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Estimating the implicit component of visuomotor rotation learning by constraining movement preparation time.

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Abstract

When sensory feedback is perturbed, accurate movement is restored by a combination of implicit processes and deliberate re-aiming to strategically compensate for errors. Here, we directly compare two methods used previously to dissociate implicit from explicit learning on a trial-by-trial basis: 1) asking participants to report the direction that they aim their movements, and contrasting this with the directions of the target and the movement that they actually produce, 2) manipulating movement preparation time. By instructing participants to re-aim without a sensory perturbation, we show that re-aiming is possible even with the shortest possible preparation times, particularly when targets are narrowly distributed. Nonetheless, re-aiming is effortful and comes at the cost of increased variability, so we tested whether constraining preparation time is sufficient to suppress strategic re-aiming during adaptation to visuomotor rotation with a broad target distribution. The rate and extent of error reduction under preparation time constraints were similar to estimates of implicit learning obtained from self-report without time pressure, suggesting that participants chose not to apply a re-aiming strategy to correct visual errors under time pressure. Surprisingly, participants who reported aiming directions showed less implicit learning according to an alternative measure, obtained during trials performed without visual feedback. This suggests that the process of reporting can affect the extent or persistence of implicit learning. The data extend existing evidence that restricting preparation time can suppress explicit re-aiming, and provide an estimate of implicit visuomotor rotation learning that does not require participants to report their aiming directions.

New and Noteworthy

During sensorimotor adaptation, implicit, error-driven learning can be isolated from explicit strategy-driven re-aiming by subtracting self-reported aiming directions from movement directions, or by restricting movement preparation time. Here, we compared the two methods. Restricting preparation times did not eliminate re-aiming, but was sufficient to suppress re-aiming during adaptation with widely-distributed targets. The self-report method produced a discrepancy in implicit learning estimated by subtracting aiming directions, and implicit learning measured in no-feedback trials.

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Introduction

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When we move, perturbations to our body or the environment can elicit discrepancies between predicted and actual outcomes. We readily adapt our movements to compensate when such discrepancies are systematic, and this process is commonly termed sensorimotor adaptation. Sensorimotor adaptation was traditionally thought to occur largely via implicit mechanisms involving updating of an internal model (Wolpert et al. 1995) in order to compensate for sensory prediction errors (i.e. mismatches between predicted and observed behaviour). It has long been recognized, however, that explicit processes can influence the behavioural response to sensorimotor perturbation (e.g., Keisler and Shadmehr 2010; Mazzoni and Krakauer 2006; Redding and Wallace 1996; Uhlarik 1973). For example, if a rotation of visual feedback results in a participant noticing systematic reaching errors to one side of a target, she might deliberately aim to the opposite side of the target to compensate. One way to disentangle such strategic re-aiming from implicit learning is to require participants to report their aiming directions throughout adaptation, and then to infer implicit adaptation by subtracting verbally reported aiming directions from actual movement directions (Bond and Taylor 2015; Brudner et al. 2016; McDougle et al. 2015; Taylor et al. 2014). This method also provides a measure of explicit re-aiming, which is estimated as the difference between the reported aiming direction and the target direction. Studies using this approach suggest that explicit re-aiming dominates the rapid initial error reduction typically seen in most sensorimotor adaptation studies, but then contributes progressively less to behaviour as an implicit *remapping* between motor commands and expected sensory outcomes develops with extended exposure to perturbation.

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The capacity to decompose sensorimotor adaptation into implicit and explicit components represents an important advance in the understanding of how the brain responds to systematic discrepancies between desired and actual motor behaviour (Taylor et al. 2014). In particular, the demonstration that explicit re-aiming dominates the initial error reduction phase of sensorimotor adaptation presents challenges for those interested in assessing the rate of implicit remapping. A method of disentangling explicit and implicit processes that relies upon subject reports of aiming

81 directions may have limitations, however. Firstly, the approach requires faithful reports of
82 intended aiming directions from study participants, which may be imprecise, difficult to obtain in
83 some contexts, and time-consuming. Secondly, the instruction to report aiming directions results
84 in faster error reduction than occurs in the absence of such instructions (Taylor et al. 2014),
85 presumably because the reporting requirement alerts participants to the benefits of re-aiming to
86 achieve task success. This raises the question of whether the reporting procedure might also
87 impact implicit processes, because the reduced task errors that accompany explicit strategy use
88 might affect the rate or extent of implicit adaptation via reward or reinforcement-related
89 processes (Reichenthal et al. 2016).

90 An alternative approach to probe implicit processes in sensorimotor adaptation is to
91 suppress the expression of explicit processes. This can be done either by employing dual-task
92 paradigms to limit attentional resources that can be devoted to explicit re-aiming (Galea 2010;
93 Keisler and Shadmehr 2010; Malone and Bastian ; Taylor and Thoroughman 2007; Taylor and
94 Thoroughman 2008), or by restricting the amount of time available to prepare a movement
95 (Fernandez-Ruiz et al. 2011; Haith et al. 2015). Restricting preparation time appears to be a
96 particularly promising approach, as there is a relationship between preparation time and
97 movement accuracy even without a sensorimotor perturbation (Georgopoulos and Massey 1987b;
98 Marinovic et al. 2017). Furthermore, there is a time cost of explicitly preparing movements
99 toward locations that are offset from the physical location of a target (Georgopoulos and Massey
100 1987b). In one such approach, Haith et al. (2015) carefully controlled movement preparation
101 time to dissociate learning resulting from explicit and implicit processes during adaptation to a
102 visuomotor rotation. They showed significantly slower error reduction when they restricted
103 movement preparation time by suddenly shifting target position in 20% of trials approximately
104 300ms before the imperative to move (Haith et al. 2015). The data suggest that explicit re-aiming
105 was suppressed by the preparation time constraint. The approach also has the benefit that it
106 provides a within-subject contrast between presumed implicit remapping (from errors on the
107 short preparation trials) and combined implicit and explicit adaptation (from errors on the long
108 preparation trials). However, some aspects of this approach merit further consideration. First, it
109 is unclear whether 300 ms is sufficiently brief to prevent entirely strategy use during adaptation.
110 Second, the switch in target location might introduce an additional processing demand, and may

111 not be desirable in some experimental designs. More generally, it is unknown whether assays of
112 implicit sensorimotor adaptation obtained via preparation time manipulation differ from those
113 obtained via reporting procedures. Here, we compared implicit learning assayed by restricting
114 movement preparation time to implicit learning assayed via reporting procedures.

115 The first aim of the study was to determine the extent to which the capacity to explicitly
116 re-aim is suppressed by reducing the amount of time available to prepare movement. We asked
117 people to explicitly re-aim 30° clockwise or counter-clockwise to targets, under increasing time
118 pressure, but in the absence of a perturbation. We expected that there would be a minimum time
119 for movement preparation below which people would be unable to aim accurately to one side of
120 a target. However, we also wondered whether advance knowledge of the approximate location of
121 potential targets would influence the capacity to re-aim. To this end, voluntary re-aiming was
122 performed either to a narrow (0-35° range) (Experiment 1A) or uniform 360° distribution of
123 target directions (Experiment 1B). We predicted that people would be able to re-aim with shorter
124 preparation times when targets were distributed narrowly. We found that participants could re-
125 aim by 30° even at the shortest preparation times tested with a narrow target distribution, but at
126 the expense of increased movement variability. For a broad 360° target distribution, participants
127 could at least partially re-aim whenever movement time was sufficient to produce directionally
128 tuned movements (i.e., as opposed to randomly directed movements), but at more dramatic cost
129 to movement variability. Thus, the motor system is capable of systematic re-aiming to one side
130 of a target irrespective of time constraints. However, we noted that participants found re-aiming
131 at short preparation times extremely effortful. Given this, the purpose of Experiment 2 was to
132 determine whether people would choose to re-aim under time pressure in order to improve
133 performance on a visuomotor rotation task.

134 In Experiment 2, we compared adaptation to a 30° visuomotor rotation with a 360° target
135 distribution under three alternative conditions. Separate groups of participants were either
136 allowed: (1) a short time to prepare movement, (2) a longer time to prepare movement, but also
137 asked to report their aiming direction, or (3) a longer time to prepare movement, without
138 reporting aiming direction. If people chose not to re-aim reaches to counter the visuomotor
139 rotation when preparation time was constrained, then we expected the rate of error reduction in
140 this condition to resemble the rate of implicit adaptation estimated from the self-report procedure.

141 We were also interested in the effects of the three different conditions on an alternative measure
142 of implicit adaptation obtained from reaches made in the absence of visual feedback. We found
143 that the rate and extent of error compensation with short preparation time closely matched
144 implicit error compensation, as estimated from subtracting movement directions from self-
145 reported aiming directions. This suggests that restriction of preparation time can suppress
146 explicit re-aiming, and provide an estimate of implicit learning that does not require participants
147 to report their aiming directions. Surprisingly, in the post-perturbation no-feedback trials, less
148 implicit learning was shown in participants who reported aiming directions than participants who
149 did not report aiming directions. This raises the possibility that the reporting procedure itself
150 increased engagement of explicit learning, which inadvertently reduced engagement of implicit
151 learning.

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Method

154 Participants

155 A total of 74 participants completed this study (Experiment 1A: n=14, mean age = 19.93,
156 range = 17-42 years, 12 females, 2 left-handed; Experiment 1B: n=14, mean age = 19.07, SD =
157 3.53, range = 17-31 years, 11 females, 2 left-handed; Experiment 2: n=36, 30 females, 2 left
158 handed, mean age =19.85, SD = 1.82). In Experiment 2, 36 people were initially assigned either
159 to a short preparation time condition or a long preparation time condition in which they had to
160 report aiming direction. Subsequently, in order to test whether differences in post-perturbation
161 estimates of implicit learning were due to the preparation time conditions or the reporting
162 procedure, a further 10 people were recruited to a long preparation time condition without
163 reporting (mean age 21, SD=4.7, range=18 to 34 years, all right-handed). For all experiments,
164 the participants were randomly assigned either to clockwise or counter-clockwise visuomotor
165 rotation conditions in equal proportions. All participants were naïve to visuomotor rotation and
166 force-field adaptation tasks. This study was approved by the Human Research Ethics Committee
167 at The University of Queensland. All participants provided written informed consent.

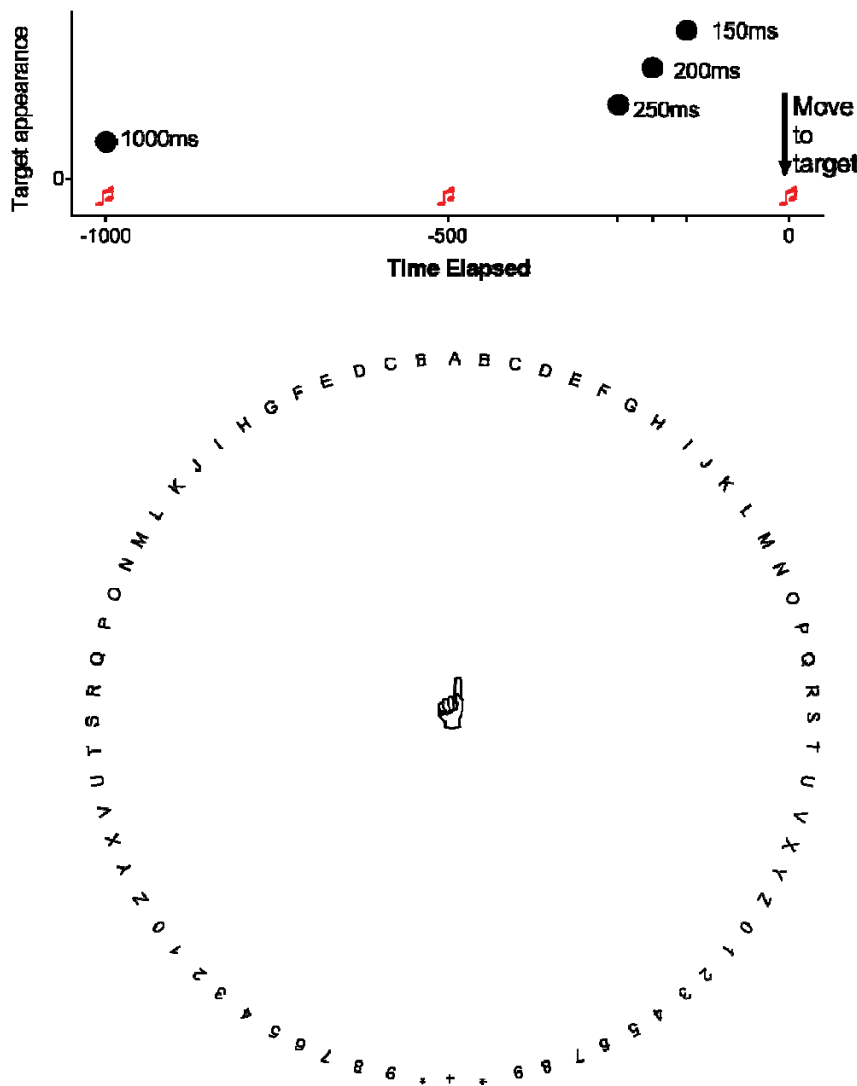
168 **Apparatus and General Trial Structure**

169 Participants completed the task using the vBOT planar robotic manipulandum, which has
170 a low-mass, two-link carbon fibre arm and measures position with optical encoders sampled at
171 1,000 Hz (Howard et al. 2009). Participants were seated on a height-adjustable chair at their ideal
172 height for viewing the screen for the duration of the experiment. Visual feedback was presented
173 on a horizontal plane on a 27" LCD computer monitor (ASUS, VG278H, set at 60Hz refresh rate)
174 mounted above the vBOT and projected to the subject via a mirror in a darkened room,
175 preventing direct vision of their hand. The mirror allowed the visual feedback of the target (a 0.5
176 cm radius circle), the starting location (a 0.5 cm radius circle), and hand cursor (0.25 cm radius)
177 to be presented in the plane of movement, with a black background. The start circle was aligned
178 10cm to the right of the participant's mid-sagittal plane at approximately mid-sternum level.

179 **General Trial Structure**

180 Participants made centre-out reaching movements by moving the robot arm from the start
181 circle to the target. Targets appeared in random order at one of eight locations 9cm away from
182 the start circle—target locations were clustered either in a small range (Experiment 1A:
183 17.5°,12.5°,7.5°,2.5°,-2.5°,-7.5°,-12.5°,-17.5° from straight ahead), or distributed uniformly
184 throughout 360° (Experiment 1B & Experiment 2: 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°).
185 At the start of each trial, the central start circle was displayed. If participants failed to move the
186 hand to within 1cm of the start circle after 1 second, the robotic manipulandum passively moved
187 the participant's hand to the start circle (using a simulated 2 dimensional spring with the spring
188 constant magnitude increasing linearly over time). A trial was initiated when the cursor remained
189 within the home location at a speed below 0.1 cm/s for 200 ms. We used a timed-response
190 paradigm (Ghez et al. 1989; Haith et al. 2015; Marinovic et al. 2014; Marinovic et al. 2008;
191 Schouten and Bekker 1967) to manipulate movement preparation time. Across all conditions, a
192 sequence of three tones spaced 500 ms apart was presented at a clearly audible volume via
193 external speakers. Participants were instructed to time the onset of their movements with the
194 onset of the third tone (see Figure 1). They were instructed not to stop on the target, but to slice
195 through it. Movement initiation was defined online as when hand speed exceeded 2cm/s. Targets
196 appeared at 1000ms, 250ms, 200ms, 150ms, or 100ms, minus a display latency (27.6 ± 1.8 ms),
197 prior to the third tone. Thus target direction information became available 972.4, 222.4, 172.4,

198 122.4, or 72.4 ms before the desired initiation time. When movements were initiated 50 ms later
 199 than the third tone, the trial was aborted: the screen was blanked and a “Too Late” on-screen
 200 error signal appeared. Similarly, when movements were initiated more than 100 ms before the
 201 desired initiation time, the trial was aborted: the screen was blanked and a “Too Soon” on-screen
 202 error signal appeared. No visual feedback about movements was available when trials were
 203 aborted. Thus, all movements recorded and analysed were made according to the following “hard
 204 cut-off” times: within 1022.4, 272.4, 222.4, 172.4, 122.4 ms after target presentation.



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 206 Figure 1. Top panel: A schematic representing the timed-response paradigm. Three tones spaced
 207 500 ms apart were presented, and participants were instructed to time the onset of their
 208 movements with the onset of the third tone. Targets appeared at different latencies prior to the
 209 third tone (Experiment 1a: 1000ms, 250ms, 200ms, 150ms, or 100ms; Experiment 1b: 1000ms,
 210 250ms, 200ms, 150ms; Experiment 2: Long preparation time condition: 1000ms, short

211 preparation time condition: 250ms). Note that these latencies were minus a display latency of
212 27.6 ± 1.8 ms. Bottom panel: Experiment 2 landmark layout for the LongReport conditions.

213 **Experiment 1.** The aim was to test re-aiming performance under progressively shorter
214 preparation times, to determine whether restricting movement preparation can prevent strategic
215 re-aiming. This paradigm of asking participants to re-aim by a specified angle relative to a visual
216 target is similar to that used by Georgopoulos and Massey (1987a). In each trial, participants
217 encountered one of eight targets which either spanned a small range of 35° (-17.5° , -
218 $12.5^\circ \dots 17.5^\circ$) in Experiment 1A, or a distribution of 360° (0° , $45^\circ \dots 360^\circ$) in Experiment 1B.
219 Targets were presented in random order. In all trials, thirty-six “landmarks” were presented on-
220 screen as white circles spaced 10° apart throughout the 360° range, 10 cm from the start circle. In
221 the re-aiming condition, half of the participants were instructed to re-aim to the third landmark
222 located clockwise from the target, and half were instructed to re-aim to the third landmark
223 counter-clockwise to the target (i.e., 30° either side of the target). All participants completed the
224 aiming condition before the re-aiming condition in blocks of 48 trials for each preparation time
225 condition. The preparation times were progressively shortened, such that the trial schedule was:
226 1000ms aiming, 1000ms re-aiming, 250ms aiming, 250ms re-aiming, 200ms aiming, 200ms re-
227 aiming, 150ms aiming, 150ms re-aiming, 100ms aiming, 100ms re-aiming. The 100ms condition
228 was not included in Experiment 1B because most participants could not initiate target-directed
229 movements prior to the deadline.

230 **Experiment 2.** To examine whether shortening preparation time can provide a sufficient
231 assay of implicit learning, we compared adaptation behaviour with short preparation time to an
232 estimate of implicit learning obtained by subtracting self-reported aiming direction from the
233 actual direction of hand movement (Bond and Taylor 2015; Brudner et al. 2016; McDougle et al.
234 2015; Taylor et al. 2014). Participants were assigned either to a 250ms preparation time
235 condition (Short), or one of two 1000ms preparation time conditions. In the LongReport
236 condition, they had to verbally report aiming directions by stating which of 72 landmarks spaced
237 5° apart most closely corresponded to the direction that they were aiming towards (Bond and
238 Taylor 2015; Taylor et al. 2014). Previous studies exclusively used numerical landmarks (Bond
239 and Taylor 2015; Brudner et al. 2016; Morehead et al. 2015; Taylor et al. 2014), which allowed
240 the use of mental addition or subtraction strategies in some participants (Bond and Taylor 2015).
241 We thus avoided using only number landmarks. Landmarks consisted of the letters A to Z, the

242 numbers 1-9, and the symbol “*” (reported as “star”). For ease of reporting, multiple-syllable
 243 characters (i.e., W) were not used. Landmarks rotated with the target, such that the same
 244 landmarks would always appear in the same location relative to the target, because rotating
 245 landmarks are more sensitive to explicit processes than fixed-location landmarks (Bond and
 246 Taylor 2015). Because of this, only a subset of the possible landmark values (A, B...G, *, 1,
 247 2, ...9) were actually used by participants when reporting their aiming directions. Participants
 248 were allowed to report their aiming direction at any time between target appearance and
 249 movement completion. Verbal reports of aiming directions were recorded online by the
 250 experimenter. To estimate implicit learning, these self-reported aiming directions were
 251 subtracted from actual movement directions. A third control group (LongNoReport) had a
 252 1000ms preparation time, but did not have to report aiming directions. We did not apply the
 253 reporting manipulation to the Short condition, as piloting showed that it was extremely difficult
 254 to report the aiming direction when the target appeared 250 ms prior to the imperative signal to
 255 move.

256 Prior to the start of the experiment, participants were given no information about the
 257 nature of the rotation; they were only told that a disturbance of the cursor would be present in
 258 some trials, which may increase task difficulty. Participants in all conditions first completed a
 259 **pre-rotation** block of 6 cycles (48 trials) with veridical feedback of their movement trajectories
 260 to familiarize them with the task. LongReport participants began to verbally report their aiming
 261 direction in last 24 trials in the pre-rotation block to familiarize them with the reporting
 262 procedure. The pre-rotation block was followed by a **rotation** block (60 cycles, i.e., 480 trials)
 263 with either a 30° clockwise or counterclockwise rotation of visual feedback relative to the centre
 264 of the start circle. Halfway through this block, participants were given a 30 second break. The
 265 rotation block was followed by a **no-feedback** block of 6 cycles (i.e., 48 trials), where visual
 266 feedback of the cursor position was hidden immediately after the cursor left the start circle.
 267 Crucially, before commencing this block, participants were explicitly instructed that there was no
 268 longer any disturbance of visual feedback, and that they should aim straight towards the target
 269 (Heuer and Hegele 2008; Taylor et al. 2014). The no-feedback block therefore provides an
 270 alternative assay of implicit remapping. Finally, participants completed a **washout** block of 6
 271 cycles (48 trials) where unrotated visual feedback was available to enable participants to return

272 movements back to the unadapted state. Landmarks were removed from the no-feedback block
273 and the washout block, and participants were no longer required to report aiming direction in
274 these blocks. The same preparation time constraints were maintained throughout the entire
275 experiment for each group.

276 **Data analysis**

277 Movement onset time was taken as the time at which hand speed first exceeded 2 cm/s.
278 Movement direction was quantified 100ms after movement onset, prior to the potential influence
279 of online corrections. For Experiment 2, data from the counterclockwise rotation group were
280 sign-transformed to allow us to collapse the dataset with data from the clockwise rotation group.
281 Negatively signed angles indicate that the deviation in hand direction relative to the target was
282 opposite to the direction of the rotation (i.e., to reduce visual error).

283 **Experiment 1:** To determine which of the preparation times was sufficiently short to
284 suppress strategic re-aiming, we first quantified movement directions relative to the target as
285 mean vectors and variability of movement directions as mean vector lengths, denoted as r for all
286 preparation times tested using circular statistics. In the aiming condition, mean vectors values
287 close to zero suggest that movement directions were close to the target. In the re-aiming
288 condition, values close to 30° indicate that movement directions were close to the instructed re-
289 aiming direction. Longer mean vectors indicate less variable movement directions, with a value
290 of 1 indicating all directions aligned, and a value of 0 indicating an absence of directional tuning
291 (i.e. a uniform distribution throughout all possible directions). We then compared movement
292 directions and variability for the aiming conditions to the re-aiming conditions. When directional
293 data is normally distributed, one can use the Hotelling's Paired Test, which is the equivalent of
294 the paired t-test for circular statistics (Zar 2010). However, as aiming directions were not
295 normally distributed, we used a non-parametric alternative (Moore's paired sample second order
296 tests) to determine whether mean vectors differed reliably between aiming and re-aiming
297 conditions (Zar 2010). Similarly, mean vector lengths typically show skewed distributions close
298 to 1, and thus Wilcoxon-Rank analyses were used to compare variability between the aiming and
299 re-aiming conditions. Circular statistics analyses were conducted with the software Oriana. For
300 Experiment 1a (narrow target distribution), we also tested whether participants re-aimed by
301 moving towards the middle of a (hypothetical) re-aiming target distribution by measuring the

302 errors made to each target, for the two shortest preparation time conditions (100 ms & 150 ms).
303 If re-aiming errors were smallest at the central 0° target and largest at the surrounding targets,
304 then this would suggest that participants adopted a strategy to re-aim to the middle of the
305 hypothetical re-aiming target distribution by initiating movements prior to full integration of
306 target direction information.

307 **Experiment 2.** Prior to statistical analyses, movements further than 90° clockwise or
308 counterclockwise away from the target (i.e., outside of a 180° range) were deemed as outliers,
309 and were discarded from the analysis. This procedure excluded a small proportion of trials
310 (Short: 4.00%, LongReport: 0.58%, LongNoReport: 0.39%). We evaluated whether the direction
311 of hand movement relative to the target, under reduced movement preparation time conditions,
312 was similar to the estimate of implicit learning obtained by subtracting self-reported aiming
313 directions from actual movement directions (Taylor et al. 2014). To this end, we recoded verbal
314 reports of landmarks into angular aiming directions, and then estimated implicit learning by
315 subtracting reported aiming directions from actual movement directions. Trials were averaged in
316 cycles of eight (one trial for each target angle) for statistical analysis. To compare adaptation
317 behaviour between conditions, ANOVAs with the within-subjects factor Cycle and two between-
318 subjects factors of Condition and Rotation Direction (clockwise, counterclockwise) were run on
319 relevant cycles. For the early adaptation phase, the relevant cycles were cycles 1-30 of the
320 adaptation block. For the late adaptation phase, the relevant cycles were cycles 31-60 of the
321 adaptation block. For the no-feedback block, the relevant cycles were all 6 cycles of the no-
322 feedback block. For the washout block, the relevant cycles were all 6 cycles of the washout
323 block. For all ANOVAs, when Mauchly's test of sphericity was statistically significant, the
324 Greenhouse-Geisser correction was used to adjust degrees of freedom.

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Results

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Experiment 1: Re-aiming away from a target at very short preparation times

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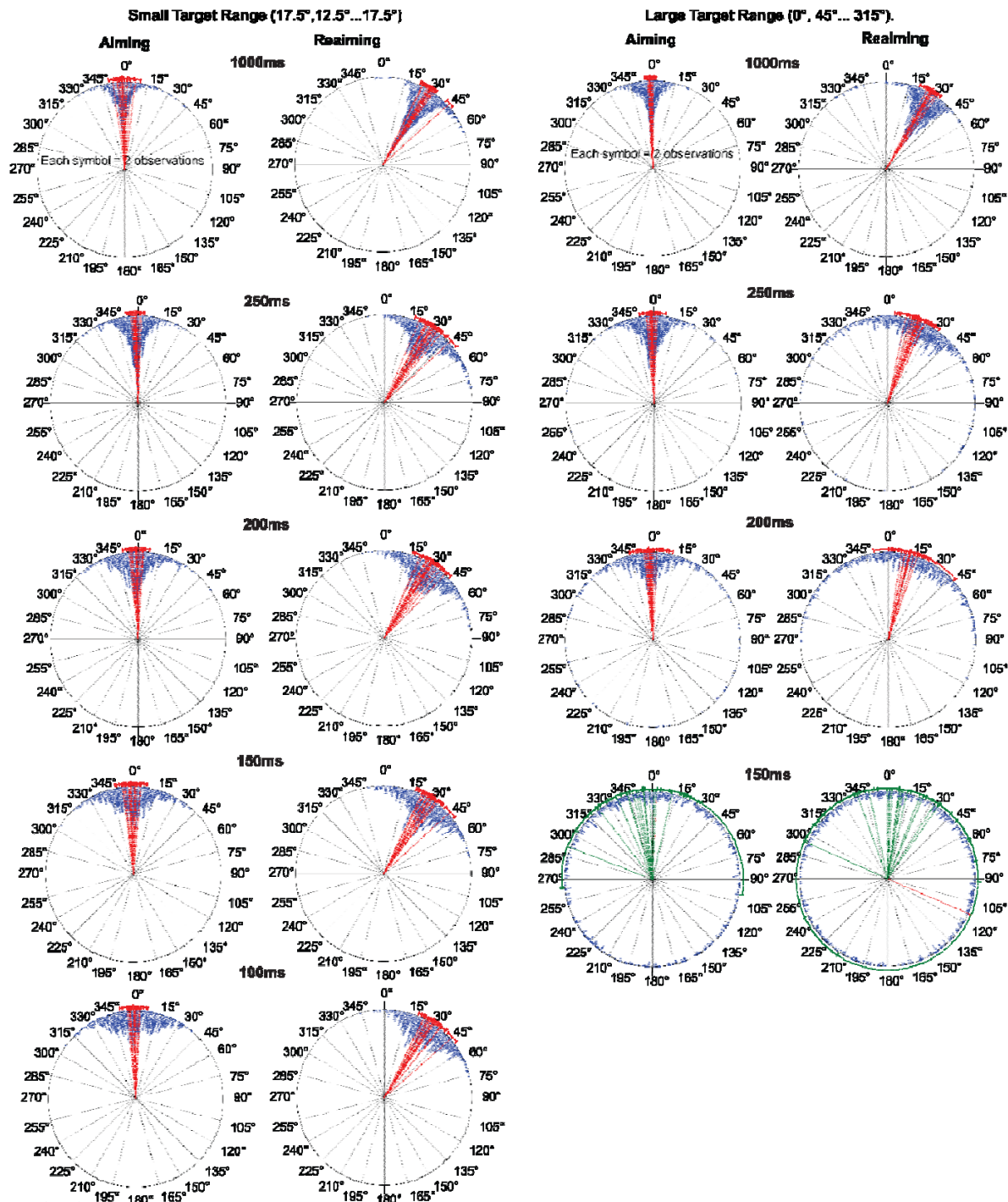
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Movement directions for all trials pooled across all subjects are shown in Figure 2 for Experiment 1A (small target range) and for Experiment 1B (large target range). With the small target range, movement directions were close to the target directions when aiming, and approximated the required 30° offset when re-aiming, even with the shortest preparation time condition of 100ms (i.e., hard initiation cut-off of 122.4ms). Rao's tests run for each participant's dataset within each preparation time condition indicated that movement directions were directionally tuned for all conditions, even for the shortest 100ms preparation time condition (all $p < .0001$). With the large target range, re-aiming movements were directed progressively closer to the original target (i.e., further from the instructed 30° offset) as preparation times were shortened. Rao's tests run for each participant's dataset within each preparation time condition indicated that movement directions were not directionally tuned for 5 of the 13 participants who completed the 150ms aiming condition and 10 of the 13 participants who completed the 150ms re-aiming conditions.

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344 Figure 2. Movement directions for the narrow target range (-17.5° to 17.5°) and large target range (0° to 360°) plotted relative
 345 to target direction at 0°, in the aiming and re-aiming conditions. Data from participants in the counterclockwise re-aiming
 346 condition were normalized to the clockwise direction and collapsed with data from participants in the clockwise re-aiming
 347 condition. Symbols represent movement directions in individual trials for all participants across the preparation time conditions
 348 (1000ms, 250ms, 200ms, 150ms to 100 ms). Note that the hard cut-off times for movement initiation in these conditions were:

349 1022.4, 272.4, 222.4, 172.4, 122.4 ms after target appearance. Red vectors represent individual mean vectors for each
 350 participant, and error bars represent the mean and 95% confidence intervals of mean movement direction for each participant.
 351 Green vectors represent individual mean vectors that were not significantly directionally tuned according to a Rayleigh's test.

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354 Table 1.

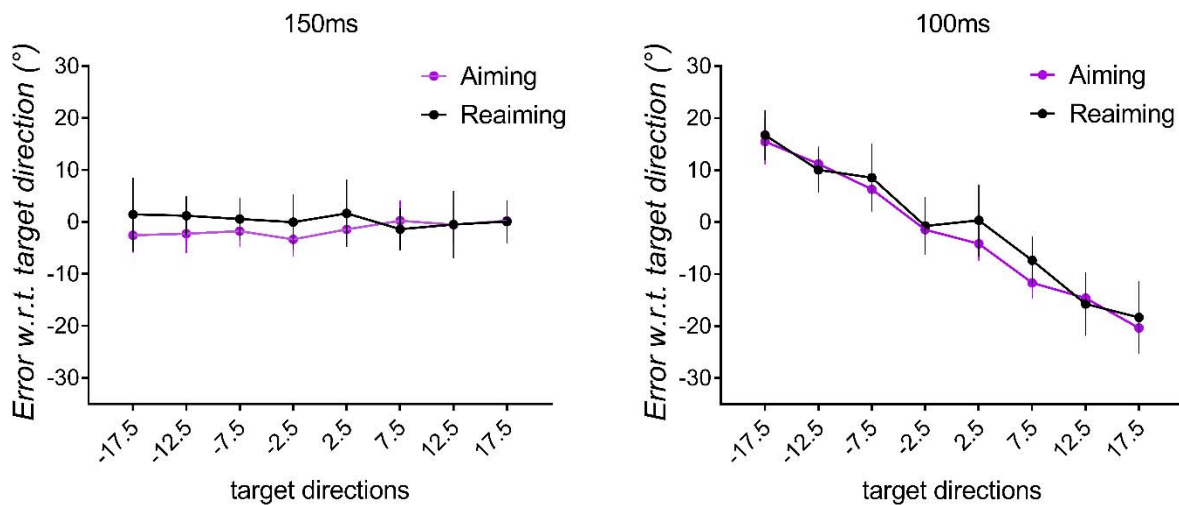
355 Statistical analyses comparing aiming and re-aiming accuracy (assessed via mean movement
 356 direction) and variability (assessed via vector length—longer vectors indicate less variability),
 357 as the amount of time available to prepare movements was progressively shortened.

Movement Preparation Time	Direction Variability (vector length)	Mean Vector Angle	Movement Time (mean+/- SEM)	Direction Variability (vector length)	Mean Vector Angle	Movement Time (mean+/-SEM)
Exp. 1A: Small target range: -17.5 ° to 17.5 °			Exp. 1B: Large target range: 0, 45°,... 315°			
1000 ms	Aiming: 0.99 Re-aiming: 0.99 z = -.32, p = 0.759	Aiming: 358.5° Re-aiming: 32.3° 2.00, p < 0.001	Aiming: 268+/- 18 ms Re-aiming: 262+/-22 ms	Aiming: 0.99 Re-aiming: 0.98 z =-2.98, p = 0.003	Aiming: 358.3° Re-aiming: 30.1° 1.48, p < 0.01	Aiming: 352+/- 19ms Re-aiming: 322+/-14ms
250 ms	Aiming: 0.99 Re-aiming: 0.97 z = -3.21, p = 0.001	Aiming: 358.2° Re-aiming: 32.6° 2.00, p < 0.001	Aiming: 262+/- 20ms Re-aiming: 278+/-16 ms	Aiming: 0.97 Re-aiming: 0.88 z = -3.41, p =0.001	Aiming: 358.4° Re-aiming: 20.1° 1.97, p < 0.01	Aiming: 235+/- 18ms Re-aiming: 250+/-22ms
200 ms	Aiming: 0.98 Re-aiming: 0.97 z = -2.52 , p = 0.012	Aiming: 358.4° Re-aiming: 32.2° 2.00, p < 0.001	Aiming 261+/- 18 ms Re-aiming= 253+/-16 ms	Aiming: 0.89 Re-aiming: 0.66 z = -3.35, p = 0.001	Aiming: 357.8° Re-aiming: 14.6° 1.81, p < 0.01	Aiming: 218+/- 17ms Re-aiming: 233+/-17ms
150 ms	Aiming: 0.97 Re-aiming: 0.96 z = -.79 , p = 0.432	Aiming: 358.8° Re-aiming: 32.2° 1.99, p < 0.001	Aiming: 260+/- 15 ms Re-aiming: 251+/-14 ms	Aiming: 0.46 Re-aiming: 0.27 z = 3.11, p =0.002	Aiming: 354.3° Re-aiming: 351.9° 1.54, p < 0.01	Aiming: 236+/- 18 Re-aiming: 235+/-18
100ms	Aiming: 0.97 Re-aiming: 0.96 z = -2.61, p = 0.009	Aiming: 358.5° Re-aiming: 32.4° 2.00, p < 0.001	Aiming: 262+/-18 ms, Re-aiming: 258+/-16 ms	n/a	n/a	n/a

359 Table 1 summarizes statistical comparisons between aiming and re-aiming across
360 preparation times for both the narrow target distribution (Experiment 1A) and the full 360° target
361 distribution (Experiment 1b). For both target distributions, movement directions were more
362 variable (shorter vector lengths) when re-aiming away from the target than when aiming to the
363 target across all preparation times. When errors were averaged across all targets in the narrow
364 range (Experiment 1a), it appears that participants could re-aim away from the target in all
365 preparation times tested (even when movements were initiated within 122.4 ms of target
366 preparation). That is, mean vector angles were on average approximately 30° away from the
367 target across all preparation times tested. We were surprised at this apparent success in re-
368 aiming, since Haith et al (2016) showed that directionally tuned movements to a unique target
369 require approximately 130 ms, and the process of re-aiming (and preparing movements to a
370 direction offset by 30° to the target) should require at least some additional processing (Haith et
371 al. 2016). We therefore examined errors for each target in the distribution individually, to search
372 for evidence that participants might have been able to achieve task success by aiming toward the
373 middle of the re-aiming target distribution (i.e. 30° away from the central visual target
374 distribution). In this case, movement could be initiated prior to integration of target direction
375 information, but average errors collapsed across targets would be close to zero.

376 Figure 3 shows clear evidence that subjects adopted such a strategy for the shortest
377 preparation time condition, under both aiming and re-aiming conditions. Errors were similar for
378 all targets in the 150ms preparation time condition, indicating that there were no large inherent
379 biases in reaching performance. There were no statistically significant differences in error size
380 across targets ($F(7,91) = 1.10$, $p = 0.39$, partial η -squared = 0.08) or conditions ($F(1,13) = 1.1$, p
381 = 0.3, partial η -squared = 0.08), nor an interaction between target and condition ($F(7,91) = 1.2$, p
382 = 0.3, partial η -squared = 0.09). By contrast, with 100ms preparation time (122.4 ms hard cut-
383 off), errors were systematically larger in absolute terms as the angle from the centre of the
384 distribution increased for the aiming condition (main effect of target $F(7,91) = 199$, $p < 0.001$,
385 partial η -squared = 0.94). The signs of errors indicate that participants made reaching movements
386 that were biased towards the central target. The pattern of errors for aiming and re-aiming
387 conditions were similar for the aiming and re-aiming conditions, with no statistically significant
388 main effect of condition ($F(1,13) = 0.6$, $p = 0.45$, partial η -squared = 0.04) or interaction between

389 condition and target ($F(7,91) = 1.6, p = 0.15, \text{partial } \eta\text{-squared} = 0.11$). Note that errors from the
 390 required (re-aiming) target are plotted and analysed, rather than errors relative to the presented
 391 target. Critically, the similarity in error directions and magnitudes for the aiming and re-aiming
 392 conditions, across all preparation time conditions, suggests that if participants had sufficient time
 393 to aim towards the target, then they also had time to re-aim to one side of the target by a
 394 specified angle. Although this process of re-aiming must require some additional processing, our
 395 data suggest that such processing is extremely rapid, to the point that we were not able to detect a
 396 time-cost for re-aiming under the conditions of our experiment. The data also suggest that people
 397 are able to apply a re-aiming strategy to an anticipated target location when there is insufficient
 398 time to adequately process visual information related to the actual target. This indicates that the
 399 approach of restricting strategic re-aiming through preparation time constraints might be
 400 especially problematic for single or dual target paradigms.



401
 402 *Figure 3. Movement errors for each target direction from -17.5° to 17.5° with respect to (w.r.t) the required*
 403 *reaching direction (i.e., presented target or re-aiming target depending on condition). Data from participants in the*
 404 *counterclockwise re-aiming condition were normalized to the clockwise direction and collapsed with data from*
 405 *participants in the clockwise re-aiming condition. Separate plots are shown for the 150ms to 100 ms preparation*
 406 *time conditions. Note that the hard cut-off times for movement initiation in these conditions were 172.4 and 122.4*
 407 *ms after target appearance. Values are group mean errors and error bars represent 95% confidence intervals.*

408 In Experiment 1b, which involved the broad target distribution, participants were less
 409 accurate at re-aiming away from the target (20.1°) with 250ms preparation, although re-aiming
 410 away from the target was still possible with 200 ms (14.6°) and 150ms (7.7°) preparation. This

411 confirms that voluntary re-aiming is not absolutely prevented by shortening movement
412 preparation time, irrespective of whether potential targets lie within a narrow or large angular
413 range. Self-reports from our participants indicated, however, that re-aiming was extremely
414 effortful at short preparation times, especially when targets were distributed around the circle.
415 Moreover, the accuracy cost of re-aiming was dramatically greater when targets were distributed
416 around the circle. Given this, in Experiment 2, we considered whether participants would choose
417 to re-aim under time pressure in order to improve performance in a visuomotor rotation task. For
418 this experiment, targets were radially arranged throughout the circle (0° , 45° ... 315°) and
419 movement preparation time was restricted to 250ms. We decided to use 250ms as an arbitrary
420 trade-off between a sufficient time to allow accurate aiming to the presented target, and
421 sufficient time-pressure to make re-aiming effortful.
422

423

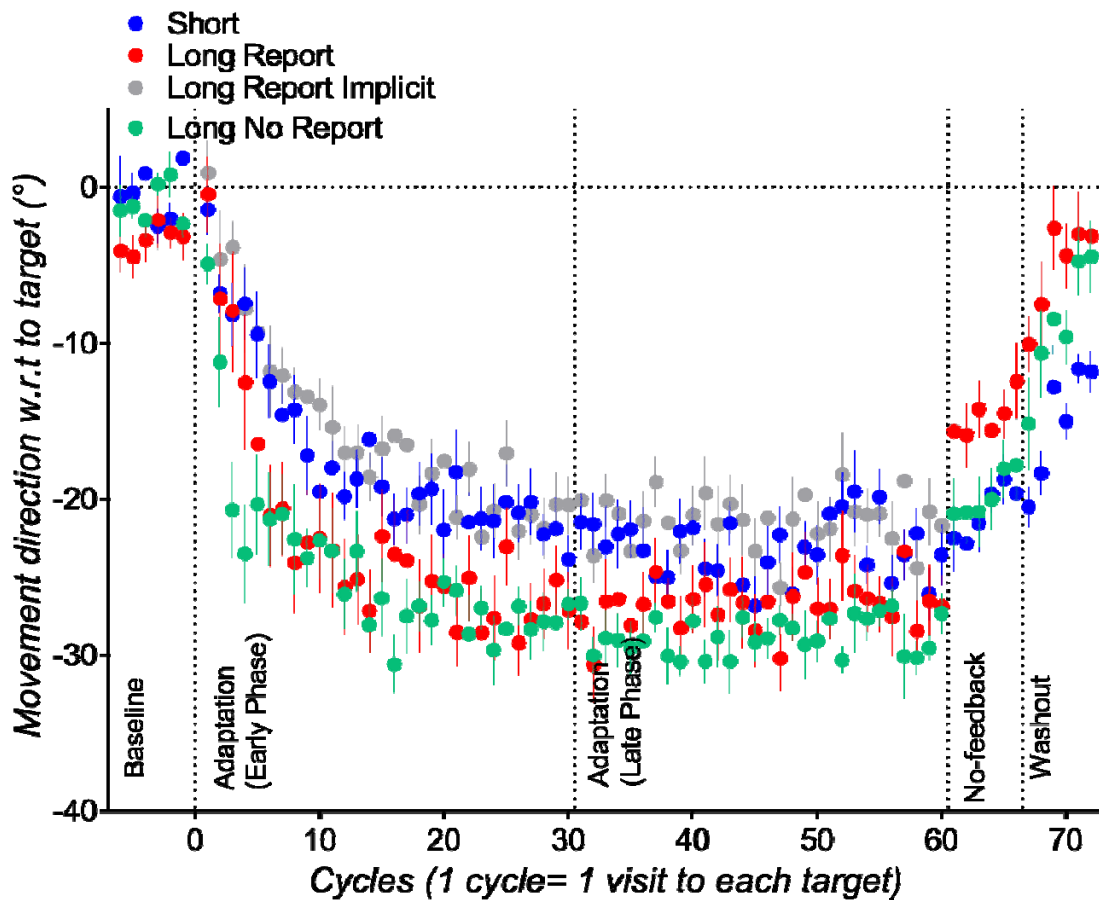
424 **Experiment 2: Suppressing strategic re-aiming with short preparation time constraints**
425 **reduces the rate and extent of error compensation.**

426 Figure 4 shows the group mean, cycle-averaged, movement directions across different
427 phases of the experiment. To evaluate whether the discrepancy between the measures of implicit
428 learning (i.e., implicit learning estimated from subtracting aiming directions from movement
429 directions and implicit learning estimated from the no-feedback trials) is related to the process of
430 reporting explicit aiming angles or the preparation time constraints, we compared this data to 10
431 additional task-naïve participants (5 counterclockwise, 5 clockwise) who completed the
432 visuomotor rotation task with the same 1000ms preparation time constraints via the same timed-
433 response paradigm, but who did not report aiming directions and had no visual landmarks
434 throughout the task (LongNoReport). In the baseline block (i.e., before encountering the
435 perturbation) a counterclockwise bias was evident in the Long preparation time group, as Cycle
436 (Cycle 1...6) x Condition (Long, Short, LongNoReport) x Rotation Direction (clockwise,
437 counterclockwise) ANOVA revealed a significant main effect of Condition, $F(2,30) = 4.267$, $p =$
438 0.023 , partial η -squared = 0.221. To estimate the bias, we averaged mean movement directions
439 from baseline cycles 2-6 (baseline cycle 1 was not included as participants were still
440 familiarising themselves with the vBOT at this stage). To eliminate the influence of this bias on
441 the subsequent test phases, we subtracted the bias from mean movement directions from each
442 subsequent cycle (i.e., the first cycle of the adaptation block to the last washout cycle). The
443 adaptation phase was arbitrarily separated into Early (Cycle 1-30) and Late blocks (Cycle 31-60).
444 ANOVAs were run on each block for all three conditions (LongReport, Short, LongNoReport),
445 according to a mixed within-between effects model (Cycle x Rotation Direction x Condition
446 [LongReport, Short, LongNoReport]). In the Early phase, there was a significant main effect of
447 Condition, $F(2,30) = 6.25$, $p = 0.005$, partial η -squared = 0.294, as well as a significant Cycles x
448 Condition interaction, $F(24.6,370.2) = 1.59$, $p = 0.037$, partial η -squared = 0.09, as less error
449 compensation was evident with Short ($-17.3 \pm 1.3^\circ$) compared to LongReport, ($-22.4 \pm 1.3^\circ$,
450 $p = .033$) and compared to LongNoReport ($-24.4 \pm 1.8^\circ$, $p = .009$). Error compensation in this early
451 phase did not differ reliably between LongReport and LongNoReport ($p = .75$). Similarly, for the
452 Late phase, there was a significant main effect of Condition, $F(2,30) = 4.77$, $p = 0.016$, partial η -

453 squared = 0.241; as less error compensation was evident with short preparation time (-23.1+/-
454 1.1°) compared to LongNoReport (-28.7+/-1°, $p = .007$) and compared to LongReport (-26.7+/-
455 1.1°, $p = .036$). Error compensation was also more complete for clockwise than counterclockwise
456 rotations, as evident in significant main effect of Rotation across all phases: Early: $F(1,30) =$
457 21.643, $p < 0.001$, partial η -squared = 0.419, Late: $F(1,30) = 10.96$, $p = 0.002$, partial η -squared
458 = 0.268]. There were no other significant interactions.

459 **Preparation time constraint as an assay of implicit learning**

460 The implicit component of error compensation observed for the Long preparation group
461 was estimated by subtracting the participants' reported aiming direction from their actual
462 movement direction, similar to previous work (Bond and Taylor 2015; Brudner et al. 2016;
463 McDougale et al. 2015; Taylor et al. 2014). This measure of error is hereafter termed
464 "LongImplicit", and was compared to angular errors observed between the target and movement
465 for the short preparation time condition. There were no significant differences between
466 LongImplicit and Short, as shown by Condition (LongImplicit, Short) x Cycle (Cycle 1...30) x
467 Rotation Direction (CW, CCW) ANOVAs run for the early adaptation phase [main effect of
468 Condition, $F(1,24) = 1.33$, $p = 0.26$, partial η -squared = 0.05, Cycle x Condition $F(12.6,303.9) =$
469 1.05, $p = 0.4$, partial η -squared = 0.04 interaction], as well as the late adaptation phase
470 [Condition, $F(1,24) = 1.44$, $p = 0.2$, partial η -squared = 0.06, Cycles x Condition, $F(11.9,287.1)$
471 = 1.4, $p = 0.16$, partial η -squared = 0.05]. The main effect of rotation direction was statistically
472 significant for the early adaptation phase, $F(1,24) = 26.29$, $p < 0.001$, partial η -squared = 0.52 as
473 well as for the late adaptation phase: $F(1,24) = 11.473$, $p = 0.002$, partial η -squared = 0.32. There
474 were no significant interactions. Thus, the extent and rate of implicit learning did not differ
475 reliably between estimates based on subtracting self-reported aiming directions and restriction of
476 preparation time.



477

478 *Figure 4. Experiment 2 mean movement direction in every cycle, averaged across each condition. Data*
 479 *from participants who encountered counterclockwise rotations were sign-transformed to allow collapsing*
 480 *with data from participants who encountered clockwise rotations. Error bars are standard errors of the*
 481 *mean. Negative values indicate movements that were opposite from the direction of rotation, positive*
 482 *values indicate movements that were in the same direction as the rotation. Note that Long Report Implicit*
 483 *is not an additional experimental condition, but is derived from subtracting self-reported aiming*
 484 *directions from movement directions in the Long Report condition.*

485

486 **Difference in estimate of implicit learning from subtracting aiming directions and estimate**
 487 **of implicit learning from no-feedback trials**

488 An alternative measure of implicit remapping is provided by the no-feedback trials that
 489 participants performed after the final adaptation phase block. Here, participants received no
 490 visual feedback about their movements, and were explicitly instructed that the perturbation was
 491 removed and that they should aim straight to the target (Taylor et al. 2014), (similar to Heuer and
 492 Hegele 2015). For the LongReport group (Figure 3) the measure of implicit learning obtained

493 from this no-feedback block appears substantially lower (i.e., movements were less adapted) than
494 the measure of implicit learning obtained by subtraction of reported aiming direction in the last
495 adaptation cycle. In contrast, for the Short group, errors in the last adaptation cycle were similar
496 to those in the first no-feedback cycle. To compare implicit learning (estimated by subtracting
497 aiming direction or by shortening preparation times) to implicit learning estimated by no-
498 feedback trials, we compared the last adaptation cycle (after subtracting aiming directions for the
499 LongReport group) to the first no-feedback cycle for the LongReport group and the Short group,
500 via a Condition (LongReport, Short) x Rotation Direction (CW, CCW) x Phase (last adaptation
501 cycle, first no-feedback phase cycle) ANOVA. There was a significant Phase x Condition
502 interaction, $F(1, 24) = 4.36$, $p = .047$, partial eta-squared = .15. Follow-up Rotation Direction x
503 Phase (last adaptation cycle, first no-feedback phase cycle) ANOVAs were run separately for the
504 LongReport and the Short condition. For LongReport, implicit learning estimated by subtracting
505 aiming direction in the last adaptation cycle ($21.7 \pm 1.8^\circ$) was more than implicit learning
506 estimated in the first no-feedback cycle ($15.8 \pm 1.6^\circ$), as shown by a significant main effect of
507 phase $F(1, 12) = 6.94$, $p = 0.022$, partial η -squared = 0.37. In contrast, for the short preparation
508 time, the last adaptation cycle ($-23.5 \pm 1.8^\circ$) did not differ reliably from the first no-feedback
509 cycle ($-22.5 \pm 1.9^\circ$): the main effect of Phase was not significant ($F(1, 12) = 0.33$, $p = 0.57$,
510 partial η -squared = 0.02), and did not interact significantly with any other factor. Thus, for the
511 LongReport group, there was a discrepancy between the estimates of implicit learning provided
512 by the reporting method, obtained in the presence of the rotation, and the no-feedback condition,
513 obtained after the final movement performed under the visuomotor rotation. There was no
514 discrepancy between implicit learning estimates for the short preparation time group, even
515 though the final estimate of implicit learning at the end of adaptation was similar to that obtained
516 after subtracting aiming directions for LongReport group, and despite the fact that both groups
517 had explicit knowledge that the rotation was removed.

518 This discrepancy between the estimates of implicit learning from reporting, in the last
519 adaptation cycle, and from no-feedback trials in which participants were instructed that the
520 rotation was absent, was also evident in previous work using the reporting procedure (c.f. Fig 2C,
521 Fig 5C Bond and Taylor 2015). Taylor et al. (2014) attributed the effect to trial-by-trial decay of
522 adaptation within the first no-feedback cycle, because there was no statistically significant

523 difference between the last adaptation trial and the first no-feedback trial (Taylor et al. 2014).
 524 Our LongReport group similarly showed no reliable difference in estimated implicit learning
 525 from the last adaptation trial to the first no-feedback trial (Trial x Rotation Direction ANOVA on
 526 the LongReport group showed a non-significant main effect of Trial $F(1,12)=.30$, $p = .59$, partial
 527 η -squared = .03). However, we hesitate to make inferences from this non-significant effect,
 528 because comparing trial-by-trial data in multi-target designs can be problematic: target directions
 529 were likely to differ between the last adaptation trial and the first no-feedback trial between-
 530 subjects, and directional accuracy differs between targets (Gordon et al. 1994). Moreover,
 531 movements were also less adapted on average over all six no-feedback cycles for the LongReport
 532 than the Short group, as shown by a significant main effect of Condition, $F(1,24) = 6.91$, $p =$
 533 0.01 , partial η -squared = 0.22 in a Condition x Rotation Direction x Cycle ANOVA. This
 534 suggests that the extent or persistence of implicit learning was less for the long preparation with
 535 reporting condition than the short preparation condition.

536 To evaluate whether the discrepancy between measures of implicit learning is related to
 537 the reporting procedure (i.e., the process of reporting explicit aiming angles and/or the presence
 538 of visual landmarks), we compared error compensation data from the Long Report group to the
 539 LongNoReport group. Error compensation during exposure to the rotation did not differ reliably
 540 between this LongNoReport group and the LongReport group, as Cycle x Reporting
 541 (LongNoReport, LongReport) x Rotation Direction (CW, CCW) ANOVAs run separately for the
 542 early adaptation phase (Cycles 1...31) and the late adaptation phase (Cycles 31...60) showed a
 543 non-significant main effect of reporting for the early adaptation phase [$F(1,18) = 0.67$, $p = 0.424$,
 544 partial η -squared = 0.036], and no significant interactions, as well as for the late adaptation phase,
 545 $F(1,18) = 0.843$, $p = 0.371$, partial η -squared = 0.045 , no significant interactions]. However, the
 546 estimate of implicit learning obtained from no-feedback trials was greater for the LongNoReport
 547 group than the LongReport condition: Cycle (Cycle 1-6) x Reporting (LongNoReport,
 548 LongReport) x Rotation Direction (CW, CCW) ANOVA on the no-feedback block showed a
 549 significant main effect of reporting, $F(1,18) = 7.32$, $p = 0.015$, partial η -squared = 0.289 . There
 550 were no other significant interactions. The main effect of Rotation Direction was significant
 551 $F(1,18) = 16.64$, $p = 0.001$, partial η -squared = 0.48 —similar to the adaptation phase,
 552 movements were more adapted with the clockwise direction ($-21.0 \pm 1.0^\circ$) than the

553 counterclockwise direction ($13.4 \pm 1.0^\circ$). Performance in the no-feedback trials did not differ
554 significantly between the LongNoReport and the Short group—a Cycle (Cycle 1-6) x Condition
555 (LongNoReport, Short) x Rotation Direction ANOVA showed a non-significant main effect of
556 condition [$F(1,18) = 0.449$, $p = 0.511$, partial η -squared = 0.024], and no significant interactions
557 with condition, all $p > 0.5$. The main effect of rotation direction was significant $F(1,18) = 15.98$,
558 $p = 0.001$, partial η -squared = 0.47.

559

Discussion

560 This study aimed to evaluate a previously established method of assaying implicit
561 learning by restricting the time available to prepare movement (Fernandez-Ruiz et al. 2011;
562 Haith et al. 2015). Experiment 1 showed that restricting time available to prepare movements
563 does not prevent people from applying a deliberate strategy to re-aim to one side of a target,
564 particularly when targets are distributed within a narrow angular range. However, Experiment 2
565 showed that restricting movement preparation time effectively reduces strategic re-aiming during
566 adaptation to visuomotor rotation when targets are distributed throughout 360° , as shown by
567 slower and less complete error compensation compared to when movement preparation times
568 were not shortened. Moreover, the errors made by participants when preparation time was
569 shortened were indistinguishable from an assay of implicit learning obtained by subtracting self-
570 reported aiming directions from movement directions (Bond and Taylor 2015; Brudner et al.
571 2016; McDougle et al. 2015; Taylor et al. 2014). Surprisingly, despite this similarity in estimates
572 of implicit learning obtained for the two methods during exposure to the visuomotor rotation,
573 participants who reported aiming directions showed less implicit remapping in the post-
574 perturbation no-feedback trials than those who did not report aiming directions. This suggests
575 that the process of reporting aiming direction reduces the extent or persistence of implicit
576 learning.

577 Suppressing the expression of explicit learning by restricting preparation time

578 Despite a long history of studies on implicit and explicit processes in sensorimotor
579 adaptation (Jakobson and Goodale 1989; Uhlarik 1973), our understanding of how these
580 processes interact to determine behaviour remains incomplete. Here, we further evaluated the
581 method of assaying implicit learning by restricting movement preparation time (Fernandez-Ruiz

582 et al. 2011; Haith et al. 2015). We showed that when there is intention to re-aim (i.e., when
 583 participants were explicitly instructed to re-aim) and potential targets were distributed within a
 584 small (35°) range, accurate re-aiming is possible irrespective of the time between target
 585 presentation and movement initiation. The accuracy cost of re-aiming in such conditions was
 586 modest. Moreover, for the shortest preparation time condition (movement initiation constrained
 587 to occur within 123 ms of target presentation), it appears that participants initiated movement
 588 prior to complete integration of visual information about the actual target, and were able to
 589 achieve task success by aiming or re-aiming to the centre of the (required) target distribution.
 590 When target direction (and thus re-aiming direction) was less predictable (targets distributed
 591 throughout 0-360°), however, re-aiming accuracy declined with progressively shorter preparation
 592 times. Participants were still able to partially re-aim away from the target whenever they had
 593 sufficient time to produce directionally tuned movements, but at the expense of dramatically
 594 increased movement variability. Hence, compressing preparation time does not introduce an
 595 absolute limit upon the capacity for re-aiming, particularly for narrow target distributions.

596 However, during sensorimotor adaptation to a perturbation, restricting preparation time
 597 appeared to suppress re-aiming when targets were distributed about 360°, such that error
 598 compensation was indistinguishable from the assay of implicit learning obtained from
 599 subtracting reported aiming direction from actual movement direction. This suggests that people
 600 choose not to apply re-aiming strategies to correct for visuomotor perturbations under time
 601 pressure, presumably to avoid the increases in effort and variability associated with re-aiming
 602 under such conditions.

603 This interpretation prompts a formal definition of the distinction between implicit and
 604 explicit processes. Here, consistent with others (Huberdeau et al. 2015), we define explicit
 605 processes as those which can be deliberately engaged and disengaged. By contrast, implicit
 606 processes are automatic and difficult to deliberately disengage. We do not distinguish between
 607 explicit processes from implicit processes based on awareness of the perturbation or a re-aiming
 608 strategy, as classically defined (Reber 1967). Indeed, many of our participants in the short
 609 preparation time condition were able to accurately describe the nature of the rotation and could
 610 articulate a compensatory strategy, but found it simply too difficult to implement the strategy
 611 when preparation times were restrained.

612 Our findings that asymptotic error levels were greater for short than long preparation time
613 conditions differ from those of Haith et al. (2015). In their task, which involved two potential
614 targets, participants were eventually able to reduce errors to a similar degree for the short and
615 long preparation time targets. This discrepancy in findings probably relates to the predictability
616 of the target locations. Targets only appeared in two locations in Haith et al. (2015), with
617 preparation time of ~300 ms. However, our Experiment 1A shows that explicit re-aiming is
618 possible even at 123 ms when the target direction was predictable within a small 35° range.
619 Hence, although the target-switch protocol in Haith et al. (2015) appears to have restricted
620 explicit processes initially, the method may not have been sufficient to suppress re-aiming by the
621 end of the adaptation block.

622 **Discrepancy between different estimates of implicit learning.**

623 In Experiment 2, the extent of implicit learning inferred from aiming reports in the long
624 preparation time condition was similar to the extent of error compensation observed for the short
625 preparation time condition. However, for the long preparation condition, there was a difference
626 between estimates of implicit learning obtained from reporting during exposure to the rotation,
627 and estimates of implicit learning obtained from subsequent movements made without feedback.
628 A discrepancy has been reported previously between measures of implicit learning measured via
629 movement directions after subtracting aiming directions, and via movement directions in
630 subsequent no-feedback trials (c.f. Fig 2C, Fig 5C Bond and Taylor 2015). However, we found
631 that there was no such decay between errors in the last perturbation trials and first no-feedback
632 trials for the short preparation time condition. Furthermore, the overall amount of implicit
633 remapping (indicated by adapted movements in the no-feedback block despite explicit
634 knowledge that the rotation had been removed), was less in the reporting group than in either of
635 two groups that did not report aiming directions (i.e., the LongNoReport group and the Short
636 group), irrespective of movement preparation time. We note that this difference might result
637 from either the act of reporting aiming directions, and/or the presence of visual landmarks,
638 however, as the original reporting procedure often requires the use of landmarks, we did not
639 attempt to dissociate between the two possibilities.

640 We propose two possibilities to account for these observations. One possibility is that
641 implicit learning is more labile (i.e., more sensitive to decay due to a change in task context or

642 the passage of time) when it is acquired in a context in which people report their re-aiming
 643 strategies to compensate for errors. The proposal that explicit processes reduce the persistence of
 644 implicit remapping is consistent with findings in prism adaptation, where explicit knowledge of
 645 the nature of the perturbation reduces the extent of implicit remapping measured in post-
 646 perturbation no-feedback trials (Jakobson and Goodale 1989; Uhlarik 1973). One caveat to this
 647 interpretation is that, although all three groups experienced the same change in context (i.e., from
 648 having feedback of cursor position with visuomotor rotation to having no cursor feedback and
 649 explicit knowledge that the rotation had been removed), the LongReport group experienced an
 650 additional context change (i.e., from having to report aiming directions to no longer having to
 651 report aiming directions). Thus, we cannot rule out the possibility that the extent of context
 652 change, rather than sensitivity to change, was the key factor underlying a reduced estimate of
 653 implicit learning in the LongReport condition.

654 An alternative possibility that could explain our data is that people may have
 655 systematically under-reported their aiming angle (i.e., people re-aimed to a greater extent than
 656 they reported). This would result in an underestimation of explicit learning and an
 657 overestimation of implicit learning in the error compensation phase. In this case, the no-feedback
 658 trials would provide a more accurate measure of implicit learning than the reporting trials, which
 659 in turn would imply that the reporting procedure enhanced explicit learning and impaired
 660 implicit learning relative to non-reporting conditions. The possibility that the reporting procedure
 661 enhanced explicit re-aiming is supported by previous findings of faster error compensation with
 662 the reporting procedure than without (Taylor et al. 2014). Such a situation would suggest a
 663 competitive push-pull relationship between implicit and explicit processes in sensorimotor
 664 adaptation. A push-pull relationship between implicit and explicit processes has been shown for
 665 other motor learning tasks. For example, in sequence learning, disrupting explicit awareness of a
 666 sequence to be learned, by performing a concurrent verbal declarative task, improved post-task
 667 recall of implicitly acquired sequences (Brown and Robertson 2007). Similarly, in force-field
 668 adaptation, engaging a declarative verbal memory task resulted in poorer recall of a fragile,
 669 possibly explicit memory created by a fast process, and improved recall of a robust, possibly
 670 implicit memory created by a slow process (Keisler and Shadmehr 2010).

671 By contrast, implicit adaptation to visuomotor rotation has been argued to be inflexible,
672 such that it develops in parallel with, but independently from, explicit learning (Bond and Taylor
673 2015). Although it is difficult to test whether self-reports of aiming direction are accurate,
674 discrepancies between self-reported aiming directions and actual aiming directions seem possible.
675 Georgopoulos and Massey (1987a) showed that when participants were explicitly instructed to
676 re-aim by a specified angle, their re-aiming was in excess of the instructed angle, particularly
677 with smaller instructed re-aiming angles of less than 35°. Thus, the question of whether implicit
678 and explicit processes operate independently or competitively in visuomotor rotation learning
679 warrants further attention.

680 **Summary**

681 This study evaluated the method of dissociating implicit and explicit learning by
682 manipulating the amount of time available to prepare movements. The method has previously
683 been shown to unmask implicit visuomotor rotation learning on a trial-by-trial basis (Haith et al.
684 2015). We found that although shortening preparation time does not prevent people from
685 voluntarily aiming to one side of a target, it appears sufficient to suppress strategic re-aiming
686 during visuomotor adaptation when targets are distributed about a broad angular range.
687 Estimating implicit learning by subtracting aiming directions from movement directions yielded
688 a discrepancy between the estimate of implicit error compensation obtained during exposure to
689 the perturbation, and the estimate of implicit learning obtained from post-perturbation trials
690 without feedback. It is possible that the reporting procedure inadvertently increased explicit re-
691 aiming and decreased implicit learning, which would suggest a push-pull relationship between
692 explicit and implicit learning. In contrast, shortening movement preparation time did not result in
693 a discrepancy between the estimate of implicit learning obtained from self-report during
694 exposure to the perturbation, and the estimate of implicit learning obtained from trials performed
695 subsequently without visual feedback.

696

697

698 *References*

- 699 **Bond KM, and Taylor JA.** Flexible explicit but rigid implicit learning in a visuomotor
700 adaptation task. *J Neurophysiol* 113: 3836-3849, 2015.
- 701 **Brown RM, and Robertson EM.** Inducing motor skill improvements with a declarative task.
702 *Nature neuroscience* 10: 148-149, 2007.
- 703 **Brudner SN, Kethidi N, Graeupner D, Ivry RB, and Taylor JA.** Delayed feedback during
704 sensorimotor learning selectively disrupts adaptation, but not strategy use. *J Neurophysiol* jn
705 00066 02015, 2016.
- 706 **Fernandez-Ruiz J, Wong W, Armstrong IT, and Flanagan JR.** Relation between reaction
707 time and reach errors during visuomotor adaptation. *Behav Brain Res* 219: 8-14, 2011.
- 708 **Galea JM.** Secondary tasks impair adaptation to step- and gradual-visual displacements. *Exp*
709 *Brain Res* 202: 473-484, 2010.
- 710 **Georgopoulos AP, and Massey JT.** Cognitive spatial-motor processes - 1. The making of
711 movements at various angles from a stimulus direction. *Exp Brain Res* 65: 361-370, 1987a.
- 712 **Georgopoulos AP, and Massey JT.** Cognitive spatial-motor processes. 1. The making of
713 movements at various angles from a stimulus direction. *Exp Brain Res* 65: 361-370, 1987b.
- 714 **Ghez C, Hening W, and Favilla M.** Gradual Specification of Response Amplitude in Human
715 Tracking Performance. *Brain Behav Evol* 33: 69-74, 1989.
- 716 **Gordon J, Ghilardi MF, and Ghez C.** Accuracy of planar reaching movements - I.
717 Independence of direction and extent variability. *Exp Brain Res* 99: 97-111, 1994.
- 718 **Haith AM, Huberdeau DM, and Krakauer JW.** The influence of movement preparation time
719 on the expression of visuomotor learning and savings. *The Journal of neuroscience : the official*
720 *journal of the Society for Neuroscience* 35: 5109-5117, 2015.
- 721 **Heuer H, and Hegele M.** Adaptation to visuomotor rotations in younger and older adults.
722 *Psychol Aging* 23: 190-202, 2008.
- 723 **Heuer H, and Hegele M.** Explicit and implicit components of visuo-motor adaptation: An
724 analysis of individual differences. *Consciousness and cognition* 33: 156-169, 2015.
- 725 **Howard IS, Ingram JN, and Wolpert DM.** A modular planar robotic manipulandum with end-
726 point torque control. *Journal of Neuroscience Methods* 181: 199-211, 2009.
- 727 **Huberdeau DM, Krakauer JW, and Haith AM.** Dual-process decomposition in human
728 sensorimotor adaptation. *Curr Opin Neurobiol* 33: 71-77, 2015.
- 729 **Jakobson LS, and Goodale MA.** Trajectories of reaches to prismatically-displaced targets:
730 evidence for "automatic" visuomotor recalibration. *Experimental brain research* 78: 575-587,
731 1989.
- 732 **Keisler A, and Shadmehr R.** A shared resource between declarative memory and motor
733 memory. *Journal of Neuroscience* 30: 14817-14823, 2010.

- 734 **Malone La, and Bastian AJ.** Thinking about walking: effects of conscious correction versus
735 distraction on locomotor adaptation. *Journal of neurophysiology* 103: 1954-1962.
- 736 **Marinovic W, Cheung FL, Riek S, and Tresilian JR.** The effect of attention on the release of
737 anticipatory timing actions. *Behav Neurosci* 128: 548, 2014.
- 738 **Marinovic W, Plooy A, and Tresilian JR.** The time course of amplitude specification in brief
739 interceptive actions. *Exp Brain Res* 188: 275-288, 2008.
- 740 **Marinovic W, Tresilian J, Chapple JL, Riek S, and Carroll T.** Unexpected acoustic
741 stimulation during action preparation reveals gradual re-specification of movement direction.
742 *Neuroscience* 2017.
- 743 **Mazzoni P, and Krakauer JW.** An implicit plan overrides an explicit strategy during
744 visuomotor adaptation. *Journal of Neuroscience* 26: 3642-3645, 2006.
- 745 **McDougle SD, Bond KM, and Taylor JA.** Explicit and implicit processes constitute the fast
746 and slow processes of sensorimotor learning. *The Journal of Neuroscience* 35: 9568-9579, 2015.
- 747 **Morehead JR, Qasim SE, Crossley MJ, and Ivry R.** Savings upon Re-Aiming in Visuomotor
748 Adaptation. *The Journal of neuroscience : the official journal of the Society for Neuroscience* 35:
749 14386-14396, 2015.
- 750 **Reber AS.** Implicit learning of artificial grammars. *Journal of verbal learning and verbal*
751 *behavior* 6: 855-863, 1967.
- 752 **Redding GM, and Wallace B.** Adaptive Spatial Alignment and Strategic Perceptual-Motor
753 Control. 22: 1996.
- 754 **Reichenthal M, Avraham G, Karniel A, and Shmuelof L.** Target size matters: Target errors
755 contribute to the generalization of implicit visuomotor learning. *Journal of neurophysiology* jn.
756 00830.02015, 2016.
- 757 **Schouten JF, and Bekker JAM.** Reaction time and accuracy. *Acta Psychologica* 27: 143-153,
758 1967.
- 759 **Taylor JA, Krakauer JW, and Ivry RB.** Explicit and implicit contributions to learning in a
760 sensorimotor adaptation task. *The Journal of neuroscience : the official journal of the Society for*
761 *Neuroscience* 34: 3023-3032, 2014.
- 762 **Taylor JA, and Thoroughman KA.** Divided Attention Impairs Human Motor Adaptation But
763 Not Feedback Control. *Journal of Neurophysiology* 98: 317-326, 2007.
- 764 **Taylor JA, and Thoroughman KA.** Motor adaptation scaled by the difficulty of a secondary
765 cognitive task. *PLoS ONE* 3: 2008.
- 766 **Uhlarik JJ.** Role of cognitive factors on adaptation to prismatic displacement. *J Exp Psychol* 98:
767 223-232, 1973.
- 768 **Wolpert DM, Ghahramani Z, and Jordan MI.** An internal model for sensorimotor integration.
769 *Science* 269: 1880-1882, 1995.
- 770 **Zar JH.** *Biostatistical analysis*. Upper Saddle River, N.J.: Upper Saddle River, N.J. : Prentice-
771 Hall/Pearson, 2010.

PREPARATION TIME CONSTRAINTS CAN ASSAY IMPLICIT VISUOMOTOR
ADAPTATION

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775 Figure Legends

776 Figure 1. Top panel: A schematic representing the timed-response paradigm. Three tones spaced
777 500 ms apart were presented, and participants were instructed to time the onset of their
778 movements with the onset of the third tone. Targets appeared at different latencies prior to the
779 third tone (Experiment 1a: 1000ms, 250ms, 200ms, 150ms, or 100ms; Experiment 1b: 1000ms,
780 250ms, 200ms, 150ms; Experiment 2: Long preparation time condition: 1000ms, short
781 preparation time condition: 250ms). Note that these latencies were minus a display latency of
782 27.6 ± 1.8 ms. Bottom panel: Experiment 2 landmark layout for the LongReport conditions.

783

784 Figure 2. Movement directions for the narrow target range (-17.5° to 17.5°) and large target
785 range (0° to 360°) plotted relative to target direction at 0° , in the aiming and re-aiming conditions.
786 Data from participants in the counterclockwise re-aiming condition were normalized to the
787 clockwise direction and collapsed with data from participants in the clockwise re-aiming
788 condition. Symbols represent movement directions in individual trials for all participants across
789 the preparation time conditions (1000ms, 250ms, 200ms, 150ms to 100 ms). Note that the hard
790 cut-off times for movement initiation in these conditions were: 1022.4, 272.4, 222.4, 172.4,
791 122.4 ms after target appearance. Red vectors represent individual mean vectors for each
792 participant, and error bars represent the mean and 95% confidence intervals of mean movement
793 direction for each participant. Green vectors represent individual mean vectors that were not
794 significantly directionally tuned according to a Rayleigh's test.

795

796 Figure 3. Movement errors for each target direction from -17.5° to 17.5° with respect to (w.r.t)
797 the required reaching direction (i.e., presented target or re-aiming target depending on condition).
798 Data from participants in the counterclockwise re-aiming condition were normalized to the
799 clockwise direction and collapsed with data from participants in the clockwise re-aiming
800 condition. Separate plots are shown for the 150ms to 100 ms preparation time conditions. Note
801 that the hard cut-off times for movement initiation in these conditions were 172.4 and 122.4 ms
802 after target appearance. Values are group mean errors and error bars represent 95% confidence
803 intervals.

804

805 Figure 4. Experiment 2 mean movement direction in every cycle, averaged across each condition.
806 Data from participants who encountered counterclockwise rotations were sign-transformed to
807 allow collapsing with data from participants who encountered clockwise rotations. Error bars are
808 standard errors of the mean. Negative values indicate movements that were opposite from the
809 direction of rotation, positive values indicate movements that were in the same direction as the
810 rotation. Note that Long Report Implicit is not an additional experimental condition, but is
811 derived from subtracting self-reported aiming directions from movement directions in the Long
812 Report condition.

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