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2 Competition between parallel sensorimotor learning systems

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18 **Abstract**

19 Sensorimotor adaptation benefits from learning in two parallel systems: one that has access to explicit
20 knowledge, and another that relies on implicit, unconscious correction. However, it is unclear how these
21 systems interact: does enhancing one system's contributions, for example through instruction, impair the
22 other, or do they learn independently? Here we illustrate that certain contexts can lead to competition
23 between implicit and explicit learning. In some cases, each system is responsive to a task-related visual
24 error. This shared error appears to create competition between these systems, such that when the explicit
25 system increases its response, errors are siphoned away from the implicit system, thus reducing its
26 learning. This model suggests that explicit strategy can mask changes in implicit error sensitivity related
27 to savings and interference. Other contexts suggest that the implicit system can respond to multiple error
28 sources. When these error sources conflict, a second type of competition occurs. Thus, the data show that
29 during sensorimotor adaptation, behavior is shaped by competition between parallel learning systems.

30

31 **Introduction**

32 When we reach towards an object, unexpected perturbations to the arm engage multiple corrective
33 systems. Some systems are reactive and respond online to counter the perturbation^{1–3}, whereas others
34 are predictive, changing their output to anticipate the perturbation^{4–6}. When multiple predictive systems
35 operate together, how do they coordinate their responses to error?

36 One possibility is that each learning system operates on a separate error source. For example,
37 when people adapt to a visual perturbation and an inertial perturbation simultaneously, the brain engages
38 parallel circuits⁷ that respond to each error separately without interference⁸. In other cases, however,
39 separate corrective systems may respond to a common error. For example, current models suggest that
40 a given sensory error simultaneously engages multiple adaptive systems, each with their own timescale
41 of learning: some fast and others slow^{9,10}.

42 Presence of multiple learning systems in the brain makes it crucial to understand how they are
43 coordinated to seamlessly improve behavior. First, suppose two learning systems are driven by the same
44 error and produce an output that reduces that error (Fig. 1A). In this case, when one system adapts, it
45 reduces the error that is available to drive learning in the other system; thus, these two parallel systems
46 will compete to “consume” a common error. Second, suppose two systems are driven by distinct errors,
47 each producing an output to minimize its own error (Fig. 1B). In this case, when one system adapts to its
48 error, the resulting action could increase the other system's error, thus producing another type of
49 competition where only one system can minimize its error. These ideas illustrate that a given system's
50 behavior will depend not only on its own error source, but the error sources that drive parallel learning
51 systems.

52 Here we consider how these competitive interactions may couple together neural systems that
53 respond to visual errors. Multiple lines of evidence suggest that the brain engages two parallel systems
54 during motor learning: a strategic explicit system that can be guided by instruction^{11,12}, as well as an
55 implicit system that adapts without our conscious awareness^{12,13}. How might these learning systems
56 interact^{14–16} during sensorimotor adaptation?

57 The answer depends on their respective error sources. Current models suggest that implicit and
58 explicit systems are differentially engaged by two distinct error sources: a task error^{17–19}, and a prediction
59 error^{4,12,20}. One theory suggests that the explicit system acts to decrease errors in task performance, while

60 the implicit system acts to reduce errors in predicting sensory outcomes^{12,21,22}. However, other models
61 have suggested that both systems are at least partly engaged by errors in task outcome^{14,17,23,24}. Here we
62 show that both errors drive implicit learning, but their relative contributions vary across different
63 experiments. Some experiments reveal how learning systems exhibit competition due to a common error
64 source as in Fig. 1A, but in others, they interfere given a conflict between separate errors as in Fig. 1B.

65 Critically, one's viewpoint can lead to contrasting interpretations of the same data. Consider the
66 case where implicit and explicit systems share at least one common error source. Suppose some
67 experimental condition facilitates explicit strategy. In this case, increases in explicit strategy will siphon
68 away the error that the implicit system needs to adapt, thus reducing implicit learning without actually
69 changing implicit learning properties.

70 Changes in implicit learning might occur not solely across two distinct environments, but across
71 two moments in time. For example, when two opposing perturbations are learned in sequence, the rate
72 of learning decreases due to interference²⁵⁻²⁷. On the other hand, when the perturbations are the same,
73 the rate of learning increases due to savings²⁸⁻³². If implicit and explicit systems share an error source,
74 each system's current response can be shaped not solely by past experience, but also by changes in the
75 other system. This may explain a potential disconnect between studies that have suggested that
76 experience-dependent increases in learning rate are subserved solely by flexible explicit strategies^{28,33-36},
77 and studies that have pointed to concomitant changes in implicit learning systems^{17,37,38}.

78 Here, we mathematically^{9,14,24,39,40} consider the extent to which implicit and explicit systems are
79 engaged by common errors, or separate errors. The hypotheses make diverging predictions, which we
80 then test in various contexts. In some contexts, the data suggest that the two systems are mostly driven
81 by a common error. This shared error produces competition as in Fig. 1A, such that increases^{15,16} or
82 decreases^{41,42} in explicit strategy indirectly exert the opposite effect on implicit learning. This competitive
83 relationship suggests an alternate way that implicit systems may exhibit two hallmarks of learning: savings
84 and interference. However, in other contexts, a single common error cannot explain implicit behavior. In
85 these cases, the data are more consistent with the idea that multiple error sources (e.g., a prediction and
86 a task error) drive comparable levels of implicit learning, leading to competition resembling Fig. 1B.

87 Together, our results illustrate that changes in behavior during sensorimotor adaptation are
88 shaped by multiple types of competition between parallel learning systems.

89

90 **Results**

91 In visuomotor rotation paradigms, participants move a cursor with their hand (Fig. 1C), but experience a
92 perturbation that changes the canonical relationship between hand motion and cursor motion. The
93 perturbation induces adaptation, resulting in a change in reach direction. This adaptation is supported by
94 both implicit and explicit processes^{11,12,21,43}; participants can intentionally re-aim their reach angle (Fig. 1C,
95 aim), and also change their reach via implicit recalibration (Fig. 1C, implicit). Together, these two systems
96 determine the hand's path (Fig. 1C, hand).

97 Suppose that a rotation r alters the cursor's path (Fig. 1C, cursor). Current models suggest that
98 this perturbation creates two distinct error sources. One error source is created by the deviation between
99 the cursor and the target: a target error¹⁷⁻¹⁹. Notably, this target error (Fig. 1C, target error) is altered by
100 both implicit (x_i) and explicit (x_e) adaptation:

101
$$e_{target}^{(n)} = r^{(n)} - (x_i^{(n)} + x_e^{(n)}) \quad (1)$$

102 Under normal circumstances, the brain expects that the cursor will move toward the aimed
103 location. This expectation gives rise to a second error: a sensory prediction error (SPE)^{4,12,20}. This SPE is
104 created by the deviation between where we aimed our hand (the expected cursor motion) and where we
105 observed the cursor's actual motion (Fig. 1C, sensory prediction error). Critically, because this error is
106 anchored to our aim location, it is altered solely by changes in the implicit system:

107
$$e_{SPE}^{(n)} = r^{(n)} - x_i^{(n)} \quad (2)$$

108 These errors create two different objective functions: (1) maximize success by eliminating target
109 error, and (2) improve our predictions by eliminating SPE. How does the brain's subconscious learning
110 system respond to these disparate directives? State-space models describe implicit adaptation as a
111 process of learning and forgetting^{9,14,24,39,40}:

112
$$x_i^{(n+1)} = a_i x_i^{(n)} + b_i e^{(n)} \quad (3)$$

113 Forgetting is controlled by the retention factor (a_i) which specifies how strongly we retain the adapted
114 state. Learning is controlled by one's error sensitivity (b_i) which determines the amount we adapt in
115 response to an error – but which error?

116 To answer this question, consider how Eq. (3) behaves following an extended training period. Like
117 adapted behavior^{23,37,44,45}, Eq. (3) approaches an asymptotic limit when the processes of learning and
118 forgetting balance each other (Fig. 1B, implicit). In the extreme case where the implicit system responds
119 solely to target error, total implicit learning is determined by Eqs. (1) and (3):

120
$$x_i^{ss} = \frac{b_i}{1 - a_i + b_i} (r - x_e^{ss}) \quad (4)$$

121 Eq. (4) demonstrates a competition between implicit and explicit systems; the total amount of implicit
122 adaptation (x_i^{ss}) is related to the difference between the perturbation r and the total amount of explicit
123 adaptation (x_e^{ss}).

124 On the other extreme, when the implicit system responds solely to SPE, total implicit learning is
125 determined by Eqs. (2) and (3):

126
$$x_i^{ss} = \frac{b_i}{1 - a_i + b_i} r \quad (5)$$

127 Eq. (5) demonstrates an independence between implicit and explicit systems; the total amount of implicit
128 adaptation depends solely on the rotation's magnitude, not one's explicit strategy.

129 In summary, the competition (Eq. (4)) and independence (Eq. (5)) equations make predictions that
130 can answer a critical question: which errors drive implicit adaptation? If implicit learning is predominantly
131 driven by SPE, the implicit system will depend only on the perturbation's magnitude according to the
132 independence equation (Eq. (5)). On the other hand, if implicit learning is predominantly driven by target
133 error, the implicit system will compete with explicit strategies according to the competition equation (Eq.
134 (4)). Here, we investigate these predictions across several experimental paradigms and explore their
135 limitations in describing the behavior of the implicit learning system.

136

137 *Enhancement in explicit strategy reduces the amount of implicit adaptation*

138 Suppose that in one condition, participants adapt to a visual rotation with some fixed explicit strategy (Fig.
139 1D, aim, solid magenta line). But in a second condition, the participant is coached about the

140 perturbation^{16,46}, enhancing their explicit strategy (Fig. 1D, aim, dashed magenta line). If the implicit
141 system learns only from SPE (Eq. (5)), then changes in explicit strategy will have no impact on implicit
142 learning (Fig. 1D, H1, compare solid black and dashed blue implicit lines). On the other hand, if the implicit
143 system learns only from target error, it competes with the explicit system (Eq. (4)). Coaching explicit
144 strategy suppresses implicit learning (Fig. 1D, H2, compare dashed blue and solid black implicit lines).

145 To test this prediction, we considered an experiment performed by Neville and Cressman¹⁵.
146 Participants were exposed to either a 20°, 40°, or 60° visuomotor rotation (Fig. 1E), and separated into
147 instructed and non-instructed conditions. Non-instructed groups (Fig. 1E, gray) adapted without any initial
148 instruction regarding the perturbation. Instructed participants were briefed about the upcoming rotation
149 and how they should compensate to hit the target (Fig. 1E, yellow). This instruction sharply increased the
150 rate of adaptation over that of the non-instructed group (Fig. 1E, compare yellow and gray curves).

151 To determine how instruction accelerated adaptation, participants were asked to reach with and
152 without explicit strategy (Fig. S1). The marginal effects of instruction (average across rotation magnitudes)
153 and perturbation magnitude (average over instruction conditions) are shown in Figs. 1F and 1G
154 respectively. Unsurprisingly, instructed participants learned faster due to an enhancement in explicit re-
155 aiming, which increased by approximately 10° across each rotation magnitude (Fig. 1F, explicit).

156 Curiously, while instruction enhanced explicit learning, it appeared to impair implicit adaptation,
157 decreasing the total implicit aftereffect (Fig. 1F, implicit learning, data). Even more puzzling, whereas
158 contributions of the explicit system increased with rotation magnitude (Fig. 1G, explicit), implicit learning
159 did not, as one might intuitively expect (Fig. 1G, implicit learning, data).

160 To interpret the implicit response to awareness and perturbation magnitude, we fit both the
161 competition (Eq. (4)) and independence equations (Eq. (5)) to the behavior across all groups, under the
162 assumption that the implicit system's sensitivity to error and retention (b_i and a_i) were identical across all
163 rotation sizes, and across the instructed and non-instructed conditions.

164 The independence and competition models made contrasting predictions (see individual
165 predictions in Figs. S1B&C). Because SPE does not depend on explicit aiming, Eq. (5) incorrectly predicted
166 the same level of implicit learning irrespective of explicit awareness (Fig. 1F, implicit learning, indep.).
167 Furthermore, because implicit adaptation is driven solely by the rotation magnitude in the independent
168 model, Eq. (5) also incorrectly predicted that implicit learning should increase with rotation size (Fig. 1G,
169 implicit learning, indep.).

170 The opposite was true of the competition model. Eq. (4) correctly predicted less implicit learning
171 in instructed participants who used greater explicit strategy (Fig. 1F, implicit learning, competition).
172 Remarkably, the competition model also predicted that the implicit aftereffect should remain similar
173 across rotation magnitudes (Fig. 1G, implicit learning, competition). How was this possible? Critically, the
174 competition equation suggests that the driving force for implicit learning is not solely the rotation, but the
175 difference between the rotation and explicit strategy. Therefore, because the total amount of explicit re-
176 aiming increased as the rotation magnitude increased (Fig. 1G, explicit), their difference remained roughly
177 constant across all perturbation sizes (Fig. S1D). Thus, Eq. (4) predicted similar implicit aftereffects
178 irrespective of rotation size.

179 In summary, when explicit learning is enhanced through instruction, implicit learning is impaired.
180 As perturbation magnitude increases, contributions of explicit learning increases, but not the

181 contributions of implicit learning. These observations are consistent with the competition model (Eq. (4)),
182 suggesting that the implicit and explicit systems are primarily driven by a common target error.

183

184 *Suppression of explicit learning increases the amount of implicit adaptation*

185 The competition equation predicts that enhancing explicit strategy should decrease implicit learning (Fig.
186 1). What should happen when explicit learning is suppressed? Suppose participants adapt with an explicit
187 strategy (Fig. 2B, aim, solid magenta line), but this strategy is then suppressed (Fig. 2B, aim, dashed
188 magenta line). Because SPE learning does not depend on explicit strategy, Eq. (5) predicts no change in
189 implicit learning (Fig. 2B, H1, left, compare solid black and dashed blue implicit lines) (Eq. (5)). However,
190 because target errors do depend on explicit strategy, Eq. (4) predicts that suppressing explicit aiming will
191 increase implicit learning (Fig. 2B, H2, right, compare dashed blue and solid black implicit lines).

192 One way to suppress explicit learning is to make participants unaware by introducing the
193 perturbation gradually. In an earlier experiment, Saijo and Gomi (2010)⁴² exposed participants to either
194 an abrupt (Fig. 2A, abrupt) or gradual (Fig. 2A, gradual) perturbation. The abrupt perturbation was
195 immediately set to 60°, but the gradual perturbation reached this magnitude over time.

196 Participants in the abrupt condition adapted rapidly to the perturbation, greatly decreasing their
197 target error to about 5° over about 10 perturbation cycles (Fig. 2C, abrupt). Participants in the gradual
198 group, experienced small target errors throughout training, but adapted less by the end of the rotation
199 period, exhibiting a terminal error nearly 3 times greater than the abrupt condition (Fig. 2C, gradual).

200 At this point, the perturbation was abruptly removed, revealing large aftereffects in each group.
201 However, even though participants in the gradual group had adapted less completely to the rotation, they
202 paradoxically exhibited larger aftereffects (Fig. 2F, data), which remained elevated throughout the entire
203 washout period (Fig. 2C, aftereffect). If these aftereffects reveal the total amount of implicit adaptation,
204 given that strategies are rapidly disengaged when the perturbation is removed³⁴ (Fig. S2), how could more
205 complete adaptation in the abrupt group lead to less implicit adaptation?

206 To investigate this phenomenon, we considered how implicit and explicit systems might behave
207 according to the independence (Eq. (5)) and competition (Eq. (4)) frameworks. To simulate these models,
208 we estimated the explicit strategies in each group. Neville and Cressman¹⁵ had measured the explicit
209 response to a 60° rotation, demonstrating that participants re-aimed their hand approximately 35°
210 consistently over the adaptation period (see yellow points in Figs. 2D&E, explicit aim). This estimate
211 agreed well with the data; participants in the abrupt condition adapted 55°, and exhibited an aftereffect
212 of approximately 20° (Fig. 2F, data, abrupt), suggesting about 35° of re-aiming. In the gradual group, we
213 assumed that little to no re-aiming occurred. This also seemed consistent with the data; participants in
214 the gradual group adapted approximately 40°, and exhibited an aftereffect of approximately 38° (Fig. 2F,
215 data, gradual) suggesting <5° of re-aiming. Using these estimates, we constructed hypothetical explicit
216 learning timecourses, as shown in Figs. 2D&E, explicit aim).

217 We next used the state-space model to simulate the implicit learning timecourse, in cases where
218 the implicit system learned solely due to SPE (Fig. 2D, implicit angle) or solely due to target error (Fig. 2E,
219 implicit angle), under the assumption that participants in both the abrupt and gradual groups had the
220 same implicit error sensitivity (b_i) and retention factor (a_i). The parameter sets that yielded the closest
221 match to the measured behavior (Fig. 2C) are shown in Figs. 2D&E (directional error). In both cases, the
222 models predicted abrupt and gradual learning timecourses that resembled the data.

223 However, the implicit states predicted by SPE learning and target error learning possessed a
224 critical difference. According to Eq. (4), the target error model predicted that the total extent of implicit
225 learning would be suppressed by explicit strategy in the abrupt condition, yielding a smaller aftereffect
226 (Fig. 2E, implicit angle). However, according to Eq. (5), the SPE model predicted that implicit learning
227 should reach the same level, yielding identical aftereffects (Fig. 2D, implicit angle).

228 In summary, the differences in aftereffects across the abrupt and gradual conditions (Fig. 2F, data)
229 were accurately predicted by the competition model (Fig. 2F, competition), but not the independence
230 model (Fig. 2F, indep.). Suppressing the explicit strategy revealed competition between implicit and
231 explicit systems which suggested that the implicit system predominantly responded to target error.

232

233 *Subject-to-subject correlations reveal competition between implicit and explicit systems*

234 Data in Figs. 1 and 2 suggested that the implicit system was altered by competition with explicit strategy.
235 Is this competition observed at the level of individual participants? In other words, the competition model
236 would predict that participants who use larger strategies will naturally exhibit less implicit adaptation.

237 To investigate this possibility, we considered earlier work where Fernandez-Ruiz and colleagues⁴¹
238 exposed participants to a 60° rotation (Fig. 3A). The large rotation appeared to induce substantial variation
239 in strategic re-aiming. Consider for example Subjects A and B (Figs. 3B&C). Upon rotation onset, Subject
240 A rapidly reduced their directional error (Fig. 3B, Subject A) and exhibited two characteristics that
241 suggested the use of large explicit re-aiming angles: (1) their reach angle varied greatly from one cycle to
242 the next^{14,44,47} and (2) their movement preparation time (Fig. 3C, Subject A) greatly increased upon onset
243 of the perturbation^{18,28,37,47}. On the other hand, Subject B reduced directional errors slowly and
244 consistently (Fig. 3B, Subject B), with little to no increase in movement preparation time (Fig. 3C, Subject
245 B). Thus, Subjects A and B appeared to engage explicit strategies to differing extents. How did differences
246 in their explicit strategy impact implicit learning?

247 When the perturbation was removed, reaction time returned to baseline levels (Fig. 3C), revealing
248 each participant's aftereffect (Fig. 3B, aftereffect). Paradoxically, though Subject A adapted more
249 completely to the rotation during the adaptation period, they exhibited a far smaller aftereffect (Fig. 3B).
250 A possible explanation is that because Subject A used greater explicit strategy during adaptation, their
251 implicit system adapted less due to competition, producing a smaller aftereffect. Indeed, although
252 participants who increased their preparation time exhibited smaller reach errors (Fig. S3), engaging
253 explicit strategies appeared to inhibit their implicit system, as revealed by a decrease in the aftereffect
254 during the washout period (Fig. 3D; $p=0.87$, $p<0.01$).

255 The competition model (Eq. (4)) provides a way to quantify these subject-to-subject correlations.
256 The left-most term in this equation is a learning gain that varies between 0 and 1, which depends on
257 implicit learning properties: retention (a_i) and error sensitivity (b_i). Thus, the competition equation
258 predicts that implicit and explicit learning will negatively co-vary according to a line whose slope and bias
259 are determined by the properties of the implicit learning system (a_i and b_i). To test the model's accuracy,
260 we exposed participants to a 30° visuomotor rotation (Fig. 3E) under two conditions (Experiment 1). In
261 one group, we strictly limited preparation time to inhibit time-consuming explicit strategies^{41,47} (Fig. 3F,
262 Limit PT). In the other group, we imposed no preparation time constraints (Fig. 3F, No PT limit). Our goal
263 was to measure a_i and b_i in the Limit PT group which putatively relied on implicit learning, and use these
264 values to predict the implicit-explicit relationship across No PT limit participants.

265 As expected, PT Limit participants dramatically reduced their reach latencies throughout the
266 adaptation period, whereas No PT limit participants exhibited a sharp increase in movement preparation
267 time after perturbation onset (Fig. 3G), indicating explicit re-aiming^{18,28,37,41,47}. Consistent with suppression
268 of explicit strategy, learning proceeded more slowly and was less complete with the PT Limit (Fig. 3F; two-
269 sample t-test on last 10 adaptation epochs: $t(30)=2.14$, $p=0.041$, $d=0.77$).

270 Next, we empirically measured the putative implicit retention factor (a_i) and error sensitivity (b_i)
271 associated with the PT Limit learning curve. We measured the retention factor during a terminal “no
272 feedback” period (Fig. 3F, dark gray, no feedback) and error sensitivity (b_i) during the adaptation period
273 (see Methods). Together, this retention factor ($a_i=0.943$) and error sensitivity ($b_i=0.35$), produced a
274 specific form of Eq. (4), namely, $x_i = 0.86 (30 - x_e)$, which we could use to predict how implicit and explicit
275 learning should vary across participants in the No PT limit group (Fig. 3H, blue line).

276 To measure No PT limit implicit and explicit learning we instructed participants to move their hand
277 through the target without any re-aiming at the end of the adaptation period (Fig. 3F, no aiming). The
278 precipitous change in reach angle revealed the terminal amounts of implicit and explicit adaptation (post-
279 instruction reveals implicit; total drop reveals explicit). To verify the accuracy of this explicit measure, we
280 asked participants to verbally report their re-aiming angles (see Methods). Participants that demonstrated
281 greater explicit strategy indeed reported larger re-aiming angles at the end of adaptation (Fig. S4A,
282 $p=0.709$) and also appeared to require greater movement preparation time (Fig. S4B, $p=0.708$).

283 How did subject-to-subject variations in implicit and explicit learning compare to the model’s
284 prediction? We observed a striking correspondence between the No PT limit implicit-explicit relationship
285 (Fig. 1H, black dot for each participant; $p=-0.95$) and that predicted by the competition model (Fig. 3H,
286 blue). The slope and intercept predicted by Eq. (4) (-0.86 and 25.74°, respectively) differed from the
287 measured linear regression (Fig. 1H, black line, $R^2=0.91$; slope = -0.9 with 95% CI [-1.16, -0.65] and
288 intercept = 25.46° with 95% CI [22.54°, 28.38°]) by only about 5% and 1%, respectively.

289 Lastly, we tested two alternate explanations that could also explain the observed correlations
290 between implicit and explicit learning. First, explicit (total adaptation minus no aiming probe) and implicit
291 (no aiming probe) learning measures inherently share variance which could lead to spurious correlation.
292 Second, in the event that participants exhibit nearly identical learning asymptotes, say approximately 26°
293 in our experiment, these implicit and explicit learning measures could be trivially constrained to lie along
294 the regression line: $x_i + x_e \approx C$, where $C = 26^\circ$.

295 To test these possibilities, we conducted a control experiment (Experiment 2). Participants
296 adapted to a 30° rotation again (Fig. 3I), but this time, we measured implicit adaptation using the no-
297 aiming instruction over an extended 20-cycle period (Fig. 3J, no aiming). We calculated early (first no-
298 aiming cycle; Fig. 3J, measure early implicit) and late (last 15 no-aiming cycles; Fig. 3J, measure late
299 implicit) implicit learning measures. As in Fig. 3H, we calculated total explicit strategy as the difference
300 between total adaptation and the first no-aiming cycle (Fig. 3J, measure explicit).

301 Critically, our explicit measure and late implicit measure were now properly decoupled, as they
302 depended on separate cycles. Remarkably, late implicit learning exhibited patterns that matched the
303 group-level interventions observed by Neville and Cressman¹⁵ (Fig. 1) and Saijo and Gomi⁴² (Fig. 2).
304 Namely, participants that compensated most for the perturbation utilized large explicit strategies (Fig. 3K;
305 $p=0.79$, $p<0.001$). But enhancements in overall learning came at the cost of reductions in implicit

306 adaptation (Fig. 3L; $\rho=-0.68$, $p=0.003$), due to a competition between implicit and explicit learning (Fig. 307 3M, $\rho=-0.79$, $p<0.001$).

308 Secondly, we considered the relationship between explicit strategy and early implicit learning, 309 and again observed a strong negative linear relationship (Fig. 3L, $\rho=-0.79$): $x_i + 0.6x_e = 19.1$. Notably, the 310 explicit regression coefficient's (0.6) 95% CI, [0.42,0.77] did not contain 1. Equivalently, this indicates that 311 there was substantial variation in asymptotic learning across participants (range 16-29°), ruling out the 312 trivial possibility that $x_i + x_e = C$, described above. To the contrary, participants who showed greater explicit 313 learning had better overall compensation for the perturbation, but had less implicit learning.

314 In summary, consistent with the idea that the two learning systems share a common error, we 315 found that when a subject's performance depends more on the contributions of the explicit system, their 316 implicit system learns less.

317

318 *Competition predicts increases in both implicit and explicit error sensitivity during savings*

319 When participants are exposed to the same perturbation twice, they adapt more quickly the second time. 320 This phenomenon is known as savings and is a hallmark of sensorimotor adaptation^{9,48,49}. Multiple studies 321 have attributed this process solely to changes in explicit strategy^{28,33,34,36,50}.

322 For example, in an earlier work²⁸, we trained participants ($n=14$) to reach to one of two targets, 323 coincident with an audio tone (Fig. 4A). By shifting the displayed target approximately 300 ms prior to 324 tone onset on a minority of trials (20%), we forced participants to execute movements with limited 325 preparation time (Low preparation time; Fig. 4A, middle). On trials in which subjects had high preparation 326 time, i.e. trials without a target switch (Fig. 4B, left), adaptation exhibited savings; the rate of learning 327 increased across exposures (Fig. 4B, right, High PT; Wilcoxon signed rank, $p=0.0085$, Cohen's $d=0.683$). 328 Learning differences were most pronounced on the first 40 trials after perturbation onset (Fig. 4C, left; 329 Fig. 4C, right, paired t-test, $p=0.0044$, Cohen's $d=0.920$).

330 To test for changes in implicit learning, we focused on short PT trials where explicit strategy is 331 suppressed^{41,47}. Unlike the High PT trials, adaptation expressed on short PT trials was similar during the 332 two exposures (Fig. 4B, middle); we found no difference in the rate of short PT learning (Fig. 4B, right, 333 Wilcoxon signed rank, $p=0.903$). Similarly, the difference in learning curves for exposures 1 and 2 (Fig. 4C, 334 middle) did not show any change after perturbation onset (Fig. 4C, right, Low PT, paired t-test, $p=0.624$).

335 These results suggested that savings relied solely on a time-consuming explicit strategy. Does this 336 mean that implicit learning was completely unaltered by prior exposure to the perturbation? The answer 337 depends on which errors drive implicit adaptation.

338 In the competition model, implicit learning is driven by target errors (Eq. (1)) that are also shared 339 with the explicit system. We fit this model to the behavior of each participant under the assumption that 340 the reach angle on low preparation time trials revealed the implicit state of adaptation, and the reach 341 angle on high preparation time trials revealed the sum of the implicit and explicit states of adaptation. 342 The model generated implicit (Fig. 4D, left and middle, blue) and explicit (Fig. 4D, left and middle, 343 magenta) states that tracked the behavior well in high PT trials (Fig. 4D, left and middle, solid black line) 344 as well as low PT trials (Fig. 4D, left and middle, dashed black line).

345 Unsurprisingly, given that High PT trials exhibited savings but Low PT trials did not, the model 346 predicted that explicit error sensitivity increased across exposures, thus leading to an increased rate of 347 adaptation (Fig. 4D, right, explicit; paired t-test, $p=0.016$, Cohen's $d=0.738$). However, the model

348 unmasked a surprising possibility; even though the implicit system showed no increase in learning rate on
349 Low PT trials (Figs. 4B&C, right), the model still indicated that the implicit system had increased its error
350 sensitivity across exposures (Fig. 4D, right, implicit, paired t-test, $p=0.023$, Cohen's $d=0.686$).

351 In contrast, when we fit the same data assuming that implicit adaptation was driven by SPE rather
352 than target error (Eq. (2), learning depends on rotation but not explicit strategy), the model (not shown
353 in Fig. 4) predicted that only explicit (paired t-test, $p=0.026$, Cohen's $d=0.673$) but not implicit (paired t-
354 test, $p=0.099$) error sensitivity had increased.

355 In summary, when we reanalyzed our earlier data, Eqs. (4) and (5) suggested that the same data
356 could be interpreted in two different ways. If we assumed that implicit learning is independent of explicit
357 strategy (independence equation), then only explicit strategy contributed to savings. This is in fact what
358 we had concluded in our original report. However, if we assumed that the implicit and explicit systems
359 learned from the same error (competition equation), then both implicit and explicit systems contributed
360 to savings. How can we determine which interpretation is more parsimonious with measured behavior?

361

362 *Competition with explicit strategy can alter measurement of implicit learning*

363 Suppose you arrive at your family dinner, but on this occasion are feeling particularly famished. Yet after
364 the meal, you are surprised to find that you ate the same amount as last week despite feeling hungrier.
365 Does this mean your hunger level was actually the same? No, not necessarily; because you are sharing the
366 meal with others, changes in their consumption rates alter the food available to you. So, eating the same
367 amount could mean that your sister sitting next to you was also hungrier than usual, taking more than
368 their normal share, and thus leaving less for you.

369 The competition equation (Eq. (4)) presents an analogous scenario, except here the "family" in
370 question is the implicit and explicit adaptive states, and the "food" that is available for consumption is
371 error. The competition model provides the insight that when the explicit system learns faster than before
372 (Fig. 4D, Day 2 vs. Day 1), it leaves less error to drive implicit learning. However, despite this reduced error
373 for the implicit system, performance on Low PT trials on Day 2 was comparable to Day 1 (Fig. 4B, right).
374 Thus, error sensitivity of the implicit system must also have increased from Day 1 to Day 2.

375 To understand how our ability to detect changes in implicit adaptation can be altered by explicit
376 strategy we constructed a competition map (Fig. 5A). Imagine that we want to compare behavior across
377 two timepoints or conditions. Fig. 5A shows how change in implicit error sensitivity (x-axis) and explicit
378 error sensitivity (y-axis) both contribute to measured implicit aftereffects (denoted by map colors), based
379 on the competition equation (Eq. (4)). The left region of the map (cooler colors) denotes combinations of
380 implicit and explicit changes that decrease implicit adaptation. The right region of the map (hotter colors)
381 denotes combinations that increase implicit adaptation. The middle black region represents combinations
382 that manifest as a perceived invariance in implicit adaptation (<5% absolute change in implicit adaptation).

383 Practically, this map defines several distinct regions (Fig. 5B). In Region A, there is a "true
384 decrease" in implicit adaptation; that is, implicit error sensitivity decreases between Timepoints 1 and 2
385 as does the total amount of implicit learning. Region D is similar, but for simultaneous increases in implicit
386 error sensitivity and total implicit learning ("true increase").

387 The other regions describe more surprising situations. In Region B, there is only a "perceived
388 decrease" in implicit learning; that is, implicit learning decreases, even though the implicit error sensitivity

389 has actually increased or remained the same. In Region E, there is only a “perceived increase” in implicit
390 learning; implicit learning increases, even though its error sensitivity decreased or remained the same.

391 Indeed, we have already explored these phenomena in Figs. 1 and 2. In Fig. 1, enhancing explicit
392 strategy decreased implicit learning without changing any implicit learning properties. The scenario is
393 equivalent to moving up the y-axis of the map (Fig. 5C, top). The same implicit system will decrease its
394 output (Fig. 5C, bottom) when normal levels of explicit strategy are increased (Fig. 5C, middle). On the
395 other hand, suppressing explicit strategy by gradually changing the perturbation appeared to increase
396 implicit learning without changing any implicit learning properties (Fig. 2). This scenario is equivalent to
397 moving down the y-axis of the map (Fig. 5D, top). The same implicit system will increase its output (Fig.
398 5D, bottom) when normal levels of explicit strategy are then suppressed (Fig. 5D, middle).

399 Now, let us consider the savings task in Fig. 4. The target error-driven (Eq. (1)) state space model
400 predicted (Fig. 3D) that explicit error sensitivity increased by approximately 70.6% during the second
401 exposure, whereas the implicit system’s error sensitivity increased by approximately 41.5% (Fig. 5E,
402 middle). These changes in implicit and explicit adaptation describe a single point in the competition map,
403 denoted by the gray circle in Fig. 5E (top). This experiment occupies Region C, which indicates that despite
404 the 41.5% increase in implicit error sensitivity, the total amount of implicit learning will increase by less
405 than 5% (Fig. 5E, bottom). In other words, the competition equation suggests the possibility that savings
406 could have occurred in the implicit system but was hidden by a dramatic increase in explicit strategy.

407 To test this prediction, we can suppress explicit adaptation, thus eliminating competition (Fig. 5F,
408 middle). Such an intervention would move our experiment from Region C to Region D (Fig. 5F, top) where
409 we will observe greater change in the implicit process (Fig. 5D, bottom). Thus, we performed a new
410 experiment to test this prediction.

411
412 *Savings in implicit learning is unmasked by suppression of explicit strategy*

413 The key prediction is that removal of explicit strategy will unmask savings in implicit learning (Fig. 5F). We
414 exposed participants (Experiment 3) to two 30° rotations, separated by an intervening period of washout.
415 To suppress explicit strategy, we forced participants to move under strict reaction time constraints on
416 every trial. As a result, participants reached to each of the four targets with a latency of approximately
417 200 ms (Fig. 6B, top), nearly 100 ms sooner than the Low PT condition used in our earlier experiment²⁸
418 (Fig. 6A). When reaction time was limited on all trials, the learning rate during the second exposure (Fig.
419 6B, middle) exhibited a marked increase (Fig. 6C, no comp.; Wilcoxon signed rank, $p=0.014$, Cohen’s
420 $d=0.637$). This enhancement in learning developed immediately after perturbation onset (Fig. 6B, bottom;
421 Fig. 6C, bottom, no comp., paired t-test, $p=0.008$, Cohen’s $d=1.06$).

422 In summary, when explicit learning was suppressed, Low PT behavior exhibited savings (Fig. 6B).
423 But when explicit strategies remained active, Low PT behavior did not exhibit any change in learning rate
424 (Fig. 6A). One possible explanation for these observations is that an implicit system expressible at Low PT
425 exhibits savings, but this can be masked by competition with explicit strategy.

426
427 *Impairments in implicit learning lead to anterograde interference*

428 When two opposing perturbations (say A and B) are experienced in sequence, exposure to perturbation
429 A decreases the rate of learning in B (anterograde interference). Like savings^{29,32,48,49}, we recently

430 suggested that impaired learning in *B* is caused by a change in error sensitivity²⁶. Might this change in
431 error sensitivity depend on the implicit learning system?

432 We exposed two groups of participants to opposing visuomotor rotations of 30° and -30° in
433 sequence (Experiment 4). In one group, the perturbations were separated by a 5-minute break (Fig. 7A).
434 In a second group, the break was 24 hours in duration (Fig. 7B). We suppressed explicit strategies by
435 strictly limiting reaction time. Under these constraints, participants executed movements at latencies
436 slightly greater than 200 ms (Figs. 7A&B, middle, blue). These reaction times were approximately 50%
437 lower than those observed when no reaction time constraints were imposed on participants, as in Lerner
438 & Albert et al.²⁶ (Figs. 7A&B, middle, green).

439 We found that implicit adaptation during the second rotation period was significantly impaired
440 after a 5-minute break (Fig. 7A, bottom). The rate of implicit learning decreased by approximately 75%
441 (Fig. 7C, 5min, limit). Passage of time partially improved this deficit (Fig. 7B, bottom). When the rotations
442 were separated by a 24 hr break, implicit learning rate was impaired by only 55% (Fig. 7C, 24 hr, limit).

443 Thus, we can conclude that suppression of explicit strategy revealed an anterograde deficit in
444 implicit learning that did not completely resolve after 24 hours, perhaps even stronger than that observed
445 when no reaction time constraints are imposed²⁶ (Fig. 7C, Lerner et al. (2020), no limit; see Discussion).

446

447 *The implicit system may adapt to multiple target errors at the same time*

448 The idea that a single shared error drives both implicit and explicit learning is quite surprising. After all, in
449 earlier work by Mazzoni and Krakauer¹², it appeared that implicit learning was driven by outcome-
450 independent prediction errors (Eq. (2)) that were unaltered by explicit strategy. Yet, in Figs. 1-7, implicit
451 learning clearly depended, at least in part, on target error, and exhibited clear interactions with explicit
452 strategy. How does one reconcile the current results with the results of Mazzoni and Krakauer?

453 To explore this question, we revisited these earlier experiments. In Mazzoni and Krakauer, we
454 tested two sets of participants. In the no-strategy group, participants adapted to a standard 45° rotation
455 (Fig. 8A, blue, no-strategy, adaptation) followed by washout (Fig. 8A, blue, no-strategy, washout). In a
456 second group, participants made two initial movements with the rotation (Fig. 8A, red, strategy, 2
457 movements no instruction). Then we told participants to aim towards a neighboring target (45° away)
458 which entirely compensated for the rotation. Unlike the experiments described in Figs. 1-7, in which only
459 the primary target was visible, in Mazzoni and Krakauer both the primary target and the aiming target
460 were always visible. Participants immediately adopted the aiming strategy, bringing error with respect to
461 the primary target to zero (Fig. 8A, red, strategy, instruction). Surprisingly, after eliminating this error,
462 their movement angles gradually drifted beyond the primary target, overcompensating for the rotation.
463 These involuntary changes implicated an implicit process.

464 When we compared the rate of learning with and without strategy, we found that it was not
465 different over the initial exposure to the perturbation (Fig. 8B, gray, compare learning rates; compare
466 mean adaptation over first 24 movements, two-sample t-test, $p=0.223$). This suggested that implicit
467 adaptation was unaltered by the abrupt change in explicit strategy, and equally importantly, was not
468 driven by error between the cursor and target (Eq. (1)), but rather by a sensory prediction error (Eq. (2)).

469 However, there remained an unsolved puzzle. While the initial rates of adaptation were the same
470 irrespective of strategy, adaptation diverged later in learning (Fig. 8B, compare strategy and no-strategy
471 curves after the initial gray region; two-sample t-test, $p<0.005$), with the no-strategy group achieving

472 greater implicit learning (see aftereffect in Fig. 8C; two-sample t-test, $p < 0.005$). Might these late
473 differences have been caused by participants in the strategy group abandoning the explicit strategy as it
474 led to larger and larger errors? This possibility seemed unlikely. When we asked participants to stop re-
475 aiming (Fig. 8A, do not aim rotation on) their movement angle changed by 47.8° (difference between 3
476 movements before and 3 movements after instruction), indicating that they had continued to maintain
477 the instructed explicit re-aiming strategy near 45° .

478 We wondered if interactions between implicit and explicit learning could help solve these puzzles.
479 First, we considered the competition model that best described the experiments in Figs. 1-7. In this model,
480 the implicit system is driven exclusively by error with respect to the primary target (Eq. (1)), which is
481 shared with explicit strategy (Fig. 8D, top, e_1). While this model predicted learning in the standard no-
482 strategy condition, it failed to account for the drift observed when participants were given an explicit
483 strategy (Fig. 8D, no learning in strategy group). This was not surprising. If implicit learning is driven by the
484 primary target's error, it will not adapt in the strategy group because participants explicitly reduce target
485 error to zero at the start of adaptation (note that -45° in Fig. 8D actually means a 0° primary target error).

486 We next considered the possibility that implicit learning was driven exclusively by error with
487 respect to the aimed target (target 2, Fig. 8E, top, e_2), as we concluded in our original study¹². While this
488 model correctly predicted implicit learning in both the no-strategy and strategy conditions, it could not
489 account for any differences in learning that emerged later during the adaptation period (Fig. 8E, bottom).

490 Finally, we noted that participants in the strategy group were given two contrasting goals. One
491 goal was to aim for the secondary target, whereas the other goal was to move the cursor through the
492 primary target (both targets were always visible). Therefore, we wondered if participants in the strategy
493 group learned from two distinct errors: cursor with respect to target 1, and cursor with respect to target
494 2 (Fig. 8F, top). In contrast, participants in the no-strategy group attended solely to the primary target,
495 and thus learned only from the error between the cursor and target 1. Thus, we imagined that implicit
496 learning in the strategy group was driven by the two different kinds of target error:

$$497 \begin{aligned} x_{i,1}^{(n+1)} &= a_i x_{i,1}^{(n)} + b_i e_1^{(n)} \\ x_{i,2}^{(n+1)} &= a_i x_{i,2}^{(n)} + b_i e_2^{(n)} \end{aligned} \quad (6)$$

498 These two modules then combined to determine the total amount of implicit learning (i.e., $x_i = x_{i,1} + x_{i,2}$).

499 Remarkably, when we applied the dual target error model (Eq. (6)) to the strategy group, and the
500 single target error model (Eqs. (1) & (3)) to the no-strategy group, the same implicit learning parameters
501 (a_i and b_i) closely tracked the observed group behaviors (black model in Fig. 8B). These models correctly
502 predicted that initial learning would be similar across the strategy and no-strategy groups (compare curves
503 in gray region in Fig. 8F bottom), but would diverge later during adaptation. How was this possible?

504 In Fig. 8G (left), we show how the errors with respect to the primary target and the aiming target
505 evolve as a function of time for the dual target model. Due to the instructed strategy, primary target error
506 is reduced to zero at the start of adaptation (see Fig. 8G, original target error curve). Therefore, early in
507 learning, the implicit system is driven predominantly only by one error source in both the strategy and no-
508 strategy groups, leading to similar adaptation rates. However, as the error with respect to the aimed
509 target decreases, error with respect to the primary target increases but in the opposite direction (Fig. 8G;
510 see schematic in Fig. 8F for intuition). Therefore, the primary target error opposes further adaptation to

511 the aiming target error. This counteracting force causes implicit adaptation to saturate prematurely.
512 Hence, participants in the no-strategy group, who do not experience this error conflict, adapt more.

513 This re-analysis suggests that when people move a cursor to one visual target (Objective 1), while
514 aiming at another visual target (Objective 2), each target appears to contribute a separate implicit error
515 source. When these two error sources conflict with one another, the implicit learning system can exhibit
516 an unintuitive attenuation in the total amount of adaptation. Thus, while explicit strategies can suppress
517 implicit learning via competition (Figs. 1-7), a different type of suppression can occur when parallel implicit
518 learning systems attempt to solve two conflicting objectives, as in Fig. 1B.

519

520 *The persistence of sensory prediction error, in the absence of target error*

521 Our re-analysis in Figs. 8A-G, suggested that when participants use a second target to aim their reach, this
522 additional landmark creates a second implicit error source. To what extent does this error depend on the
523 target's physical presence in the workspace? Taylor & Ivry²¹ tested this idea, repeating the instruction
524 paradigm used by Mazzoni and Krakauer, though with nearly 4 times the number of adaptation trials (Fig.
525 8H, instruction with target, black). Interestingly, while the reach angle exhibited the same implicit drift
526 described by Mazzoni and Krakauer, with many more trials participants eventually counteracted this drift
527 by modifying their explicit strategies, bringing their target error back to zero (Fig. 8H, black). At the end of
528 adaptation, participants exhibited large implicit aftereffects after being instructed to no longer aim (Fig.
529 8H, right, aftereffect; $t(9)=5.16$, $p<0.001$, Cohen's $d=1.63$).

530 However, in a second experiment, participants were taught how to re-aim their reach angles
531 during an initial baseline period, but during adaptation itself, they were not provided with physical aiming
532 targets (Fig. 8H, instruction without target). Thus, in this case, only an SPE could drive implicit adaptation
533 towards the aimed location. Even without physical aiming landmarks, participants immediately eliminated
534 error at the primary target after being instructed to re-aim (Fig. 8H, middle, yellow). Remarkably however,
535 without the physical aiming target, these participants did not exhibit an implicit drift in reach angle at any
536 point during the adaptation period, and exhibited only a small implicit aftereffect during the washout
537 period (Fig. 8H, right, $t(9)=3.11$, $p=0.012$, Cohen's $d=0.985$). In fact, the aftereffect was approximately 3
538 times larger when participants aimed towards a physical target during adaptation than when this target
539 was absent (Fig. 8H, right, aftereffect; two-sample t-test, $t(18)=2.85$, $p=0.012$, Cohen's $d=0.935$).

540 Thus, these data suggested a remarkable depth to the implicit system's response to error. While
541 implicit adaptation was greatest in response to a target error, removal of the physical target still resulted
542 in what appeared to be SPE-driven learning, albeit to a smaller degree.

543

544 **Discussion**

545 Sensorimotor adaptation benefits from learning in two parallel systems: one that has access to explicit
546 knowledge^{11,51}, and another that relies on implicit, unconscious correction^{12,13,45}. Here we show that each
547 system is responsive to task-related errors between the subject's cursor and the target^{17,23}. In such cases,
548 when the error is shared competition occurs between these systems, such that when the explicit system
549 increases its response, errors are more rapidly depleted, thus decreasing the driving force for implicit
550 adaptation as in Fig. 1A. This model suggests that an explicit strategy can potentially mask changes in
551 implicit error sensitivity (Fig. 4). Indeed, suppressing the explicit strategy unveiled strong increases (Fig.

552 6) and decreases (Fig. 7) in putative implicit adaptation that were consistent with two hallmarks of
553 learning: savings and interference.

554 However, in various cases, this task error could not explain implicit adaptation by itself. For
555 example, when participants aimed their hand to one visual target, but the cursor to another visual target,
556 the implicit system appeared to balance two errors (Fig. 8): an error with respect to the primary target,
557 and an error with respect to the aimed target, an SPE. These two errors were coupled together such that
558 decreases in error with respect to the aimed target would increase error with respect to the primary
559 target. Thus, the data suggested a second way that the implicit system can exhibit competition: two
560 separate implicit learning modules can interfere with one another when they try to solve conflicting
561 objectives (Fig. 1B).

562 Describing sensorimotor adaptation in terms of explicit and implicit contributions is important
563 because these systems may rely on different neural structures. Explicit learning mechanism are likely
564 dependent on cortical involvement^{43,52,53}, whereas implicit learning mechanisms at least partly engage the
565 cerebellum^{7,20,54–58}. Our results suggest that in some learning contexts, these two systems can compete
566 with each other, as they strive to respond to a common error.

567

568 *Flexibility in the implicit response to error and the properties of savings and interference*

569 When two similar sensorimotor perturbations are experienced in sequence, the rate of relearning is
570 enhanced during the second exposure^{28,29,32,49,59}. This hallmark of memory^{60,61} is referred to as savings.
571 Savings is often quantified based on differences in the learning curves for each exposure^{28,34}, or the rate
572 of adaptation⁶². While these conventions are intuitive, they are based on an important underlying
573 assumption: when one learning component's properties change, its contribution to overall adaptation will
574 also change. Here we describe why this intuition may not always be true.

575 The state space model^{9,39,40} quantifies behavior using two process: learning and forgetting. This
576 model describes savings as a change in one's sensitivity to error^{29,32,48}. When similar errors are experienced
577 on consecutive trials, the brain becomes more sensitive to their occurrence and responds more strongly
578 on subsequent trials^{37,48,63}. Generally, as error sensitivity increases, so too does the rate at which we adapt
579 to the perturbation (e.g., High PT trials in Fig. 4). However, under certain circumstances, changes in one's
580 implicit sensitivity to error may not lead to differences in measured behavior (e.g., Low PT trials in Fig. 4).

581 The reason is competition. If implicit systems adapt to target errors (Eq. (1)), they are altered not
582 solely by the rotation but also explicit strategy. When strategy is enhanced, it reduces the error available
583 for implicit learning. Therefore, although the implicit system may become more sensitive to error, this
584 increase in sensitivity is canceled out by the decrease in error size. If true, this would mean that implicit
585 processes can change in ways that are hidden within measured behavior.

586 For example, recent lines of evidence have suggested that increases in learning rate depend solely
587 on the explicit recall of past actions. Implicit adaptation does not seem to contribute to faster re-learning,
588 whether its magnitude is measured through verbal reports³⁴, or by restricting movement preparation
589 time^{28,33} (Fig. 4). These data might suggest that the implicit system is unaltered by past experience.
590 However, when reaction time is limited during both exposures, thus suppressing explicit contributions to
591 behavior, we found that the implicit system exhibited savings (Fig. 6). This would be consistent with recent
592 evidence that savings requires the presence of task-related errors¹⁷, which can be siphoned away by the
593 explicit system. Thus, what appears to be a disconnect between studies that have detected increases in

594 only the explicit learning rate^{28,33–36}, and studies that have detected increases in the implicit learning
595 rate^{17,37,38}, may actually be consistently described by the competition equation (Eq. (4)).

596 This competition equation can be used to construct a map that describes how implicit adaptation
597 should change based on the properties of implicit and explicit systems. When both implicit and explicit
598 systems become more sensitive to error, the explicit response can hide changes in the implicit response
599 (Fig. 5B, Region C). In fact, drastic enhancement in explicit adaptation could even lead to a decrease in
600 implicit learning, even when implicit error sensitivity has increased (Fig. 5B, Region B). Indeed this
601 prediction might explain cases whereby re-exposure to a rotation increases explicit strategies, but appears
602 to attenuate implicit learning^{33,36,64}. For example, a recent study by Huberdeau and colleagues³³, seven
603 exposures to a rotation led to caching of the explicit strategy, with a simultaneous decrease in the implicit
604 aftereffect. However, such a mechanism cannot account for decreases in implicit learning seen in
605 response to invariant error-clamp perturbations³⁶, which presumably are free of explicit strategy.

606 Recent studies have shown that with multiple exposures to a visuomotor rotation, the explicit
607 response to the perturbation can be cached and expressed at lower reaction times^{33,47}. Could caching of
608 an explicit strategy have contributed to the savings we measured under reaction time constraints in
609 Experiment 3 (Fig. 6)? This possibility seems unlikely. First, there appears to be little such caching after
610 only two exposures to a rotation. Otherwise, Haith and colleagues²⁸ should also have observed savings on
611 Low PT trials. In addition, the rotation occurred at four separate targets in Experiment 3, but only one
612 target in Haith and colleagues. Lastly, reaction time constraints in Experiment 3 induced shorter reach
613 latencies (nearing 200 ms), than those used by Haith and colleagues (300 ms). These conditions would be
614 expected to suppress explicit caching. Nevertheless, future studies are needed to better understand the
615 conditions (e.g., number of targets, reaction time constraints) that permit caching of the explicit process,
616 and how these cached responses interact with implicit learning.

617 Finally, it is important to distinguish between reductions in implicit adaptation which appear to
618 be driven by explicit suppression, versus those that are caused by a direct impairment in the implicit
619 response to error. For example, when two opposing perturbations are experienced sequentially, the
620 response to the second exposure is impaired by anterograde interference^{9,25,27,65}. Recently, we linked
621 these impairments in learning rate to a transient reduction in error sensitivity which recovers over time²⁶.
622 Here, we limited reaction time to isolate the potential implicit contributions to this impairment.
623 Impairments in the implicit system were large and long-lasting (Fig. 7C), persisting even after 24 hours.

624 Interestingly, when we performed a similar experiment without restricting reaction time²⁶, we
625 found a smaller impairment in learning rate that almost fully recovered after 24 hours (Fig. 7C, no limit).
626 These differences might suggest that uninhibited explicit strategies compensate for lingering deficits in
627 implicit adaptation. In fact, Leow and colleagues¹⁷ recently demonstrated that prior exposure to task
628 errors in one direction increases the rate at which participants explicitly adapt to a visuomotor rotation in
629 the opposite direction, suggesting that explicit strategies might exhibit improvements rather than
630 impairments during interference protocols. However, it is important to point out that our reaction time-
631 limited experiment in Fig. 7, differed from our earlier work²⁶ (see Methods; reaching versus pointing as
632 well as differences in trial count). Thus, our data motivate the need for future experiments to understand
633 how explicit strategies contribute to adaptation during anterograde interference.

634

635 *Competition-driven enhancement and suppression of implicit adaptation*

636 Our data caution that when implicit learning increases or decreases, this does not necessarily mean that
637 the implicit system has altered its response to error.

638 For example, when participants are made aware of a visuomotor rotation before it is introduced,
639 their explicit response is drastically enhanced^{15,16}. These increases in explicit strategy are coupled to
640 decreases in implicit adaptation. A similar phenomenon can be observed in other experiments where
641 participants are provided with visual landmarks scattered on either side of the target. When participants
642 use these landmarks to report their intended aiming direction, reporting frequency increases explicit
643 strategy use, but decreases implicit adaptation⁶⁶⁻⁶⁸. Furthermore, participants themselves exhibit varying
644 degrees of strategy, leading to negative subject-to-subject associations between implicit and explicit
645 learning^{15,16,41} (Fig. 3).

646 Given these changes in implicit adaptation, it may at first seem surprising that in some cases,
647 implicit learning remains constant across large changes in perturbation magnitude^{15,69}. For example, in
648 Neville and Cressman¹⁵, while awareness decreased implicit adaptation, the implicit aftereffect was
649 mostly invariant across each rotation size (Fig. 1). Notably, the competition equation (Eq. (4)) can again
650 account for this observation. This equation shows that the driving force for adaptation is not the size of
651 the rotation alone, but rather the difference between the rotation and explicit strategy (Fig. S1D).

652 This competition between implicit and explicit adaptation helps to reveal the errors which drive
653 implicit learning. This competitive relationship (Eq. (4)) naturally arises when implicit systems are driven
654 by errors in task outcome (Eq. (1)), but not errors between the cursor and intended aiming angle (Eq. (2)).
655 We can observe these negative interactions not solely when enhancing explicit strategy, but also when
656 suppressing re-aiming. For example, in cases where perturbations are introduced gradually, thus reducing
657 conscious awareness, implicit “procedural” adaptation appears to increase^{38,42,70} (Fig. 2). Similarly, when
658 participants are required to move with minimal preparation time, thus suppressing time-consuming
659 explicit re-aiming^{28,41,47}, the total extent of implicit adaptation also appears to increase^{37,41}.

660 Lastly, competition may help to describe not only why implicit learning can vary across two
661 experimental conditions, but also across individuals within a single experiment as in Fig. 3H. In one prime
662 example, Miyamoto and colleagues¹⁴ exposed participants to a sum-of-sines rotation. Curiously,
663 participants with more vigorous explicit responses to the perturbation exhibited less vigorous implicit
664 learning. In a second example, Fernandez-Ruiz and colleagues⁴¹ observed that participants who increased
665 their movement preparation time rapidly counteracted a rotation, but also exhibited smaller aftereffects
666 during washout. And as a third example, when Bromberg et al.⁶⁸ measured eye movements during
667 adaptation, participants who tended to look towards their re-aiming locations not only exhibited greater
668 explicit strategies, but less implicit adaptation.

669 In other words, participants that used cognitive strategies to adapt exhibited less procedural
670 learning⁴¹. To explain these individual correlations, Miyamoto et al.¹⁴ suggested that there may be an
671 intrinsic relationship between implicit and explicit sensitivity to error: when an individual’s explicit error
672 sensitivity is high, their implicit error sensitivity is low. Here our results describe a different way to account
673 for the same observation (Fig. 3H). In Experiment 1, we used the competition equation (Eq. (4)) to predict
674 each individual’s implicit adaptation from their measured explicit strategy, assuming each participant had
675 the same sensitivity to error. This one equation accurately accounted for the inverse relationship between
676 implicit and explicit aftereffects. Thus, negative individual-level correlations between implicit and explicit

677 adaptation can arise from subject-to-subject variation in strategy, even when implicit error sensitivity is
678 invariant across participants.

679 Finally, it is important to consider how generalization may have altered our implicit learning
680 measures. Earlier studies have shown that when participants are asked to report their aiming direction
681 using a ring of visual landmarks, implicit learning generalizes around the reported aiming direction^{71,72}.
682 Thus, participants who aim further away from the target may show smaller implicit adaptation when
683 asked to “move straight to the target” simply due to generalization. However, the expected magnitude of
684 this effect ($\approx 5^\circ$; see Fig. S5B for aim-target displacement⁷¹ of 22.5° and S3A for aim-target displacement⁷²
685 of 30°) does not seem large enough to account for the large variation we measured in implicit adaptation
686 (ranges of 17° in Fig. 2F, 32° in Fig. 3D, 14° in Fig. 3H, 17° in Fig. 3L). In the studies considered here,
687 participants trained at either 3 (Fig. 1), 4 (Figs. 3H&L), 8 (Fig. 3D), or 12 (Fig. 2) targets, as opposed to 1
688 target in these earlier generalization studies^{71,72} (Figs. S3A and S3B). Thus, generalization-based decreases
689 in implicit learning would likely be smaller in the current work, given that the generalization function
690 widens with additional training targets^{73,74}.

691 Along these lines, Neville and Cressman¹⁵ asked whether implicit learning varied across their 3
692 training targets, 2 of which corresponded with an “aim solution”, 1 of which did not; they did not find any
693 change in implicit learning across each target. In addition to differences in training targets, the studies
694 considered here did not use aiming reports to measure explicit learning, which were employed on each
695 trial to measure aim direction in the earlier generalization studies. This may play another important role
696 in the generalization function. For example, in these earlier generalization studies implicit learning
697 measured via reporting was larger than that measured when reaching straight to the target (Fig. S5C), due
698 to generalization. However, in Experiment 1, when we asked participants to report their aim at the end
699 of adaptation, we found greater implicit learning on the straight-ahead reaching probes, than in the aim
700 reports (Fig. S5E), opposite the generalization expectation. A similar phenomenon was noted recently
701 when aim reports were used sparsely during adaptation⁷⁵ (Fig. S5D). All in all, while it does not seem that
702 generalization played a major role in our primary results, future studies are needed to measure how
703 generalization may differ across tasks, as well as different types of error signals (e.g., target error vs. SPE).
704

705 *Error sources that drive implicit adaptation*

706 Mazzoni and Krakauer¹² exposed participants to a visuomotor rotation, but also provided instructions for
707 how to re-aim their hand to achieve success. While participants immediately used this strategy to move
708 the cursor through the target, the elimination of task error failed to stop implicit adaptation. These data
709 suggested that implicit systems responded to errors in the predicted sensory consequence of their
710 actions^{20,76}, rather than errors in hitting the target.

711 However, such a model, where implicit systems learn solely based on the angle between aiming
712 direction and the cursor (Eq. (2)), could not account for the implicit-explicit interactions we observed in
713 some of the data (Figs. 1-3). These interactions could only be described by an implicit error source that is
714 altered by explicit strategy, such as the angle between the cursor and the target (Eq. (1)). For example, in
715 Experiments 1&2, participants did not aim straight to the target, but rather adjusted their aiming angle
716 by $5\text{--}20^\circ$ (Fig. 3). These changes in re-aiming appeared to alter implicit adaptation via errors between the
717 cursor and the target. This target-cursor error source (Eq. (1)) used in our state-space model (Eq. (3))

718 appeared to provide an accurate account of short-term visuomotor adaptation across a number of
719 studies^{14–16,24,37,41,42}.

720 We do not mean to suggest however, that implicit adaptation is solely driven by a single target
721 error. In fact, there are many cases where this idea fails^{11,12,21}, beyond the Mazzoni and Krakauer study.
722 We speculate that one feature which alters implicit learning is the simultaneous presence of multiple
723 visual targets. In Figs. 1–7, there was only one visual target on the screen at a time. However, in Mazzoni
724 and Krakauer (Fig. 8), there were two important visual targets: the adjacent target towards which
725 participants explicitly aimed their hand, and the original target towards which the cursor should move.
726 Thus, in theory there were two potential visual target errors. Interestingly, when we considered the
727 possibility that the implicit system adapted to both errors at the same time, we could more completely
728 account for these earlier data (Fig. 8F).

729 The idea that both kinds of visual error (cursor with respect to the primary target, and cursor with
730 respect to the aimed target) drive implicit learning, could potentially help to describe other confounding
731 observations. For example, in cases where landmarks are provided to report explicit aiming^{11,24,72}, target-
732 cursor error is often rapidly eliminated, but implicit adaptation continues to increase over time. Our dual-
733 error model (Eq. (6)) would explain this continued adaptation based on persistent aim-cursor error.

734 However, the nature of this aim-cursor error remains rather uncertain. For example, while this
735 error source generates strong adaptation when the aim location coincides with a physical target (Fig. 8H,
736 instruction with target), implicit learning is observed even in the absence of a physical aiming landmark²¹
737 (Fig. 8H, instruction without target), albeit to a smaller degree. This latter condition strongly implicates an
738 SPE learning mechanism. Thus, it may be that the aim-cursor error is actually an SPE that is enhanced by
739 the presence of a physical target. In this view, implicit learning is driven by a target error module and an
740 SPE module that is enhanced by a visual target error^{17,23,77}. These various implicit learning modalities are
741 likely strongly dependent on both implicit and explicit contexts, in ways we do not currently understand.

742 We speculate that the cerebellum might play an important role in this model of implicit
743 adaptation^{55,57,78–80}. Current models propose that complex spikes in Purkinje cells (P-cells) in the cerebellar
744 cortex lead to LTD (Marr-Albus-Ito hypothesis). These complex spikes are reliably evoked by olivary input
745 in response to a sensory error^{79,81,82}. However, different P-cells are activated by different error directions,
746 thus organizing P-cells into error-specific subpopulations^{81,82}. Therefore, our model suggests that two
747 different sources of error might simultaneously transduce learning in two different P-cell subpopulations,
748 which then combine their adapted states into a total implicit correction at the level of the deep nuclei.
749 Thus, errors based on the original target, and the aiming target, might simultaneously activate two implicit
750 learning modules in the cerebellum (Fig. 8G).

751 Alternatively, it is equally possible that these aim-cursor errors and target-cursor errors engage
752 separate brain regions both inside and outside the cerebellum. In this view, an interesting possibility is
753 that patients with cerebellar disorders^{20,54,56,83,84} may have learning deficits specific to one error but not
754 the other⁵⁶. These possibilities remain to be tested.

755
756

757 **Methods**

758 Here we describe the experiments and corresponding analysis reported in the main text. Much of this
759 work involves reevaluation of earlier literature; this includes data from Haith and colleagues²⁸ in Figs. 4&6,
760 data from Lerner and Albert et al.²⁶ in Fig. 7, data from Neville and Cressman¹⁵ in Fig. 1, data from Saijo
761 and Gomi⁴² in Fig. 2, data from Fernandez-Ruiz et al.⁴¹ in Fig. 3, data from Mazzoni and Krakauer¹² in Fig.
762 8, and data from Taylor and Ivry²¹ in Fig. 8. Furthermore, some generalization data^{71,72} was considered in
763 Fig. S5. The relevant details of these studies are summarized in the sections below alongside the new data
764 collected for this work (Experiments 1-4).

765

766 *Participants*

767 A detailed description of participants in Haith and colleagues²⁸ (n=14), Lerner and Albert et al.²⁶ (n=34 for
768 5 min and 24 hr groups), Neville and Cressman¹⁵ (n=63), and Mazzoni and Krakauer¹² (n=18), Saijo and
769 Gomi⁴² (n=9 for abrupt, n=9 for gradual), Fernandez-Ruiz et al.⁴¹ (n=9), and Taylor and Ivry²¹ (n=10 for
770 instruction with visual target, n=10 for instruction without visual target) are described in their respective
771 papers. All volunteers (ages 18-62) in Experiments 1-4 were neurologically healthy and right-handed.
772 Experiment 1 include n=9 participants (5 Male, 4 Female) in the No PT limit group and included n=13
773 participants (6 Male, 7 Female) in the PT Limit group. Experiment 2 included n=17 participants (10 Male,
774 7 Female). Experiment 3 included n=10 participants (6 Male, 4 Female). Experiment 4 included n=20
775 participants (10 Male, 10 Female). Experiments 1-4 were approved by the Institutional Review Board at
776 the Johns Hopkins School of Medicine.

777

778 *Apparatus*

779 In Experiments 1, 3, and 4 participants held the handle of a planar robotic arm and made reaching
780 movements to different target locations in the horizontal plane. The forearm was obscured from view by
781 an opaque screen. An overhead projector displayed a small white cursor (diameter = 3mm) on the screen
782 that tracked the motion of the hand. Throughout testing we recorded the position of the handle at
783 submillimeter precision with a differential encoder. Data were recorded at 200 Hz. Protocol details were
784 similar for Haith and colleagues²⁸, Neville and Cressman¹⁵, Saijo and Gomi⁴², and Fernandez-Ruiz et al.⁴¹ in
785 that participants gripped a two-link robotic manipulandum, were prevented from viewing their arm, and
786 received visual feedback of their hand position in the form of a visual cursor. In Lerner and Albert et al.²⁶,
787 participants performed pointing movements with their thumb and index finger while gripping a joystick
788 with their right hand. In Mazzoni and Krakauer¹², participants rotated their hand to displace an infrared
789 marker placed on the index finger. In Taylor and Ivry²¹, hand position was tracked via a sensor attached
790 to the index finger while participants made horizontal reaching movements along the surface of a table.
791 In Experiment 2, participants were tested remotely on their personal computer. They moved a cursor on
792 the screen by sliding their index finger along the track pad.

793

794 *Visuomotor rotation*

795 Experiments 1-4 followed a similar protocol. At the start of each trial, the participant brought their hand
796 to a center starting position (circle with 1 cm diameter). After maintaining the hand within the start circle,
797 a target circle (1 cm diameter) appeared in 1 of 4 positions (0°, 90°, 180°, and 270°) at a displacement of
798 8 cm from the starting circle (in Experiment 2, 8 targets were actually used, spaced in increments of 45°).

799 Participants then performed a “shooting” movement to move their hand briskly through the target. Each
800 experiment consisted of epochs of 4 trials (or 8 trials for Experiment 2) where each target was visited once
801 in a pseudorandom order.

802 Participants were provided audiovisual feedback about their movement speed and accuracy. If a
803 movement was too fast (duration < 75ms) or too slow (duration > 325ms) the target turned red or blue,
804 respectively. If the movement was the correct speed, but the cursor missed the target, the target turned
805 white. Successful movements were rewarded with a point (total score displayed on-screen), an on-screen
806 animation, and a pleasing tone (1000 Hz). If the movement was unsuccessful, no point was awarded and
807 a negative tone was played (200 Hz). Participants were instructed to obtain as many points as possible
808 throughout the experimental session.

809 Once the hand reached the target, visual feedback of the cursor was removed, and a yellow
810 marker was frozen on-screen to provide static feedback of the final hand position. At this point,
811 participants were instructed to move their hand back to the starting position. The cursor remained hidden
812 until the hand was moved within 2 cm of the starting circle.

813 Movements were performed in one of three conditions: null trials, rotation trials, and no feedback
814 trials. On null trials, veridical feedback of hand position was provided. On rotation trials, the on-screen
815 cursor was rotated relative to the start position. On no feedback trials, the subject cursor was hidden
816 during the entire trial. No feedback was given regarding movement endpoint, accuracy, or timing.

817 As a measure of adaptation, we analyzed the reach angle on each trial. The reach angle was
818 measured as the angle between the hand and the target (relative to the start position), at the moment
819 where the hand exceeded 95% of the target displacement.

820 Experiments in Haith and colleagues²⁸, Lerner and Albert et al.²⁶, Neville and Cressman¹⁵, Taylor
821 and Ivry²¹, Saijo and Gomi⁴², Fernandez-Ruiz et al.⁴¹, and Mazzoni and Krakauer¹² were collected using
822 similar, but separate protocols. For a full description of these paradigms, please consult the corresponding
823 manuscripts. Important differences between these experiments and the rotation protocol mentioned
824 above are briefly described in the sections below.

825
826 *Statistics*
827 Parametric (t-test) and nonparametric (Wilcoxon signed-rank test) tests were performed in MATLAB
828 R2018a. For these tests, we report the p-value, and Cohen’s d as a measure of effect size.

829
830 *Competition Map*
831 To illustrate the way implicit and explicit systems might interact, we used a state space model (Eqs. (1-3))
832 where implicit and explicit learning were driven by target errors. Similar to the implicit system described
833 in Eq. (3), we modeled explicit learning as a process of learning and forgetting^{14,24}:

$$x_e^{(n+1)} = a_e x_e^{(n)} + b_e e^{(n)} \quad (7)$$

834 Here, a_e and b_e represent the explicit system’s retention factor and error sensitivity. Together Eqs. (3) and
835 (7) describe how implicit and explicit systems adapt to error between the target and cursor (Eq. (1)).

836
837 Because implicit and explicit systems share a common error source in this target error model,
838 their responses will exhibit competition. That is, increases in explicit adaptation will necessarily be coupled
839 to decreases in implicit adaptation. To summarize this interaction, we created a competition map. The

840 competition map describes common scenarios in which the goal is to compare two different learning
841 curves. For example, one might want to compare the response to a 30° visuomotor rotation under two
842 different experimental conditions. Another example would be savings, where we compare adaptation to
843 the same perturbation at two different timepoints. In these cases, it is common to measure the amount
844 of implicit and explicit adaptation, and compare these across conditions or timepoints.

845 The critical point is that changes in the amount of implicit adaptation reflect the modulation of
846 both implicit and explicit responses to error. To demonstrate this idea, we needed a way to quantify the
847 amount of implicit adaptation. For this, we chose the steady-state amount of implicit learning. As
848 described in the main text, the steady-state level of implicit adaptation can be derived from Eqs. (1-3).
849 This derivation resulted in the competition equation shown in Eq. (4). Note that Eq. (4) predicts the steady-
850 state level of implicit learning from the implicit retention factor, implicit error sensitivity, mean of the
851 perturbation, and critically, the steady-state explicit strategy. If the explicit system is also described using
852 a state space model as in Eq. (7), it is easy to show that Eq. (4) can be equivalently expressed in terms of
853 the implicit and explicit learning parameters according to Eq. (8):

$$854 \quad x_i^{ss} = \frac{b_i(1-a_e)}{(1-a_i+b_i)(1-a_e+b_e)-b_ib_e} r \quad (8)$$

855 Eq. (8) provides the total amount of implicit adaptation as a function of the retention factors, a_i and a_e , as
856 well as the error sensitivities, b_i and b_e . We used Eq. (8) to construct the competition map in Fig. 5A, by
857 comparing the total amount of implicit learning across a reference condition and a test condition.

858 For our reference condition, we fit our state space model to the mean behavior in Haith et al.²⁸
859 (Fig. 4B, Day 1, left). This model best described adaptation during the first perturbation exposure using
860 the parameter set: $a_s=0.9829$, $a_f=0.9278$, $b_s=0.0629$, $b_f=0.0632$. Next, we imagined that implicit error
861 sensitivity and explicit error sensitivity differed across the reference and test conditions. On the x-axis of
862 the map, we show a percent change in b_i from the reference condition to the test condition. On the y-axis
863 of the map, we show a percent change in b_e from the reference condition to the test condition. The
864 retention factors were held constant across conditions. Then for each condition we calculated the total
865 amount of implicit learning using Eq. (8). The color at each point in the map represents the percent change
866 in the total amount of implicit learning from the reference condition to the test condition.

867 As described in the main text, the competition map (Fig. 5A) is composed of several important
868 regions (Fig. 5B). In Region A, there is a decrease in implicit error sensitivity (from reference to test) as
869 well as a decrease in the total amount of implicit adaptation predicted by Eq. (8). In Region B, Eq. (8)
870 predicts a decrease in implicit adaptation, despite an increase in implicit error sensitivity. In Region D,
871 there is an increase both in implicit error sensitivity as well as steady-state implicit learning. In Region E,
872 there is an increase in implicit adaptation, despite a decrease in implicit error sensitivity. Finally, Region C
873 shows cases where there are changes in implicit error sensitivity, but the total absolute change in implicit
874 adaptation (Eq. (8)) is less than 5%. To determine this region, we solved for the linear bounds that describe
875 a 5% increase or a 5% decrease in the output of Eq. (8).

876

877 Neville & Cressman (2018)¹⁵

878 To understand how enhancing explicit strategy might alter implicit learning, we considered data collected
879 by Neville and Cressman¹⁵. Here the authors tested how awareness of a visuomotor rotation altered the

880 adaptation process. To do this, participants (n=63) were divided into one of many groups. In the instructed
881 groups (Fig. 1E, yellow) the nature of the perturbation as well as a compensatory strategy was provided
882 to the participants prior to the introduction of the perturbation. In other groups, no instruction was
883 provided (Fig. 1E, gray). During rotation periods, participants reached to three potential targets. Implicit
884 and explicit contributions to behavior were measured at 4 different periods using “inclusion” and
885 “exclusion” trials. During exclusion trials, the authors instructed participants to reach (without visual
886 feedback) as they did during the baseline period prior to perturbation onset (without using any knowledge
887 of the perturbation gained thus far). During inclusion trials, the authors instructed participants to reach
888 (without visual feedback) using all knowledge gained about the perturbation. In this way, the aftereffect
889 measured on exclusion trials served as a measurement of implicit adaptation, and the difference in
890 aftereffects measured on inclusion and exclusion trials served as a measurement of explicit adaptation.

891 At the start of the experiment all participants performed a baseline period without a rotation for
892 30 trials. Baseline implicit and explicit reach angles were then assayed using inclusion and exclusion trials.
893 At this point, participants in the strategy group were briefed about the perturbation with an image that
894 depicted how feedback would be rotated, and how they could compensate for it. Then all groups were
895 exposed to the first block of a visuomotor rotation for 30 trials. Some participants experienced a 20°
896 rotation (Fig. 1E, left), others a 40° rotation (Fig. 1E, middle), and others a 60° rotation (Fig. 1E, right).
897 After this first block, implicit and explicit learning were assayed with inclusion and exclusion trials. This
898 was followed by a second perturbation block, and another round of inclusion/exclusion trials. Finally, the
899 experiment ended with a third perturbation block and a final round of inclusion/exclusion trials.

900 Here we focused on the measures of implicit and explicit adaptation obtained from inclusion and
901 exclusion trials at the end of the final block. To obtain these data, we extracted the mean participant
902 response and the associated standard error of the mean, directly from the primary figures reported by
903 Neville and Cressman¹⁵ using Adobe Illustrator CS6. The implicit and explicit responses in all 6 groups are
904 shown in Fig. S1. The marginal effects of instruction (average over rotation sizes) and rotation size
905 (average over instruction conditions) are shown in Figs. 1F and 1G respectively.

906 Finally, we tested whether the competition equation (Eq. (4)) or independence equation (Eq. (5))
907 could account for the levels of implicit learning observed across rotation magnitude and awareness
908 conditions. To do this, we used a bootstrapping approach. Using the mean and standard deviation
909 obtained from the primary figures, we sampled hypothetical explicit and implicit aftereffects for 10
910 participants. We then calculated the mean across these 10 simulated participants. After this, we used
911 *fmincon* in MATLAB R2018a to find an implicit error sensitivity that minimized the following cost function:

$$912 \quad \theta_{fit} = \operatorname{argmin}_{\theta} \sum_{n=1}^6 (x_{i_n}^{ss} - \hat{x}_{i_n}^{ss})^2 \quad (9)$$

913 This cost function represents the difference between the simulated level of implicit adaptation, and the
914 amount of implicit learning that would be predicted for a given perturbation size and simulated explicit
915 adaptation, according to our competition framework (Eq. (4)) or independence framework (Eq. (5)). For
916 this process, we set the implicit retention factor to 0.9565 (see *Measuring properties of implicit learning*).
917 Therefore, only the implicit error sensitivity remained as a free parameter. In sum, we aimed to determine
918 if a single implicit error sensitivity could account for the amount of adaptation across the no instruction
919 group, instruction group, and each of the three perturbation magnitudes (20, 40, and 60°). The

920 combination of instruction and perturbation magnitude yielded 6 groups, hence the upper limit on the
921 sum in Eq. (9). We repeated this process for a total of 10,000 simulated groups.

922 In Fig. 1F, we show the marginal effect of instruction on the implicit aftereffect. This was obtained
923 by averaging across each of the 3 rotation magnitudes shown in Fig. S1, for each model. In Fig. 1G we
924 show the marginal effect on rotation size on the implicit aftereffect. This was obtained by averaging across
925 the instructed and non-instructed conditions for each rotation size shown in Fig S1, for each model.

926

927 *Saijo and Gomi (2010)*⁴²

928 To understand how suppressing explicit strategy might alter implicit learning, we considered data
929 collected by Saijo and Gomi⁴². In one of their experiments, the authors tested how perturbation onset
930 altered the adaptation process. Subjects were divided into either an abrupt (n=9) or gradual group (n=9),
931 and reached to 1 of 12 targets, which were ordered pseudorandomly in each cycle of 12 trials. After a
932 baseline period of 8 cycles, a visuomotor rotation was introduced. The perturbation period lasted 32
933 cycles. After this, the perturbation was removed for 6 cycles of a washout condition. Participants were
934 exposed to either an abrupt rotation where the perturbation magnitude suddenly changed from 0° to 60°,
935 or a gradual condition where the perturbation magnitude increased over smaller increments (10°
936 increments that lasted 3 cycles each; Fig. 2A).

937 Here, we considered why participants in the abrupt perturbation condition achieved greater
938 adaptation during the rotation period (smaller error in Fig. 2C) but exhibited a smaller aftereffect when
939 the perturbation was removed. Our theory suggested that this may be due to competition. If the gradual
940 condition suppressed explicit awareness of the rotation³⁸, then Eq. (4) would predict increases in implicit
941 learning which were observed in the aftereffects measured during the washout period (where explicit
942 strategies were disengaged). However, the SPE model (Eq. (5)) would predict the same amount of implicit
943 adaptation: the same aftereffect in each condition.

944 To test these hypotheses, we simulated implicit adaptation using the state-space model in Eq. (3).
945 In Fig. 2D, we used an SPE for the error term in Eq. (3). In Fig. 2E, we used the target error for the error
946 term in Eq. (3). We imagined that the total reach angle was determined based on the sum of implicit and
947 explicit learning. However, these authors did not directly measure explicit strategies. Fortunately, Neville
948 and Cressman¹⁵ measured explicit strategies using inclusion and exclusion trials during a 60° abrupt
949 rotation (yellow points, explicit aim in Figs. 2D&E).

950 We used these measurements in our abrupt simulations. Neville and Cressman observed that
951 explicit strategies rapidly reached 35.5° and remained stable during adaptation. To approximate these
952 data, we simulated abrupt explicit strategy using the exponential curve: $x_e = 35.5 - 10e^{-2t}$ (Figs. 3D&E,
953 explicit aim, black line). Note that the nature of this exponential curve is entirely inconsequential to our
954 analysis, apart from its saturation level. Outside of the rotation period, we assumed explicit strategy was
955 zero. This is consistent with data from Morehead et al.³⁴ that showed almost immediate disengagement
956 in aiming strategy during washout (Fig. S2). For the gradual condition, we assumed explicit strategy was
957 zero throughout the entire experiment (Figs. 3D&E, explicit aim, gradual), as the participants remained
958 largely unaware of the rotation. This seemed consistent with the data; gradual participants adapted
959 approximately 40°, and exhibited an aftereffect of about 38°, indicating a re-aiming angle less than even
960 5°. Note, our primary results (Fig. 2F) were unchanged in a sensitivity test where we assumed 10° of re-
961 aiming in the gradual group (not shown).

962 Thus, our simulations included two free parameters: error sensitivity (b_i) and retention fraction (a_i)
963 for the implicit system. In each simulation, we assumed that these parameters were identical across the
964 gradual and abrupt groups. To fit these parameters, we minimized the following cost function:

965
$$\theta_{fit} = \operatorname{argmin}_{\theta} \sum_n (e_{abrupt}^{(n)} - \hat{e}_{abrupt}^{(n)})^2 + (e_{gradual}^{(n)} - \hat{e}_{gradual}^{(n)})^2 \quad (10)$$

966 Eq. (10) is the sum of squared errors between the directional errors predicted by the model (Figs. 2D&E,
967 directional error) and observed in the data (Fig. 2C) across all trials in the abrupt and gradual conditions.
968 Note that each simulation incorporated variability. We simulated noisy directional errors using the
969 standard errors shown in the data in Fig. 2C. In the explicit state, we added variability to each trial using
970 the standard error in explicit strategy reported by Neville and Cressman¹⁵. For the implicit state, we used
971 20% of the explicit variability, given that aiming strategies are more variable than implicit corrections¹⁴.
972 We repeated these simulations 20,000 times, each time resampling our noise sources and then fitting our
973 parameter set (a_i and b_i) by minimizing Eq. (10) with *fmincon* in MATLAB R2018a. The mean implicit curve
974 for the SPE learning model and target error learning model are shown in Figs. 2D and 2E respectively
975 (implicit angle; mean \pm SD). Critically, in each simulation we measured the aftereffect that occurred on
976 the first cycle of the washout period (Figs. 2D&E, aftereffect). The mean and standard deviation in these
977 aftereffects is reported in Fig. 2F.

978 Finally, note that we obtained the directional errors in Fig. 2C used in our simulations, directly
979 from the primary figure in the original manuscript (using the GRABIT routine in MATLAB R2018a). Please
980 also note in the actual experiment, on some trials (7.1% of all trials), the perturbation was introduced
981 midway during the reach to test feedback corrections at only 1 target location (the 0° target). These trials
982 were not relevant for our current analysis. Otherwise, the visuomotor rotation was applied during the
983 entire movement as in the standard paradigm. Also note that because the authors were also analyzing
984 feedback responses, participants made 15 cm movements, with a 0.6 second movement duration at
985 baseline. Here, we only wanted to consider the feedforward adaptive component. Fortunately, the
986 authors reported initial movement errors 100 ms following movement onset that could not have been
987 altered by feedback. Therefore, we used these early measures of adaptation in the current study.

988

989 *Fernandez-Ruiz et al. (2011)⁴¹*

990 In Figs. 3A-D, we show data collected and originally reported by Fernandez-Ruiz and colleagues⁴¹. In this
991 experiment, participants made 10 cm reaching movements to 1 of 8 targets, pseudorandomly arranged
992 in cycles of 8 trials. Here we report data from the unconstrained RT group described in the original
993 manuscript. The experiment started with 3 cycles of null rotation trials, followed by 40 cycles of a 60°
994 rotation. The experiment ended with a 20-cycle washout period (no rotation) where aftereffects were
995 assessed. In Figs. 3B&C we show data from 2 example participants reported in the original manuscript. In
996 Fig. 2D, the change in preparation time was calculated on the last cycle of the rotation period (relative to
997 the baseline period). The aftereffect is the reach angle on the first cycle of the washout period. In Fig. S3,
998 we report data from Fig. 3 of the original manuscript. Here the authors calculated the directional error
999 and the change in preparation time across 5-cycle periods spanning the entire rotation. The points in Fig.
1000 S3 show individual subjects for the first 5 and last 5 rotation cycles. All lines show the linear regression
1001 across individual subjects in each color-coded period. Note that each line has a negative slope, indicating
1002 that participants who increased their reaction time more consistently exhibited smaller directional errors

1003 through the entire rotation period. These data were extracted directly from the primary figures reported
1004 by Fernandez-Ruiz and colleagues⁴¹ using Adobe Illustrator CS6. The R^2 value reported in Fig. 2D was
1005 calculated from these extracted data.

1006

1007 *Experiment 1*

1008 To test whether changes in explicit strategy altered implicit learning, we recruited participants for two
1009 experiments. In the first experiment, participants adapted to a visuomotor rotation without any limits
1010 applied to preparation time (No PT limit), thus allowing participants to use explicit strategy. In a second
1011 experiment, we strictly limited preparation time in order to suppress explicit strategy (Limit PT).

1012 Participants in the No PT limit condition began with 10 epochs of null trials (1 epoch = 4 trials),
1013 followed by a rotation period of 60 epochs. Other details concerning the experiment paradigm are
1014 described in *Visuomotor rotation*. At the end of the perturbation period, we measured the amount of
1015 implicit and explicit learning. To do this, participants were instructed to forget about the cursor and
1016 instead move their hand through the target without applying any strategy to compensate for the
1017 perturbation. Furthermore, visual feedback was completely removed during these trials. All 4 targets were
1018 tested in a randomized sequence. To quantify the total amount of implicit learning, we averaged the reach
1019 angle across all targets (Figs. 3F&H). To calculate the amount of explicit adaptation, we subtracted this
1020 measure of implicit learning from the mean reach angle measured over the last 10 epochs of the
1021 perturbation prior to the verbal instruction.

1022 In the Limit PT group, we suppressed explicit adaptation for the duration of the experiment by
1023 limiting the time participants had to prepare their movements. To enforce this, we limited the amount of
1024 time available for the participants to start their movement after the target location was shown. This upper
1025 bound on reaction time was set to 225 ms (taking into account average screen delay). If the reaction time
1026 of the participant exceeded the desired upper bound, the participant was punished with a screen timeout
1027 after providing feedback of the movement endpoint. In addition, a low unpleasant tone (200 Hz) was
1028 played. This condition was effective in limiting reaction time (Fig. 3G, middle), even lower than the 300
1029 ms threshold used by Haith and colleagues²⁸. This experiment started with 10 epochs (1 epoch = 4 trials)
1030 of null trials. After this, the visuomotor rotation was introduced for 60 epochs. At the end of the
1031 perturbation period, we measured retention of the visuomotor memory in a series of 15 epochs of no
1032 feedback trials (Fig. 3F, no feedback).

1033 Our goal was to test whether the putative implicit learning properties measured in the Limit PT
1034 group could be used to predict the subject-to-subject relationship between implicit and explicit
1035 adaptation in the No PT limit group (according to Eq. (4)). To do this, we measured each participant's
1036 implicit retention factor and error sensitivity in the Limit PT condition (see *Measuring properties of implicit*
1037 *learning* below). We then averaged each parameter across participants. Next, we inserted these mean
1038 parameters into Eq. (4). With these variables specified, Eq. (4) predicted a specific linear relationship
1039 between implicit and explicit learning (Fig. 3H, model). We overlaid this prediction on the actual amounts
1040 of implicit and explicit adaptation measured in each No PT limit participant (Fig. 3H, black dots). We
1041 performed a linear regression across these measured data (Fig. 3H, black line, measured). We report the
1042 slope and intercept of this regression as well as the corresponding 95% confidence intervals.

1043 The individual differences between implicit and explicit learning in Experiment 1 (Fig. 3H) could
1044 have been due uncertainty in our empirical probe (move hand through the target without re-aiming). That

1045 is, some participants may not have understood the instruction to move their hand through the target, and
1046 instead continued to aim. These participants would appear to have very little explicit strategy, and high
1047 amounts of implicit learning. Therefore, to verify our explicit measures, we considered two additional
1048 explicit markers: movement preparation time and reported strategies. In Fig. S4B, we compared explicit
1049 re-aiming with movement preparation time. That is, we calculated how much participant changed their
1050 movement preparation time after the perturbation turned on (the mean preparation time over 20 cycles
1051 following rotation onset, relative to the mean preparation time over the 3 cycles preceding rotation
1052 onset). Changes in preparation time are known to correlate with strategic re-aim^{41,47}.

1053 Lastly, we also asked participants to verbally report their explicit strategy. After the implicit probe
1054 trials, we showed each target once again, with a ring of small white landmarks placed at an equal radial
1055 distance around the screen²⁴. A total of 108 landmarks was used to uniformly cover the circle. Each
1056 landmark was labeled with an alphanumeric string. Subjects were asked to report the nearest landmark
1057 that they were aiming towards at the end of the experiment in order to move the cursor through the
1058 target when the rotation was on. The mean angle reported across all 4 targets was calculated to provide
1059 an additional assay of explicit adaptation (Fig. S4A, explicit report angle). Explicit re-aiming is prone to
1060 erroneous selections where the hand is mentally rotated in the wrong direction⁴⁷ (errors of same
1061 magnitude, opposite sign) Therefore, for individual targets where the participant reported an explicit
1062 angle in the opposite direction, we used its absolute value when calculating their explicit recalibration.
1063 These strategy report trials were used to calculate the implicit learning estimate shown in Fig. S5E.

1064

1065 *Experiment 2*

1066 Here, we remotely tested a very similar paradigm to the No PT limit condition in Experiment 1. Participants
1067 controlled a cursor by moving their index finger across the track pad of their personal computer. The
1068 experiment was coded in Java. To familiarize themselves with the task, participants watched a 3-minute
1069 instructional video. In this video, the trial structure, point system, and feedback structure were described.
1070 After this video, there was a practice period. During the practice period, the software tracked the
1071 participant's reach angle on each trial. If the participant achieved success on fewer than 65% of trials
1072 (measured based on an angular target-cursor discrepancy $\leq 30^\circ$, reaction time ≤ 1 sec, and movement
1073 duration ≤ 0.6 sec), they had to re-watch the instructional video and re-do the practice period.

1074 After the practice period ended, the testing period began. This testing period was almost identical
1075 to the No PT limit condition in Experiment 1. On each trial, participants reached to 1 of 4 targets (up,
1076 down, left, and right). Each target was visited once pseudorandomly in a cycle of 4 targets. After an initial
1077 10-cycle null period, a 30° visuomotor rotation was imposed that lasted for 60 epochs. At the end of the
1078 rotation period, we measured implicit and explicit adaptation. The experiment briefly paused, and an
1079 audiovisual recording was played that instructed participants to not use any strategy and to move their
1080 hand straight through the target. After this, the experiment resumed, feedback was removed, and
1081 participants performed 20 cycles of no-aiming, no-feedback probe trials (Fig. 3J, no aiming).

1082 We measured subject-to-subject correlations between implicit and explicit adaptation. For this,
1083 we calculated two implicit learning measures. The early implicit aftereffect was simply the aftereffect
1084 observed on the first no-aiming, no-feedback probe cycle (Fig. 3L). The late implicit aftereffect was the
1085 average aftereffect observed on the last 15 cycles of this no-aiming, no-feedback period (Fig. 3K). To
1086 measure explicit learning, we calculated the difference between the total amount of adaptation (mean

1087 reach angle over last 10 cycles of the rotation period) and the first cycle of the no-aiming, no-feedback
1088 period. We investigated the relationship between explicit adaptation and the early and late implicit
1089 aftereffects via linear regression in Figs. 3L and 3K respectively. For the early implicit aftereffect, we
1090 measured the 95% CI for the slope and intercept. Critically, this interval did not contain 1, indicating that
1091 the subject-to-subject correlations cannot be described by the trivial case where all participants had
1092 adapted the same amount by the end of the adaptation period (see main text).

1093

1094 *Haith et al. (2015)*²⁸

1095 To understand how implicit and explicit processes contribute to savings, Haith and colleagues²⁸ designed
1096 a forced preparation time task. Briefly, participants (n=14) performed reaching movements to two targets,
1097 T1 and T2, under a controlled preparation time scenario. To control movement preparation time, four
1098 audio tones were played (at 500 ms intervals) and participants were instructed to reach coincident with
1099 the 4th tone. On high preparation time trials (High PT), the intended target was displayed during the entire
1100 tone sequence. On low preparation time trials (Low PT), the intended target was switched approximately
1101 300 ms prior to the 4th tone. High PT trials were more probable (80%) than Low PT trials (20%).

1102 After a baseline period (100 trials for each target), a 30° visuomotor rotation was introduced for
1103 target T1 only. After 100 rotations trials (Exposure 1), the rotation was turned off for 20 trials. After a 24
1104 hr break, participants then returned to the lab. On Day 2, participants performed 10 additional reaching
1105 movements without a perturbation, followed by a second 30° rotation (Target T1 only) of 100 trials
1106 (Exposure 2). The experiment then ended with a washout period of 100 trials for each target.

1107 We quantified the amount of savings expressed upon re-exposure to the perturbation, on High
1108 PT and Low PT trials. We measured savings using two metrics. First, we measured the rate of learning
1109 during each exposure to the perturbation using an exponential fit. We fit a two-parameter exponential
1110 function to both Low PT and High PT trials during the first and second exposure (we constrained the third
1111 parameter to enforce that the exponential begin at each participant's measured baseline reach angle).
1112 We compared the exponential learning rate using a paired t-test (Fig. 4B, 3rd column).

1113 We also quantified savings in a manner similar to that reported by Haith and colleagues²⁸; we
1114 calculated the difference between the reach angles before and after the introduction of the perturbation,
1115 during each exposure (Fig. 4C, 1st and 2nd columns). For High PT trials, we then computed the mean reach
1116 difference over the 3 trials preceding, and 3 trials following perturbation onset. Given their reduced
1117 frequency, for Low PT trials, we focused solely on the trial before and trial after perturbation onset. To
1118 detect savings, we compared the pre-perturbation and post-perturbation differences using a paired t-test
1119 (Fig. 4C, 3rd column).

1120 Finally, we also used a state-space model of learning to measure properties of implicit and explicit
1121 learning during each exposure. We modeled implicit learning according to Eq. (3) and explicit learning
1122 according to Eq. (7). In one model fitting procedure, we modeled error according to Eq. (1) for the
1123 competitive framework. These results are shown in Fig. 4D. In a second model fitting procedure, we
1124 modeled error according to Eq. (2) for the independent framework. These results are not shown in the
1125 Fig. 4, but relevant statistical outcomes are reported in the main text.

1126 In the model, behavior is described as the summation of implicit and explicit learning. Each system
1127 possessed a retention factor and error sensitivity. Here, we asked how implicit and explicit error sensitivity
1128 might have changed from Exposure 1 to Exposure 2. Therefore, we assumed that the implicit and explicit

1129 retention factors were constant across perturbations, but allowed a separate implicit and explicit error
1130 sensitivity during Exposures 1 and 2. Therefore, our modeling approach included six free parameters. We
1131 fit this model to the measured behavior by minimizing the following cost function using *fmincon* in
1132 MATLAB R2018a:

$$1133 \quad \theta_{fit} = \arg \min_{\theta} \sum_{n=1}^N (y_1^{(n)} - \hat{y}_1^{(n)})^2 + (y_2^{(n)} - \hat{y}_2^{(n)})^2 \quad (11)$$

1134 Here y_1 and y_2 represent the reach angles during the first and second exposure. These reach angles are
1135 composed of High PT and Low PT trials. On Low PT trials, the reach angle is equal to the implicit adaptative
1136 process. On High PT trials, the reach angle is equal to the sum of the implicit adaptive process and the
1137 explicit adaptive process.

1138 We fit this model to individual participant behavior, in the case where implicit learning was driven
1139 by target errors (Eq. (1)), and also in the alternate case where it was driven by aim-cursor errors (Eq. (2)).
1140 We report the implicit and explicit error sensitivities for the target-error learning case in Fig. 4D, right. For
1141 this model, the predicted behavior is shown in the first two columns of Fig. 4D. We also fit the target-error
1142 (Eq. (1)) model to the mean behavior across all participants in Exposure 1 and Exposure 2. We obtained
1143 the following parameter set: $a_s=0.9829$, $a_f=0.9278$, $b_{s,1}=0.0629$, $b_{s,2}=0.089$, $b_{f,1}=0.0632$, $b_{f,2}=0.1078$. Note
1144 that the subscripts 1 and 2 denote error sensitivity during Exposure 1 and 2, respectively. These
1145 parameters were used for our simulations in Fig. 5 (see *Competition Map*).

1146

1147 *Experiment 3*

1148 In Haith et al. (2015)²⁸, no savings was observed on trials where preparation time was limited (Low PT
1149 trials), consistent with the possibility that implicit learning processes are not modulated by past
1150 experiences. Here, we questioned if savings in implicit learning processes might have been suppressed by
1151 competition with explicit learning processes (see *Competition Map*). That is, if implicit and explicit
1152 processes share error sources, changes in explicit learning could mask changes in implicit learning. The
1153 way to test this possibility would be to eliminate explicit learning on all trials, to ensure that the error on
1154 each trial is expressly available for the implicit learning system. Experiment 3 tested this possibility using
1155 a limited preparation time condition.

1156 Limiting reaction time is known to suppress explicit strategy^{17,41,47}. To limit reaction time, we used
1157 the same procedure described above for Experiment 2. This condition was effective in limiting reaction
1158 time (Fig. 6B, top row), even lower than the 300 ms threshold used by Haith and colleagues²⁸.

1159 Experiment 3 used the 4-target protocol reported in *Visuomotor rotation*. Apart from that, its trial
1160 structure was similar to that of Haith et al.²⁸. After a familiarization period, subjects completed a baseline
1161 period of 10 epochs (1 epoch = 4 trials for each target). At that point, we imposed a 30° visuomotor
1162 rotation for 60 epochs (Exposure 1). At the end of this first exposure, participants completed a washout
1163 period with no perturbation that lasted for 70 epochs. At the end of the washout period, subjects were
1164 once again exposed to a 30° visuomotor rotation for 60 epochs (Exposure 2).

1165 We quantified savings in a manner consistent with Haith et al.²⁸. First, we fit a two-parameter
1166 exponential function to the reach angle during Exposures 1 and 2 (third parameter was used to constrain
1167 the fit so exponential curve started at the reach angle measured prior to perturbation onset). We analyzed
1168 any change in the rate parameter of the exponential using a paired t-test (Fig. 6C, top). Second, we also

1169 tested for differences in the initial amount of learning. To do this, we calculated the difference between
1170 reach angle during Exposures 1 and 2 (Figs. 6A&B, bottom row). We then calculated the difference in
1171 reach angle (Exposure 2 - Exposure 1) during the 4 epochs preceding and 4 epochs following rotation
1172 onset. We compared these differences for Exposures 1 and 2 using a paired t-test (Fig. 6C, bottom).
1173

1174 *Experiment 4*

1175 Lerner and Albert et al.²⁶ demonstrated that anterograde interference slows the rate of learning after 5
1176 min (also 1 hr), but dissipates over time and is nearly gone after 24 hr. Here we wondered if this reduction
1177 in learning rate could at least be in part driven by impairments in implicit learning. Because Lerner and
1178 Albert et al.²⁶ did not constrain preparation time, one would expect that participants used both implicit
1179 and explicit learning processes. In Experiment 2, we isolated the implicit component of adaptation by
1180 limiting reaction time. We used the same technique to limit reaction time reported for Experiment 2. The
1181 experiment paradigm is described in *Visuomotor rotation* above. With that said, we used 8 adaptation
1182 targets as opposed to 4 targets, to match the protocol used by Lerner and Albert et al.²⁶.

1183 The perturbation schedule is shown in Figs. 7A&B at top. We recruited two groups of participants,
1184 a 5 min group (n=9), and a 24 hr group (n=11). After familiarization, all participants were exposed to a
1185 baseline period of null trials lasting 5 epochs (1 epoch = 8 trials). Next participants were exposed to a 30°
1186 visuomotor rotation for 80 cycles (Exposure A). At this point, the experiment ended. After a break,
1187 participants returned to the task. For the 5 min group, the second session occurred on the same day. For
1188 the 24 hr group, participants returned the following day for the second session. At the start of the second
1189 session, participants were exposed to a 30° visuomotor rotation (Exposure B) whose orientation was
1190 opposite to that of Exposure A. This rotation lasted for 80 epochs.

1191 We analyzed the rate of learning by fitting a two-parameter exponential function to the learning
1192 curve during Exposures A and B (the third parameter was used to constrain the exponential curve to start
1193 from the behavior on the first epoch of the rotation). For each participant we computed an interference
1194 metric by dividing the exponential rate of learning during Exposure B, by that measured during Exposure
1195 A (Fig. 7C, at right, blue). In addition, we also analyzed the reaction time of the participants during
1196 Exposure B (Figs. 7A&B, middle, blue).

1197

1198 *Lerner and Albert et al. (2020)²⁶*

1199 Recently, Lerner and Albert et al.²⁶ demonstrated that slowing of learning in anterograde interference
1200 paradigms is caused by reductions in sensitivity to error. Here, we re-analyze some of these data.

1201 Lerner and Albert et al.²⁶ studied how learning one visuomotor rotation altered adaptation to an
1202 opposing rotation when these exposures were separated by time periods ranging from 5 min to 24 hr.
1203 Here we focused solely on the 5 min group (n=16) and the 24 hr group (n=18). A full methodological
1204 description of this experiment is provided in the earlier manuscript. Briefly, participants gripped a joystick
1205 with the thumb and index finger which controlled an on-screen cursor. Their arm was obscured from view
1206 using a screen. Targets were presented in 8 different positions equally spaced at 45° intervals around a
1207 computer monitor. Each of these 8 targets was visited once (random order) in epochs of 8 trials. On each
1208 trial, participants were instructed to shoot the cursor through the target.

1209 All experiment groups started with a null period of 11 epochs (1 epochs = 8 trials). This was
1210 followed by a 30° visuomotor rotation for 66 epochs (Exposure A). At this point, the experiment ended.

1211 After a break, participants returned to the task. For the 5 min group, the second session occurred on the
1212 same day. For the 24 hr group, participants returned the following day for the second session. At the start
1213 of the second session, participants were immediately exposed to a 30° visuomotor rotation (Exposure B)
1214 whose orientation was opposite to that of Exposure A. This rotation lasted for 66 epochs. Short set breaks
1215 were taken every 11 epochs during Exposures A and B.

1216 Here as in the earlier work²⁶, we analyzed the rate of learning by fitting a two-parameter
1217 exponential function to the learning curve during Exposures A and B (the third parameter was used to
1218 constrain the exponential curve to start from the behavior on the first epoch of the rotation). For each
1219 participant we computed an interference metric by dividing the exponential rate of learning during
1220 Exposure B, by that measured during Exposure A (Fig. 7C, green). In addition, we also analyzed the reaction
1221 time of the participants during Exposure B. The mean reaction time over the first perturbation block is
1222 shown in Figs. 7A&B (middle, green traces).

1223

1224 *Mazzoni and Krakauer (2006)*¹²

1225 In this study, subjects sat in chair with their arm supported on a tripod. An infrared marker was attached
1226 to a ring placed on the participant's index finger. The hand was held closed with surgical tape. Participants
1227 moved an on-screen cursor by rotating their hand around their wrist. These rotations were tracked with
1228 the infrared marker. On each trial, participants were instructed to make straight out-and-back movements
1229 of a cursor through 1 of 8 targets, spaced evenly in 45° intervals. A 2.2 cm marker translation was required
1230 to reach each target. Note that all 8 targets remained visible throughout the task.

1231 Two groups of participants were tested with a 45° visuomotor rotation. In the no-strategy group,
1232 participants adapted as per usual, without any instructions. After an initial null period, the rotation was
1233 turned on (Fig. 8A, blue, adaptation). After about 60 cycles of adaptation, the rotation was turned off and
1234 participants performed another 60 of washout trials (Fig. 8A, blue, washout). The break between the
1235 adaptation and washout periods in Fig. 8A, no-strategy, is simply for alignment purposes.

1236 The strategy group followed a different protocol. After the null period, participants reached for 2
1237 movements under the rotation (Fig. 8A, 2 cycles no instruction, red). At this point, the subjects were told
1238 that they made 2 errors, and that they could counter the error by reaching to the neighboring clockwise
1239 target (all targets always remained onscreen). After the instruction, participants immediately reduced
1240 their error to zero (point labeled instruction in red, Fig. 8A). They continued to aim to the neighboring
1241 target under the rotation throughout the adaptation period. Note that the direction errors became
1242 negative. This convention indicates overcompensation for the rotation, i.e., that participants are altering
1243 their hand angle by more than their strategy aim of 45°. Towards the end of the adaptation period,
1244 participants were told to stop re-aiming, and direct their movement back to the original target (Fig. 8A,
1245 do not aim, rotation on). Then after several movements, the rotation was turned off as participants
1246 continued to aim for the original target during the washout period.

1247 In Fig. 8A we show the error between the primary target (target 1) and cursor during the entire
1248 experiment. In Fig. 8B we show the error between the aimed target (target 2) and cursor during the
1249 adaptation period. Note that the aimed and primary targets are generally related by 45° when the strategy
1250 group is re-aiming. We observed that initial adaptation rates (over first 24 movements, gray area in Fig.
1251 8B) were similar, but the no-strategy group ultimately achieved greater implicit adaptation. These data

1252 were all obtained by using the GRABT routine in MATLAB 2018a to extract the mean (and standard error
1253 of the mean) performance in each group from the figures shown in the primary article.

1254 To account for behaviors, we fit 1 of 3 models to the direction error during the adaptation period
1255 shown in Fig. 8B. In all cases we modeled explicit re-aiming in the strategy group as an
1256 an aim sequence that started at zero during the initial two movements, and then 45° for the rest of the
1257 adaptation period (i.e., after the instruction to re-aim). In the no-strategy group, we modeled explicit
1258 learning as an aim sequence that remained at zero throughout the adaptation period.

1259 In Fig. 8D, we modeled implicit learning based on the state-space model in Eq. (3) and target error
1260 term defined in Eq. (1). This target error was defined as the difference between the primary target (i.e.,
1261 the initial target displayed associated with task outcome) and the cursor. In Fig. 8E, we modeled implicit
1262 learning based on the state-space model in Eq. (3) and the aim-cursor error defined in Eq. (2). This aim-
1263 cursor error was defined as the difference between the aimed target (either 0° or 45°) and the cursor. Fig.
1264 8F, shows our third and final model. In this model, implicit learning in the strategy group was modeled
1265 using the dual-error system shown in Eq. (6). That is, there were two implicit modules, one which
1266 responded to the target errors as in Fig. 8D, and the other which responded to aim-cursor errors as in Fig.
1267 8E. The evolution of these errors is shown in Fig. 8G. In the no-strategy group, we modeled implicit
1268 learning based on the primary target error alone and cursor.

1269 Each model in Figs. 8D-F were fit in an identical manner. We fit the implicit retention factor and
1270 implicit error sensitivity to minimized squared error according to:

$$1271 \theta_{fit} = \operatorname{argmin}_{\theta} \sum_{n=1}^N (y_{strategy}^{(n)} - \hat{y}_{strategy}^{(n)})^2 + (y_{no-strategy}^{(n)} - \hat{y}_{no-strategy}^{(n)})^2 \quad (12)$$

1272 In other words, we minimized the sum of squared error between our model fit and the observed behavior
1273 across both the strategy and no-strategy groups in Fig. 8B. In other words, we constrained that each group
1274 had the same implicit learning parameters. In the case of our dual-error model in Fig. 8F, we assumed that
1275 each implicit module also possessed the same retention and error sensitivity. In sum, all model fits had
1276 two free parameters (error sensitivity and retention) which were assumed to be identical independent of
1277 instruction. This fit was performed using *fmincon* in MATLAB R2018a. The predicted behavior is shown in
1278 Figs. 8D-F at bottom. For our best model (Fig. 8F), the model behavior is also overlaid in Fig. 8B.

1279

1280 *Taylor and Ivry (2011)*²¹

1281 In Fig. 8H, we show data collected and originally reported by Taylor and Ivry²¹. In this experiment,
1282 participants moved their arm at least 10 cm towards 1 of 8 targets, that were pseudorandomly arranged
1283 in cycles of 8 trials. Only endpoint feedback of the cursor position was provided. The hand was slid along
1284 the surface of a table while the position of the index finger was tracked with a sensor. After an initial
1285 familiarization block (5 cycles), participants were trained how to explicitly rotate their reach angle
1286 clockwise by 45°. That is, on each trial they were shown veridical feedback of their hand position, but were
1287 told to reach to a neighboring target, that was 45° away from the primary illuminated target. After this
1288 training and another null period, the adaptation period started where the cursor position was rotated by
1289 45° in the counterclockwise direction for 40 cycles. The first 2 movements in the rotation exhibited large
1290 errors (Fig. 8H, 2 movements no instruction). As in Mazzoni and Krakauer¹², the participants were then

1291 instructed that they could minimize their error by adopting the aiming strategy they learned at the start
1292 of the experiment. Using this strategy, participants immediately reduced their direction error to zero.

1293 Here we report data from two critical groups in this experiment. In the “instruction with target”
1294 group (Fig. 8H, black, n=10) participants were shown the neighboring targets during the adaptation period
1295 to assist their re-aiming. However, in the “instruction without target” group (Fig. 8H, yellow, n=10)
1296 participants were only shown the primary target; the neighboring targets did not appear on the screen to
1297 help guide re-aiming. Only participants in the “instruction with target” group exhibited the drift reported
1298 by Mazzoni and Krakauer¹². However, both groups exhibited an implicit aftereffect (Fig. 8H, aftereffect;
1299 first cycle of washout period as reported in Fig. 4C of the original manuscript²¹).

1300 These data were extracted directly from the primary figures reported by Taylor and Ivry²¹ using
1301 Adobe Illustrator CS6. We used the means and standard deviations for our statistical tests on the implicit
1302 aftereffect in Fig. 8H.

1303

1304 *Generalization studies*

1305 In our Discussion, we describe how generalization can alter measurements of implicit adaptation. Here
1306 we report data from many earlier studies. In Fig. S5A, we show data collected by Day et al.⁷², reported in
1307 Fig. 2 of the original manuscript. Here, participants were exposed to a 45° rotation while reaching to a
1308 single target. On each trial they were asked to report their aiming direction, using a ring of visual
1309 landmarks. In the “target” group in Fig. S5A, implicit aftereffects were periodically probed at the trained
1310 target location, by asking participants to reach to the target without aiming. In the “aim” group in Fig.
1311 S5A, implicit aftereffects were periodically probed at a target location 30° away from the trained target,
1312 consistent with the direction of the most frequently reported aim. In Fig. S5A, we show the implicit
1313 aftereffect measured on the first aftereffect trial at the end of the experiment. In Fig. S5C we again show
1314 the implicit aftereffect measured at the trained target location in the “probe” condition. The “report”
1315 condition shows the amount of implicit learning estimated by subtracting the reported explicit strategy
1316 from the reported reach angle on the last cycle of the rotation.

1317 In Fig. S5B, we show data collected by McDougle et al.⁷¹, reported in Fig. 3A of the original
1318 manuscript. Here participants were also exposed to a 45° rotation while reaching to a single target. At the
1319 end of the experiment, participants were exposed to an aftereffect block where they reached 3 times to
1320 16 different targets spaced in varying increments around the unit circle. In this aftereffect block feedback
1321 was removed and participants were told to move straight to the target without re-aiming. This aftereffect
1322 block was used to construct a generalization curve. In Fig. S5B we show data only from 2 relevant locations
1323 on this curve. The “target” condition represents aftereffects probed at the training target. The “aim”
1324 condition shows the aftereffect measured at 22.5° away from the primary target, which was the target
1325 closest to the mean reported explicit re-aiming strategy of 26.2°.

1326 Lastly, in Fig. S5D we show data collected by Maresch et al.⁷⁵, reported in Fig. 4b of the original
1327 manuscript. This study was informative to our discussion because they report implicit aftereffects
1328 measured using both exclusion trials (as in most of the data described in this manuscript) as well implicit
1329 aftereffects measured using aim reports. In Fig. S5D we specifically show data from the IR-E group in the
1330 original manuscript. We selected this group, because aim was only intermittently reported (4 trials for
1331 every 80 normal adaptation trials), and also because there were many adaptation targets (8 total). Thus,
1332 in most cases, participants only had to attend to a single target when reaching as in our primary results.

1333 The “probe” condition in Fig. S5D corresponds to the total implicit learning measured at the end of
1334 adaptation by telling participants to reach without re-aiming. The “report” condition in Fig. S5D
1335 corresponds to the total implicit learning estimated at the end of adaptation by subtracting the reported
1336 aim direction from the measured reach angle.

1337 Note that data in Figs. S5A-D were extracted directly from the primary figures reported in the
1338 original manuscripts using Adobe Illustrator CS6.

1339

1340 *Measuring properties of implicit learning*

1341 Many of our model’s predictions depended on estimates of implicit retention factor and error sensitivity.
1342 We obtained these using the Limit PT group in Experiment 2. To calculate the retention factor for each
1343 participant, we focused on the no feedback period at the end of Experiment 2 (Figs. 8D, no feedback).
1344 During these error-free periods trial errors were hidden, thus causing decay of the learned behavior. The
1345 rate of this decay is governed by the implicit retention factor according to:

$$y^{(n)} = a_i^n y_{ss} \quad (13)$$

1346 Here $y^{(n)}$ refers to the reach angle on the n -th no feedback trial, and y_{ss} corresponds to the asymptotic
1347 behavior prior to the no feedback period. We used *fmincon* in MATLAB R2018a to identify the retention
1348 factor which minimized the difference between the decay predicted by Eq. (13) and that measured during
1349 the no feedback period. We obtained an epoch-by-epoch retention factor of 0.943 ± 0.011 (mean \pm SEM).
1350 Note that an epoch consisted of 4 trials, so this corresponded to a trial-by-trial retention factor of 0.985.
1351 When modeling Neville and Cressman¹⁵ (Fig. 1), we cubed this trial-by-trial term because each cycle
1352 consisted of 3 different targets (final retention factor of 0.9565).

1353 Next, we measured implicit error sensitivity in the Limit PT group during rotation period trials. To
1354 measure implicit error sensitivity on each trial, we used its empirical definition:

$$b^{(n_1)} = \frac{y^{(n_2)} - a^{n_2 - n_1} y^{(n_1)}}{e^{(n_1)}} \quad (14)$$

1355 Eq. (14) determines the sensitivity to an error experienced on trial n_1 when the participant visited a
1356 particular target T. This error sensitivity is equal to the change in behavior between two consecutive visits
1357 to target T, on trials n_1 and n_2 divided by the error that had been experienced on trial n_1 . In the numerator,
1358 we account for decay in the behavior by multiplying the behavior on trial n_1 by a decay factor that
1359 accounted for the number of intervening trials between trials n_1 and n_2 . For each target, we used the
1360 specific retention factor estimated for that target with Eq. (13).

1361 Using this procedure, we calculated implicit error sensitivity as a function of trial in Experiment 2.
1362 To remove any potential outliers, we identified error sensitivity estimates that deviated from the
1363 population median by over 3 median absolute deviations within windows of 10 epochs. As reported by
1364 Albert and colleagues³⁷, implicit error sensitivity increased over trials. Eqs. (4) and (5) require the steady-
1365 state implicit error sensitivity observed during asymptotic performance. To estimate this value, we
1366 averaged our trial-by-trial error sensitivity measurements over the last 5 epochs of the perturbation. This
1367 yielded an implicit error sensitivity of 0.346 ± 0.071 (mean \pm SEM).

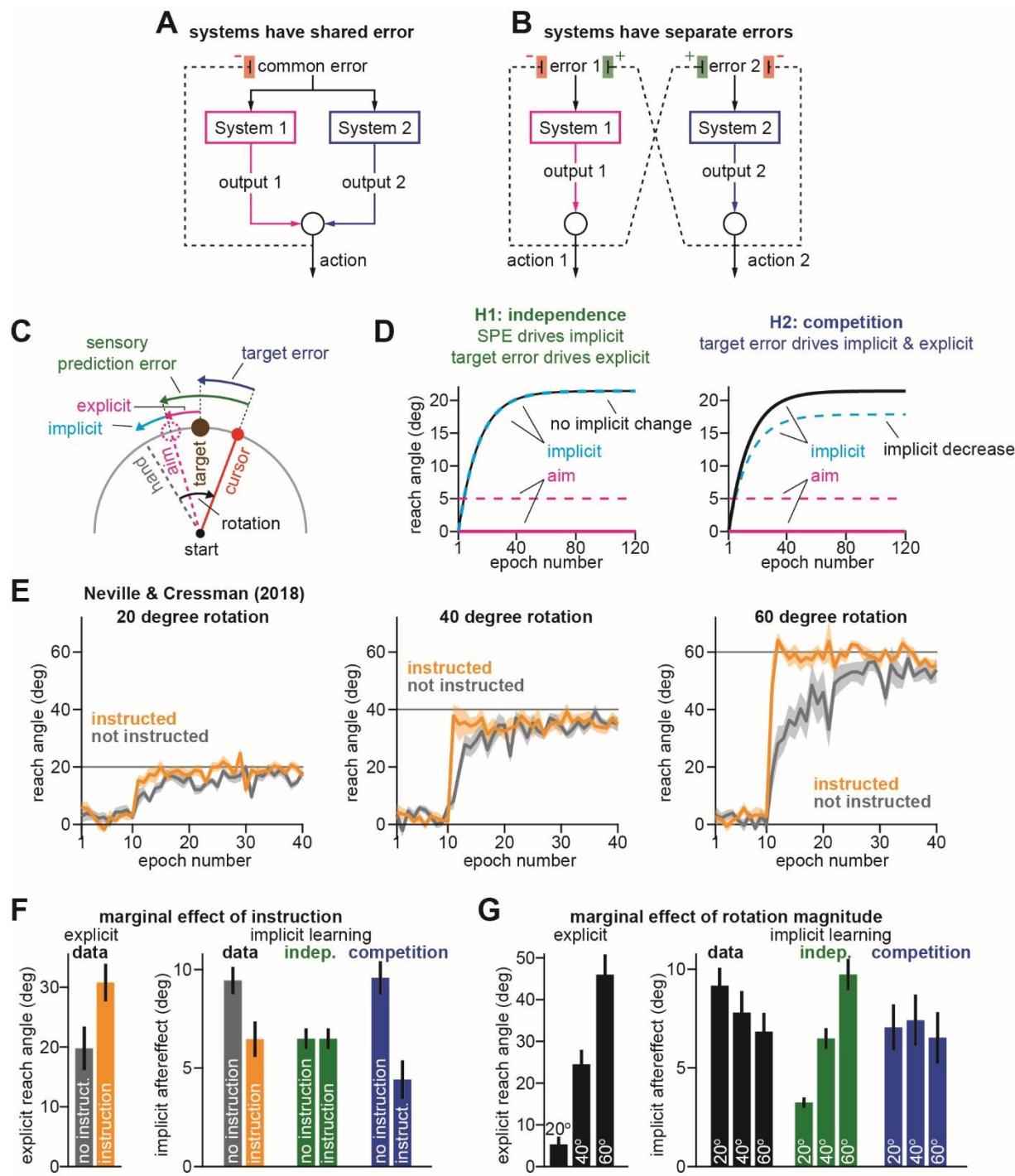
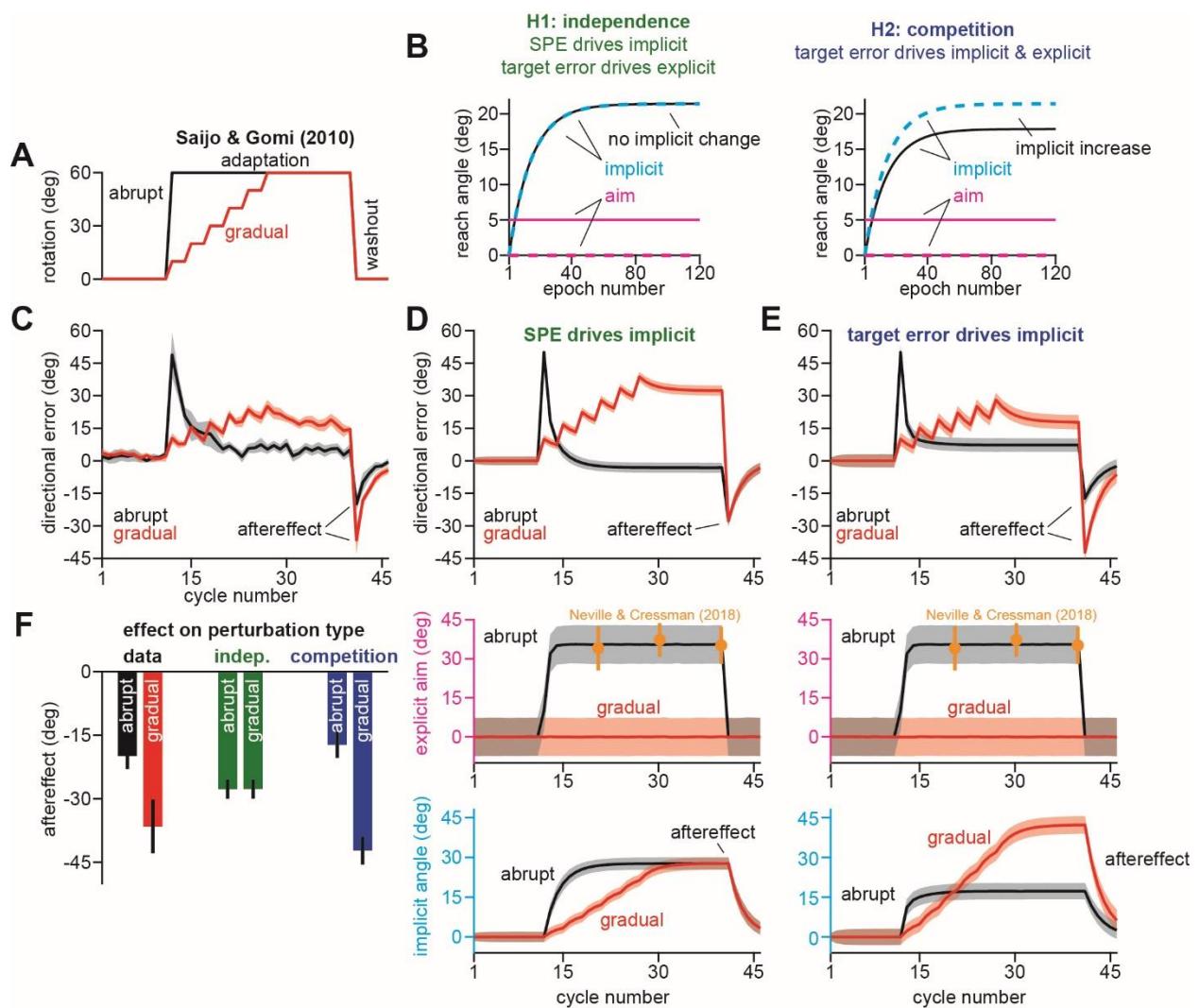
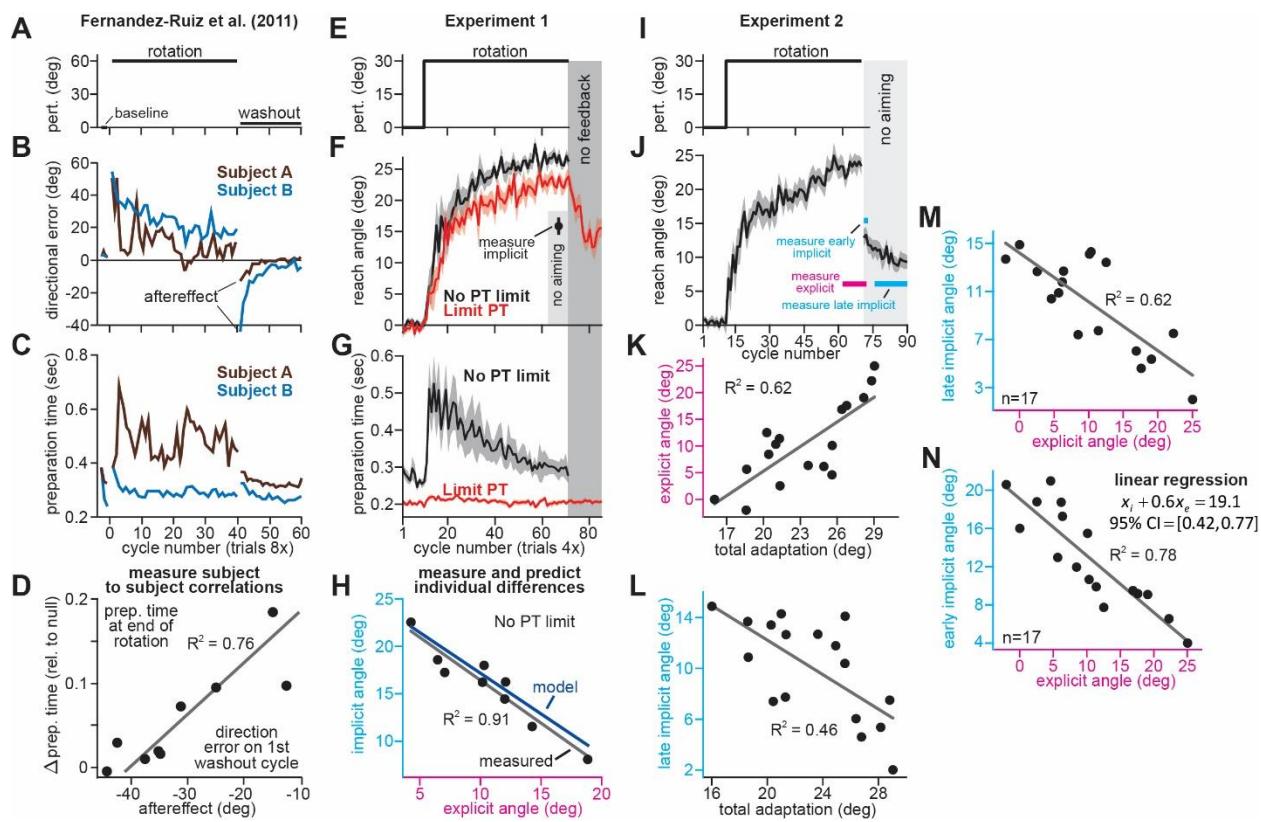


Figure 1. Enhancing explicit strategy suppresses implicit adaptation. **A.** Schematic showing competition between two cooperating parallel systems. Systems 1 and 2 receive the same error and produce outputs to reduce the error. Increases in one system's output will decrease the error source for the partner system, suppressing its adaptation. **B.** Schematic showing competition between two parallel systems with differing objectives. Systems 1 and 2 receive different errors and produce an output that tends to increase the other system's error. In this case, when one system is optimized, the other system is prevented from reducing its error. **C.** Schematic of visuomotor rotation. Participants move from S to T. Hand path is composed of explicit (aim) and implicit corrections. Cursor path is perturbed by

rotation. We explored two hypotheses: prediction error (H1, aim vs. cursor) vs. target error (H2, target vs. cursor) drives implicit learning. **D.** Prediction error hypothesis predicts that enhancing aiming (dashed magenta) will not change implicit learning (black vs. dashed cyan) according to the independence equation. Target error hypothesis predicts that enhancing aiming (dashed magenta) will decrease implicit adaptation (black vs. dashed cyan). **E.** Data reported by Neville and Cressman¹⁵. Participants were separated into 1 of 6 groups. Groups differed based on verbal instruction (instructed yellow; non-instructed gray) and rotation magnitude (20° left; 40° middle; 60° right). **F.** The marginal effect of instruction (average across 3 rotation sizes) shown for explicit adaptation at left and implicit learning at right. Learning predicted by the independence equation (green) and competition equation (blue) are shown. Models were fit assuming implicit error sensitivity and retention were identical across all 6 groups. **G.** The marginal effect of perturbation magnitude (average across instruction conditions) shown for explicit adaptation at left and implicit learning at right. Learning predicted by the independence equation (green) and competition equation (blue) are shown. Models were fit as in **F**. Error bars for data show mean \pm SEM. Error bars for model predictions refer to mean and standard deviation across 10,000 bootstrapped samples.



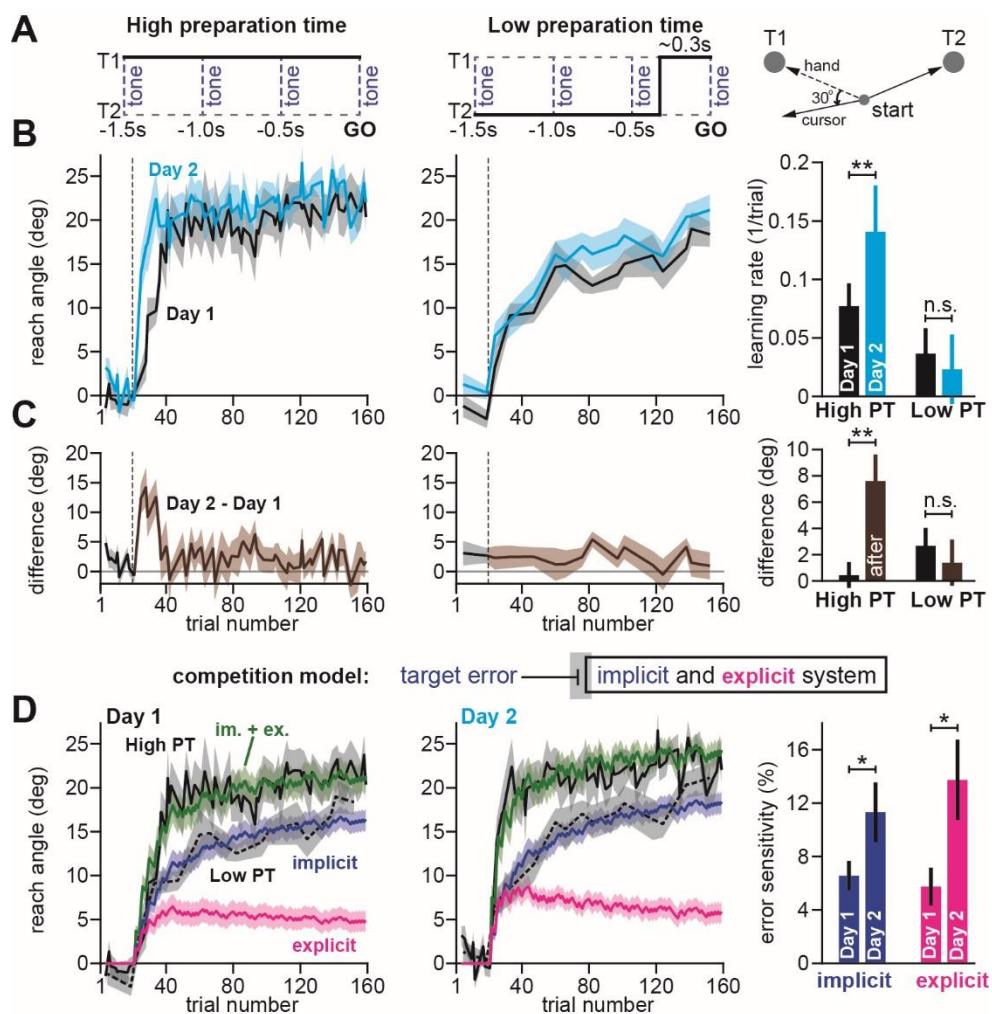
1
2 **Figure 2.** Suppressing explicit strategy increases the total amount of implicit adaptation. Data reported from Saito
3 and Gomi⁴². **A.** Participants adapted to either an abrupt or gradual 60° rotation followed by a washout period. **B.** We
4 explored two hypotheses: prediction error (H1, aim vs. cursor) vs. target error (H2, target vs. cursor) drives implicit
5 learning. Prediction error hypothesis predicts that suppressing aiming (dashed magenta) through gradual
6 perturbation onset will not change implicit learning (black vs. dashed cyan). Target error hypothesis predicts that
7 suppressing aiming (dashed magenta) will increase implicit adaptation (black vs. dashed cyan). **C.** Directional error
8 during adaptation. Note that while the abrupt group exhibited greater adaptation during the rotation, they also
9 showed a smaller aftereffect suggesting less implicit adaptation. **D.** We simulated a state-space model where the
10 implicit system learned from SPE. The model parameters were selected to best fit the data in **C**. In the middle row,
11 hypothetical abrupt explicit strategy was simulated based on data reported by Neville and Cressman¹⁵ (yellow
12 points). The gradual explicit strategy was assumed to be zero because participants were less aware. At bottom, we
13 show implicit learning predicted by an SPE error source. Note the identical saturation levels. **E.** Same as in **D**, but for
14 implicit adaptation based on target error. Note greater implicit learning in gradual condition at the bottom row.
15 Models in **D** and **E** were fit assuming that implicit error sensitivity and retention are identical across abrupt and
16 gradual conditions. **F.** Here we show the implicit aftereffect on the first washout cycle (12 total trials). Model
17 predictions for SPE learning (indep.) and target error learning (competition) are shown. Data show mean \pm SEM
18 across participants. Error bars for model are mean and standard deviation across 20,000 bootstrapped samples.



19 **Figure 3.** Strategy suppresses implicit learning across individual participants. **A-D.** Data are shown from Fernandez-
 20 Ruiz et al.⁴¹. Participants were exposed to a 60° visuomotor rotation followed by a washout period. Paradigm shown
 21 in **A**. Two learning curves for individual participants shown in **B**. Preparation time (latency between reach onset and
 22 target presentation) shown in **C**. In **D**, participants with greater increases in preparation time (relative to baseline)
 23 showed smaller aftereffects, suggesting less implicit adaptation. **E-F.** In Experiment 1, participants adapted to a 30°
 24 visuomotor rotation. The paradigm is shown in **E**. Participants in the No PT limit group had no constraint placed on
 25 their movement preparation time. Participants in the Limit PT group had to execute movements with restricted
 26 preparation time. Learning curves for each group shown in **F**. Note that Limit PT adaptation ended with a no feedback
 27 period where memory retention was measured. Note that No PT limit adaptation ended with a cycle of exclusion
 28 trials where participants were instructed to reach straight to the target without re-aiming and without any feedback
 29 (no aiming, measure implicit). Movement preparation time for each group is shown in **G**. In **H**, we show the total
 30 implicit and explicit adaptation in each participant in the No PT limit condition. Implicit learning measured during
 31 the terminal no aiming probe. Explicit learning represents difference between total adaptation (last 10 rotation
 32 cycles) and implicit probe. The black line shows a linear regression. The blue line shows the theoretical relationship
 33 predicted by the competition equation which assumes implicit system adapts to target error. The parameters for
 34 this model prediction (implicit error sensitivity and retention) were measured in the Limit PT group. **I-N.** In
 35 Experiment 2, participants performed a similar experiment remotely using a personal computer. The paradigm is
 36 shown in **I**. The learning curve is shown in **J**. Implicit learning was measured at the end of adaptation over a 20-cycle
 37 period where participants were instructed to reach straight to the target without aiming and without feedback (no
 38 aiming seen in **I** and **J**). We measured explicit adaptation as difference between total adaptation and reach angle on
 39 first no aiming cycle (**J**, measure explicit). We measured early implicit aftereffect as reach angle on first no aiming
 40 cycle (**J**, measure early implicit). We measured late implicit aftereffect as mean reach angle over last 15 no aiming
 41 cycles (**J**, measure late implicit). In **K** we show how explicit adaptation varies with total adaptation. In **L** we show how
 42

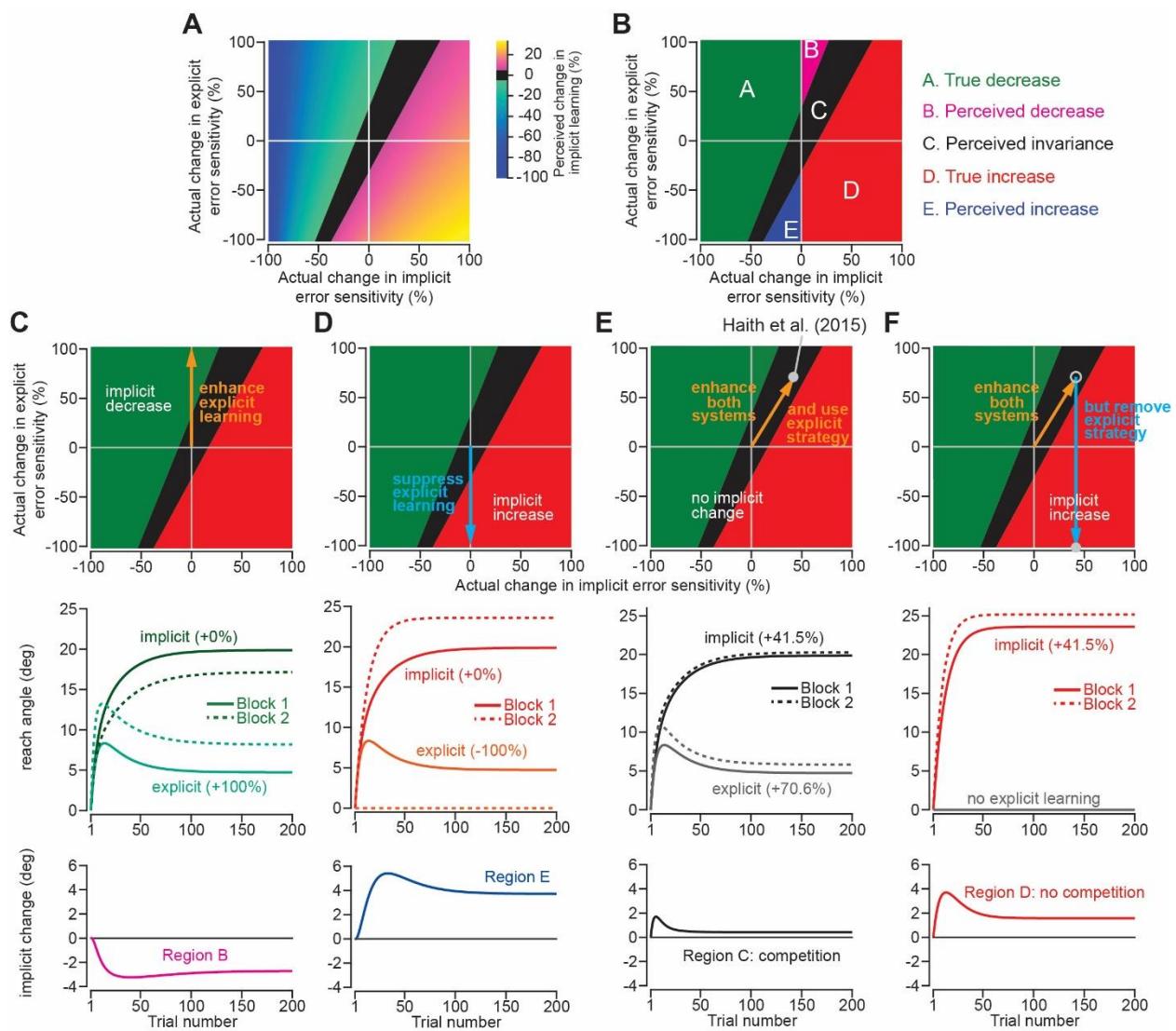
43 late implicit aftereffect varies with total adaptation. In **M** we show how explicit adaptation varies with late implicit
44 aftereffect. In **N** we show how explicit adaptation varies with early implicit aftereffect. Points in **I-N** show individual
45 participants. Lines indicate linear regressions. Error bars show mean \pm SEM across participants.

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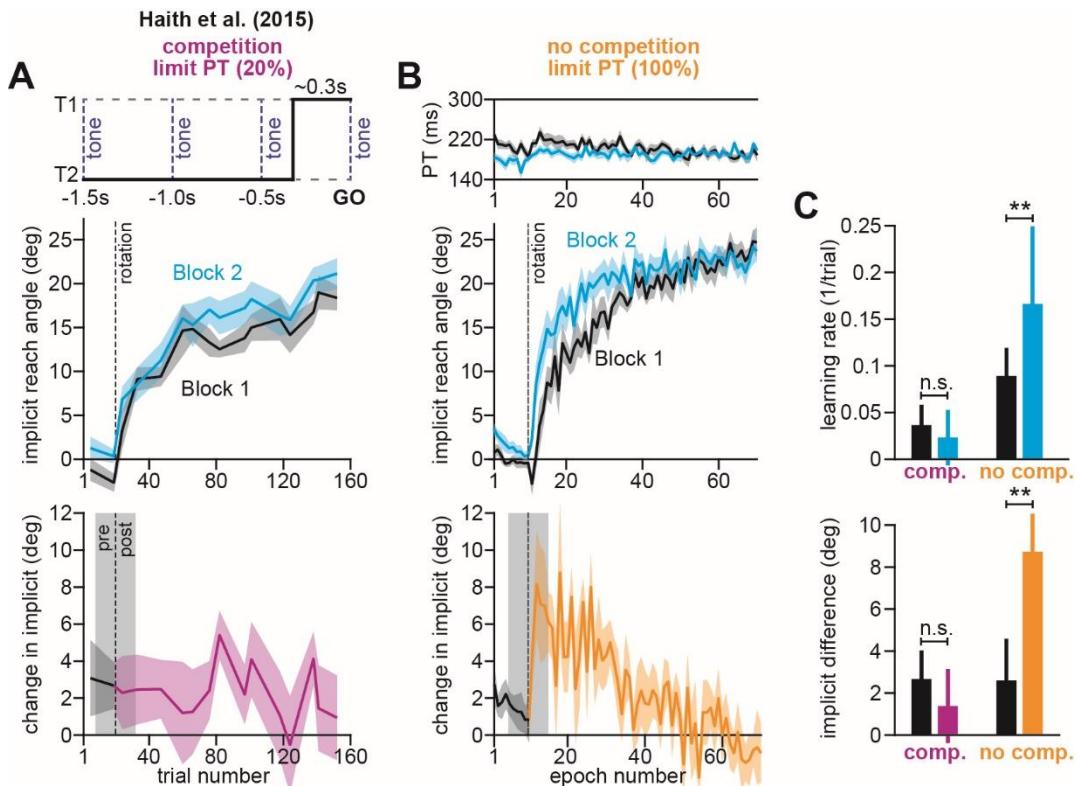
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48 **Figure 4.** Model predicts increase in implicit error sensitivity without any change in implicit learning rate. **A.** Haith
49 and colleagues²⁸ instructed participants to reach to Targets T1 and T2 (right). Participants were exposed to a 30°
50 visuomotor rotation at Target T1 only. Participants reached to the target coincident with a tone. Four tones were
51 played with a 500 ms inter-tone-interval. On most trials (80%) the same target was displayed during all four tones
52 (left, High preparation time or High PT). On some trials (20%) the target switched approximately 300 ms prior to the
53 fourth tone (middle, Low preparation time or Low PT). **B.** On Day 1, participants adapted to a 30° rotation (Block 1, black) followed by a washout period. On Day 2, participants again experienced a 30° rotation (Block 2, blue). At left, we show the reach angle expressed on High PT trials during Blocks 1 and 2. Dashed vertical line shows perturbation onset. At middle, we show the same but for Low PT trials. At right, we show learning rate on High and Low PT trials, during each block. **C.** As an alternative to the rate measure shown at right in **B**, we calculated the difference between reach angle on Blocks 1 and 2. At left and middle, we show the learning curve differences for High and Low PT trials, respectively. At right, we show difference in learning curves before (black) and after (brown) the perturbation. **D.** We fit a state space model to the learning curves in Blocks 1 and 2 assuming that target errors drove implicit adaptation. Low PT trials captured the implicit system (blue). High PT trials captured the sum implicit and explicit system (green). Explicit trace (magenta) is the difference between the High and Low PT predictions. At right, we show error sensitivities predicted by the model. Error bars show mean \pm SEM, except for the learning rate in **B** which displays the median. Paired t-tests are used in **C** and **D**. Wilcoxon signed rank test is used in **B**. Statistics: n.s. means no significant difference, * $p < 0.05$, ** $p < 0.01$.



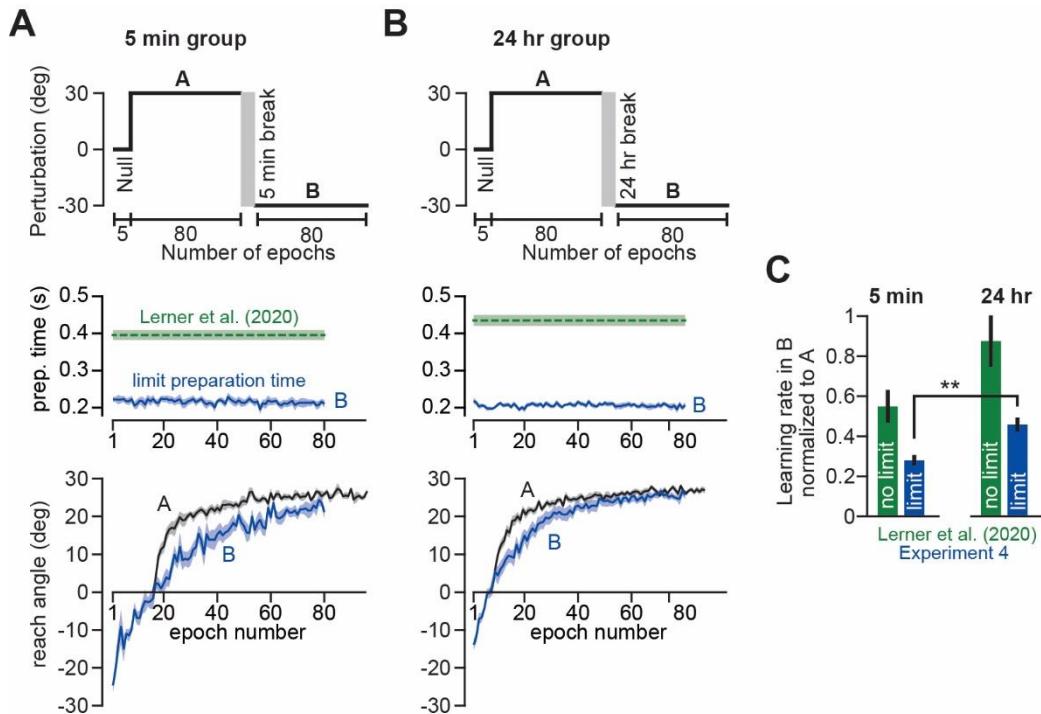
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67 **Figure 5.** Changes in implicit adaptation depend on both implicit and explicit error sensitivity. **A.** Here we depict the
68 competition map. The x-axis shows change in implicit error sensitivity between reference and test conditions. The
69 y-axis shows change in explicit error sensitivity. Colors indicate the percent change in implicit adaptation (measured
70 at steady-state) from the reference to test conditions. Black region denotes an absolute change less than 5%. The
71 map was constructed with Eq. (8). **B.** The map can be described in terms of 5 different regions. In Region A (true
72 increase), implicit error sensitivity and total implicit adaption both increase in test condition. Region D is same, but
73 for decreases in error sensitivity and total adaptation. In Region B (perceived decrease) implicit adaption decreases
74 though its error sensitivity is higher or same. In Region E (perceived increase), implicit adaption increases though
75 its error sensitivity is lower or same. Region C shows a perceived invariance where implicit adaptation changes less
76 than 5%. **C.** Top: effect of suppressing explicit learning. Middle: implicit and explicit learning shown in Blocks 1 and
77 2, where explicit error sensitivity increases 100%. Bottom: implicit learning change (Block 1 to 2). **D.** Top: effect of
78 enhancing explicit learning. Middle: implicit and explicit learning shown in Blocks 1 and 2, where only difference is
79 100% increase in explicit error sensitivity. Bottom: change in implicit learning (Block 1 to 2). **E.** Top: model simulation
80 for Haith et al.²⁸. Middle: implicit and explicit learning during Blocks 1 and 2 where implicit error sensitivity increases
81 by 41.5% and explicit error sensitivity increases by 70.6%. Bottom: negligible change in implicit learning (Block 1 to
82 2). **F.** Same as in **E** except here explicit strategy is suppressed during Blocks 1 and 2.



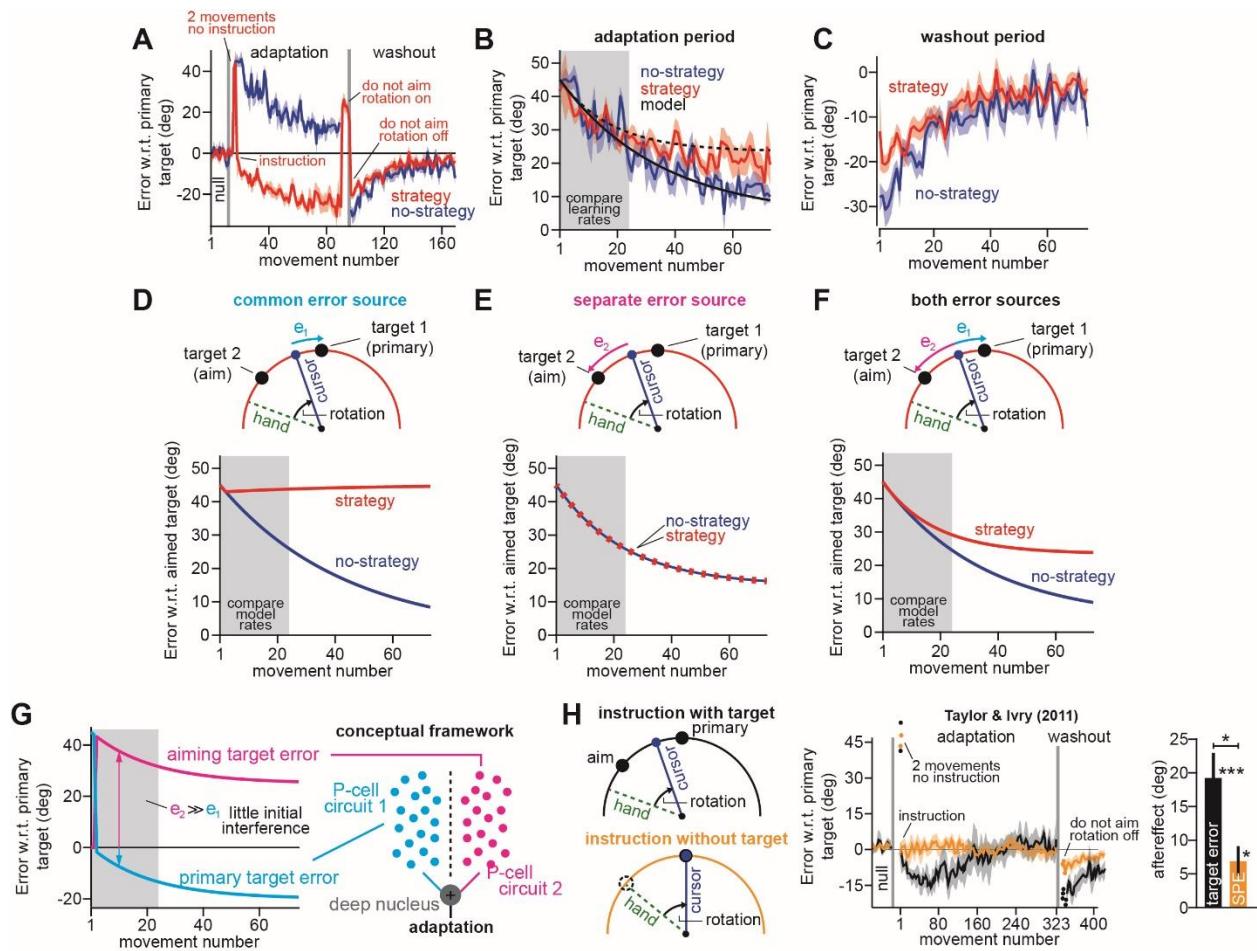
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84 **Figure 6.** Removing explicit strategy reveals savings in implicit adaptation. **A.** Top: Low preparation time (Low PT)
 85 trials in Haith and colleagues²⁸ used to isolate implicit learning. Middle: learning during Low PT in Blocks 1 and 2.
 86 Bottom: difference in Low PT learning between Blocks 1 and 2. **B.** Similar to **A**, but here (Experiment 3) explicit
 87 learning was suppressed on every trial, as opposed to only 20% of trials. To suppress explicit strategy, we restricted
 88 reaction time on every trial. The reaction time during Blocks 1 and 2 is shown at top. At middle, we show how
 89 participants adapted to the rotation under constrained reaction time. At bottom, we show the difference between
 90 the learning curves in Blocks 1 and 2. **C.** Here we measured savings in Haith et al. (20% of trials had reaction time
 91 limit) and Experiment 3 (100% of trials had reaction time limit). At top, we quantify savings by fitting an exponential
 92 curve to each learning curve. Bars show the rate parameter associated with the exponential. At bottom, we quantify
 93 savings by comparing how Blocks 1 and 2 differed before perturbation onset (black), and after perturbation onset
 94 (purple and yellow). Error bars show mean \pm SEM, except for the learning rate at the top of **C** which shows the
 95 median. Paired t-tests are used at the bottom of **C**. Wilcoxon signed rank tests are used at the top of **C**. Statistics:
 96 n.s. means no significant difference, ** $p<0.01$.



97

98 **Figure 7.** Removing explicit strategy reveals anterograde interference in implicit adaptation. **A.** Top: participants
99 were adapted to a 30° rotation (A). Following a 5-minute break, participants were then exposed to a -30° rotation
100 (B). This A-B paradigm was similar to that of Lerner & Albert et al.²⁶. Middle: to isolate implicit adaptation, we
101 imposed strict reaction time constraints on every trial. Under these constraints, reaction time (blue) was reduced by
102 approximately 50% over that observed in the self-paced condition (green) studied by Lerner & Albert et al.²⁶ Bottom:
103 learning curves during A and B in Experiment 4; under reaction time constraints, the interference paradigm produced
104 a strong impairment in the rate of implicit adaptation. To compare learning during A and B, B period learning was
105 reflected across y-axis. Furthermore, the curves were temporally aligned such that an exponential fit to the A period
106 and exponential fit to the B period intersected when the reach angle crossed 0°. This alignment visually highlights
107 differences in the learning rate during the A and B periods. **B.** Here we show the same analysis as in **A** but when
108 exposures A and B were separated by 24 hours. **C.** To measure the amount of anterograde interference on the
109 implicit learning system, we fit an exponential to the A and B period behavior. Here we show the B period exponential
110 rate parameter divided by the A period rate parameter (values less than 1 indicate a slowing of adaptation). At left
111 we show the results for the 5-minute group. At right we show the results for the 24-hr group. In green we show data
112 from Lerner & Albert et al.²⁶ where reaction time was unrestricted (no limit). In blue we show our new dataset
113 (Experiment 4) where reaction time was limited to isolate implicit learning. A two-sample t-test was used to test for
114 differences in the implicit impairment at 5 minutes and 24 hours. Error bars show mean ± SEM. Statistics: **p<0.01.
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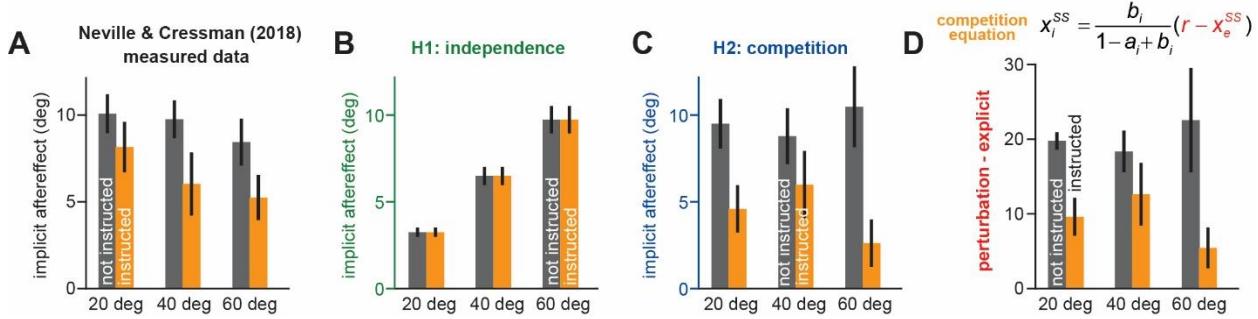


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118 **Figure 8.** Two visual targets create two implicit error sources. **A.** Figure shows data reported in Mazzoni and
119 Krakauer¹². Blue shows error between primary target and cursor during adaptation and washout. Red shows the
120 same, but in a strategy group that was instructed to aim to a neighboring target (instruction) to eliminate target
121 errors, once participants experienced two large errors (2 cycles no instruction). **B.** Here we show the error between
122 the cursor and the aimed target during the adaptation period. These curves are the same as in **A** except we use the
123 aimed target rather than primary target, so as to better compare learning curves across groups. **C.** The washout
124 period reported in **A**. Here error is relative to primary target, though in this case aimed and primary targets are the
125 same. **D.** Here we modeled behavior when implicit learning adapts to primary target errors. The primary target error
126 is shown in e_1 at top. Note that no-strategy learning resembles data. However, strategy learning exhibits no drift
127 because the implicit system has zero error. Note here that the primary target error of 0° is a 45° aimed target error
128 in the strategy group. **E.** Similar to **D**, except here the implicit system adapts to errors between the cursor and aimed
129 target. This error is schematized in e_2 at top. Note that this model predicts identical learning in strategy and no-
130 strategy groups. **F.** In this model, the strategy group adapts to both the primary target error and the aimed target
131 error (e_1 and e_2 at top). The no-strategy group adapts only to the primary target error. Learning parameters are
132 identical across groups. **G.** At left, we show how aiming target and primary target errors evolve in the strategy group
133 in **F**. At right, we imagine a potential neural substrate for implicit learning. The primary target error and aiming target
134 error engage two different sub-populations of Purkinje cells in the cerebellar cortex. These two implicit learning
135 modules combine at the deep nucleus. **H.** Figure shows data reported in Taylor and Ivry²¹. Participants performed a
136 task similar to **A**. Before adaptation, participants were taught how to re-aim their reach angles. In the “instruction
137 with target” group, participants re-aimed during adaptation with the aide of neighboring aiming targets (top-left).

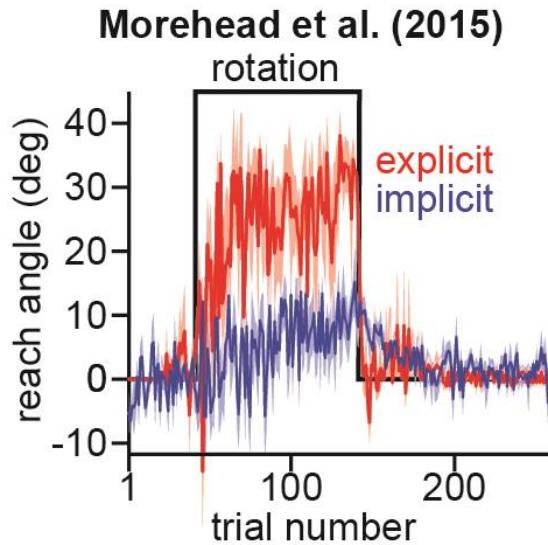
138 In the “instruction without target” group, participants re-aimed during adaptation without any aiming targets, solely
139 based on the remembered instruction from the baseline period. The middle shows learning curves. In both groups,
140 the first 2 movements were uninstructed, resulting in large errors (2 movements no instruction). Note in the
141 “instruction with target” group, there is an implicit drift as in A, but participants eventually reverse this by changing
142 explicit strategy. There is no drift in the “instruction without target” group. At right, we show the implicit aftereffect
143 measured by telling participants not to aim (first no feedback, no aiming cycle post-adaptation). Greater implicit
144 adaptation resulted from physical target. Error bars show mean \pm SEM. Statistics: * $p<0.05$, *** $p<0.001$.

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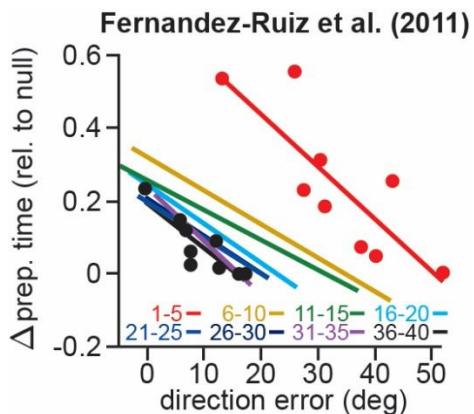


146
147 **Figure S1.** Changes in implicit adaptation in response to awareness and rotation size. Data reported from Neville and
148 Cressman (2018)¹⁵. **A.** Participants were separated into 1 of 6 groups. Groups differed based on verbal instruction
149 (instructed yellow; non-instructed gray) and rotation magnitude (20° left; 40° middle; 60° right). Here we show
150 implicit learning measured using exclusion trials (reach without re-aiming) at the end of adaptation. **B.** Here we show
151 implicit aftereffects predicted by a model where implicit system learns from SPE only. **C.** Here we show implicit
152 aftereffects predicted by a model where implicit system learns from target error only. **D.** The competition model
153 (target error learning) predicts that implicit learning will be proportional to the difference between the rotation size
154 and the total explicit strategy. Here we show this quantity for all 6 experimental groups. Note that model predictions
155 in **B** and **C** assume that implicit error sensitivity and retention factor are the same across all 6 experimental groups.
156 Error bars for data show mean \pm SEM. Error bars for model predictions refer to mean and standard deviation across
157 10,000 bootstrapped samples.

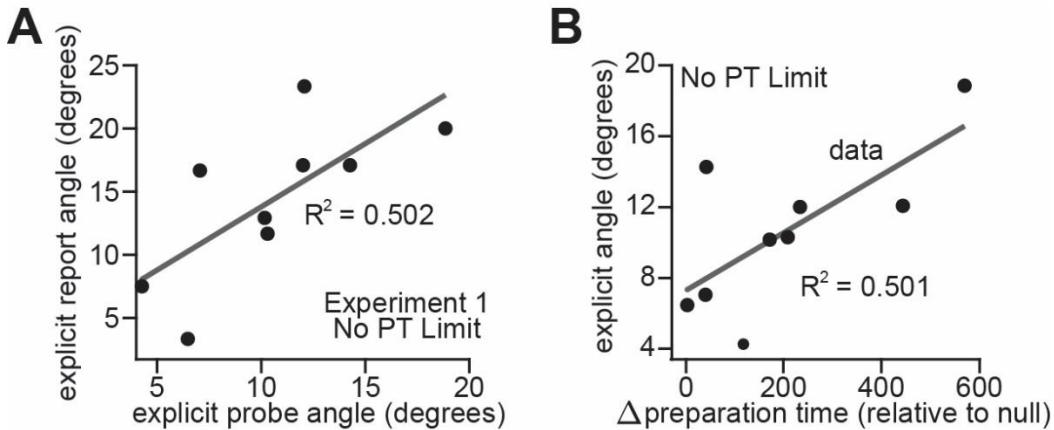
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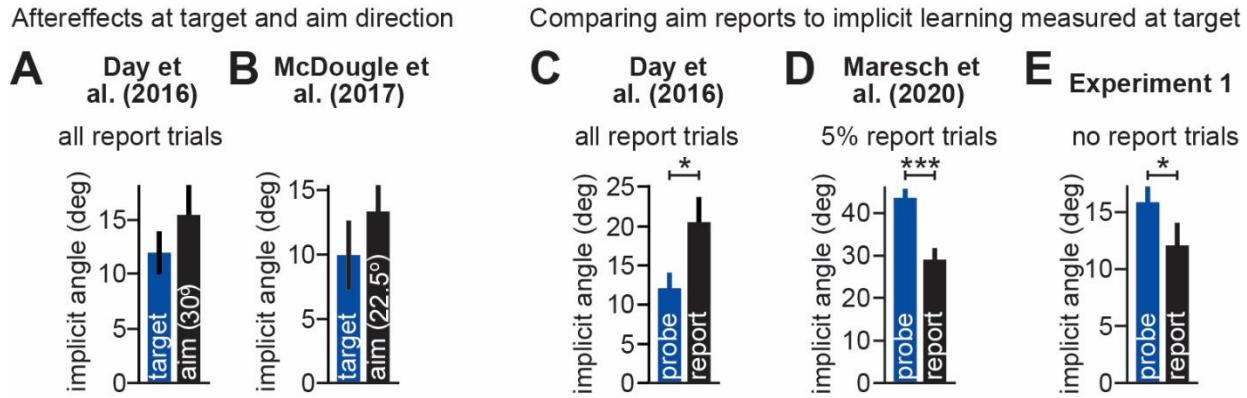


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160 **Figure S2.** Explicit strategies are rapidly disengaged during washout. Data are reported from Morehead et al.
161 (2015)³⁴. Here participants adapted to a 45° rotation, followed by an extended washout period. Explicit learning was
162 measured by asking subjects to report their aiming angle using a ring of visual landmarks. Implicit learning was
163 measured as the difference between the observed reach angle and the direction of reported aim. In this task,
164 participants reached on each trial to 1 of 4 targets. Note the sharp change in explicit angle to zero at the start of the
165 washout period. The aftereffect during a washout period is thought to reflect implicit adaptation. This requires that
166 explicit strategies are rapidly disengaged during washout, consistent with these data. Error bars show mean ± SEM.
167



168
169 **Figure S3.** Participants that increase their preparation time exhibit greater total adaptation. Data are reported from
170 Fernandez-Ruiz and colleagues⁴¹. In this experiment, participants made 10 cm reaching movements to 1 of 8 targets,
171 pseudorandomly arranged in cycles of 8 trials. Here we report data from the unconstrained RT group described in
172 the original manuscript. The experiment started with 3 cycles of null rotation trials, followed by 40 cycles of a 60°
173 rotation. The authors calculated change in movement preparation time (relative to baseline period) on each trial.
174 Here the authors calculated the directional error and the change in preparation time across 5-cycle periods spanning
175 the entire 40-cycle rotation. The points show individual subjects for the first 5 and last 5 rotation cycles. All lines
176 show the linear regression across individual subjects in each color-coded period. Note that each line has a negative
177 slope, indicating that participants who increased their reaction time more consistently exhibited smaller directional
178 errors through the entire rotation period.
179





195 **Figure S5.** Differences in generalization across visuomotor rotation tasks. **A.** Data collected by Day et al.⁷², reported
 196 in Fig. 2 of the original manuscript. Here, participants were exposed to a 45° rotation while reaching to a single
 197 target. On each trial they were asked to report their aiming direction, using a ring of visual landmarks. In the “target”
 198 group, implicit aftereffects were measured at the trained target location. In the “aim” group, implicit aftereffects
 199 were probed at a target location 30° away from the trained target, consistent with the direction of the most
 200 frequently reported aim. Here we show data from the first aftereffect cycle after the rotation period. **B.** Similar to **A**
 201 except for data reported by McDougle et al.⁷¹ (Fig. 3A of the original manuscript). Participants were also exposed to
 202 a 45° rotation while reaching to a single target. At the end of the experiment, participants were exposed to an
 203 aftereffect block where participants were told to move straight to the target without re-aiming. Here we take two
 204 relevant points from the generalization curve measured at the end of learning. The “target” condition represents
 205 aftereffects probed at the training target. The “aim” condition shows the aftereffect measured at 22.5° away from
 206 the primary target, which was the target closest to the mean reported explicit re-aiming strategy of 26.2°. **C.** Data
 207 again from Day et al.⁷². The “probe” implicit learning measure is the same as **A**. The “report” condition shows the
 208 amount of implicit learning estimated by subtracting the reported explicit strategy from the reported reach angle
 209 on the last cycle of the rotation. **D.** Similar to **C**, but for the intermittent reporting (IR-E) group reported by Maresch
 210 et al.⁷⁵ (Fig. 4b of the original manuscript). In this group aim was only intermittently reported (4 trials for every 80
 211 normal adaptation trials). Thus, in most cases, participants only had to attend to a single target when reaching. The
 212 authors also used 8 training targets (as opposed to 1 in **A-C**). The “probe” condition corresponds to the total implicit
 213 learning measured at the end of adaptation by telling participants to reach without re-aiming. The “report” condition
 214 corresponds to the total implicit learning estimated at the end of adaptation by subtracting the reported aim
 215 direction from the measured reach angle. **E.** Here we report implicit learning measured using the “probe” and
 216 “report” conditions in Experiment 1, analogous to the measures described in **D**. Error bars show mean \pm SEM.
 217

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