Kooij, K. V. D., Overvliet, K. E., & Smeets, J. B. J. (2016). Temporally stable adaptation is
567 robust, incomplete and specific. *European Journal of Neuroscience*, 44(9), 2708-2715.
568 <https://doi.org/10.1111/ejn.13355>
- 569 Lackner, J. R., & Dizio, P. (1994). Rapid adaptation to Coriolis force perturbations of arm
570 trajectory. *Journal of Neurophysiology*, 72(1), 299-313.
571 <https://doi.org/10.1152/jn.1994.72.1.299>
- 572 Magill, R. A., & Anderson, D. (2017). *Motor learning and control: concepts and*
573 *applications*. McGraw-Hill Education.
- 574 Mazzoni, P. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor
575 Adaptation. *Journal of Neuroscience*, 26(14), 3642-3645.
576 <https://doi.org/10.1523/JNEUROSCI.5317-05.2006>
- 577 McDougale, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and Implicit Processes
578 Constitute the Fast and Slow Processes of Sensorimotor Learning. *Journal of*
579 *Neuroscience*, 35(26), 9568-9579. <https://doi.org/10.1523/JNEUROSCI.5061-14.2015>
- 580 McDougale, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor
581 learning. *Nature Communications*
582 *Nat Commun*, 10(1), 40. <https://doi.org/10.1038/s41467-018-07941-0>
- 583 Miller, K. D. (2016). Canonical computations of cerebral cortex. *Curr Opin Neurobiol*, 37,
584 75-84. <https://doi.org/10.1016/j.conb.2016.01.008>
- 585 Morehead, J. R., Taylor, J. A., Parvin, D. E., & Ivry, R. B. (2017). Characteristics of implicit
586 sensorimotor adaptation revealed by task-irrelevant clamped feedback. *Journal of*
587 *cognitive neuroscience*, 29(6), 1061-1074.
588 https://www.mitpressjournals.org/doi/full/10.1162/jocn_a.01108
- 589 Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. (1978). Receptive field organization of
590 complex cells in the cat's striate cortex. *The Journal of Physiology*, 283(1), 79-99.
591 <https://doi.org/10.1113/jphysiol.1978.sp012489>
- 592 Pack, C. C., & Bensmaia, S. J. (2015). Seeing and Feeling Motion: Canonical Computations
593 in Vision and Touch. *PLoS Biology*
594 *PLoS Biol*, 13(9). <https://doi.org/10.1371/journal.pbio.1002271>
- 595 Plamondon, R., & Alimi, A. M. (1997). Speed/accuracy trade-offs in target-directed
596 movements. *Behavioral and Brain Sciences*
597 *Behav Brain Sci*, 20(2), 279-303. <https://doi.org/10.1017/S0140525X97001441>
- 598 Ratcliff, R. (2002). A diffusion model account of response time and accuracy in a brightness
599 discrimination task: Fitting real data and failing to fit fake but plausible data.
600 *Psychonomic Bulletin & Review*, 9(2), 278-291. <https://doi.org/10.3758/BF03196283>
- 601 Ringach, D. L., & Malone, B. J. (2007). The Operating Point of the Cortex: Neurons as Large
602 Deviation Detectors. *Journal of Neuroscience*, 27(29), 7673-7683.
603 <https://doi.org/10.1523/JNEUROSCI.1048-07.2007>
- 604 Schmidt, R. A., & Lee, T. D. (2011). *Motor control and learning: a behavioral emphasis*.
605 Human Kinetics.
- 606 Schween, R., & Hegele, M. (2017). Feedback delay attenuates implicit but facilitates explicit
607 adjustments to a visuomotor rotation. *Neurobiology of Learning and Memory*, 140, 124-
608 133. <https://doi.org/10.1016/j.nlm.2017.02.015>
- 609 Shadmehr, R., Brashers-Krug, T., & Mussa-Ivaldi, F. Interference in Learning Internal
610 Models of Inverse Dynamics in Humans., 8.
- 611 Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*,
612 171(3972), 701-703. <https://doi.org/10.1126/science.171.3972.701>
- 613 Shmuelof, L., Huang, V. S., Haith, A. M., Delnicki, R. J., Mazzoni, P., & Krakauer, J. W.
614 (2012). Overcoming Motor “Forgetting” Through Reinforcement Of Learned Actions.

- 615 *Journal of Neuroscience*, 32(42), 14617-14621a.
616 <https://doi.org/10.1523/JNEUROSCI.2184-12.2012>
- 617 Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting Adaptive Processes with
618 Different Timescales Underlie Short-Term Motor Learning. *PLoS Biology*
619 *PLoS Biol*, 4(6), e179. <https://doi.org/10.1371/journal.pbio.0040179>
- 620 Snoddy, G. S. (1926). Learning and stability: a psychophysiological analysis of a case of
621 motor learning with clinical applications. *Journal of Applied Psychology*, 10(1), 1-36.
622 <https://doi.org/10.1037/h0075814>
- 623 Spang, K., Wischhusen, S., & Fehle, M. (2017). Limited Plasticity of Prismatic Visuomotor
624 Adaptation. *i-Perception*
625 *Iperception*, 8(2). <https://doi.org/10.1177/2041669517701458>
- 626 Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to
627 Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, 34(8), 3023-
628 3032. <https://doi.org/10.1523/JNEUROSCI.3619-13.2014>
- 629 Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive
630 combination of motor primitives. *Nature*, 407(6805), 742-747.
631 <https://doi.org/10.1038/35037588>
- 632 Thura, D., Beauregard-Racine, J., Fradet, C.-W., & Cisek, P. Decision making by urgency
633 gating: theory and experimental support. *J Neurophysiol*, 19.
- 634 Thura, D., & Cisek, P. (2017). The Basal Ganglia Do Not Select Reach Targets but Control
635 the Urgency of Commitment. *Neuron*, 95(5), 1160-1170.e5.
636 <https://doi.org/10.1016/j.neuron.2017.07.039>
- 637 van der Kooij, K., Brenner, E., van Beers, R. J., & Smeets, J. B. J. (2015). Visuomotor
638 Adaptation: How Forgetting Keeps Us Conservative. *PLoS ONE*, 10(2).
639 <https://doi.org/10.1371/journal.pone.0117901>
- 640 Vaswani, P. A., Shmuelof, L., Haith, A. M., Delnicki, R. J., Huang, V. S., Mazzoni, P.,
641 Shadmehr, R., & Krakauer, J. W. (2015). Persistent Residual Errors in Motor
642 Adaptation Tasks: Reversion to Baseline and Exploratory Escape. *Journal of*
643 *Neuroscience*, 35(17), 6969-6977. <https://doi.org/10.1523/JNEUROSCI.2656-14.2015>
- 644 Vaswani, P. A., & Shadmehr, R. (2013). Decay of Motor Memories in the Absence of Error.
645 *The Journal of Neuroscience*
646 *J Neurosci*, 33(18), 7700-7709. <https://doi.org/10.1523/JNEUROSCI.0124-13.2013>
- 647 Vyas, S., O'Shea, D. J., Ryu, S. I., & Shenoy, K. V. (2020). Causal Role of Motor
648 Preparation during Error-Driven Learning. *Neuron*, 106(2), 329-339.
649 <https://doi.org/10.1016/j.neuron.2020.01.019>
- 650 Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics.
651 *Acta Psychologica*, 41(1), 67-85. [https://doi.org/10.1016/0001-6918\(77\)90012-9](https://doi.org/10.1016/0001-6918(77)90012-9)
- 652 Wong, A. L., Haith, A. M., & Krakauer, J. W. (2015). Motor Planning. *The Neuroscientist: A*
653 *Review Journal Bringing Neurobiology, Neurology and Psychiatry*
654 *Neuroscientist*, 21(4), 385-398. <https://doi.org/10.1177/1073858414541484>
655