1

Competition between parallel sensorimotor learning systems

Scott T. Albert[1], Jihoon Jang[1], Adrian M. Haith[2], Gonzalo Lerner[3], Valeria Della-Maggiore[3], John W. Krakauer[2,4,5], and Reza Shadmehr[1,4]

1. Department of Biomedical Engineering, Johns Hopkins School of Medicine, Baltimore MD
2. Department of Neurology, Johns Hopkins School of Medicine, Baltimore MD
3. Deparamento de Fisiología y Biofísia, Universidad de Buenos Aires, Buenos Aires, Argentina
4. Department of Neuroscience, Johns Hopkins School of Medicine, Baltimore MD
5. The Santa Fe Institute, Santa Fe, NM

Correspondence: Scott Albert, 416 Traylor Building, Johns Hopkins School of Medicine, 720 Rutland Ave., Baltimore, MD 21205, USA. Email: salbert8@jhmi.edu. Phone: 410-614-3424.

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 circuits[7] that respond to each error separately without interference[8]. 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

2

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 interference[25–27]. On the other hand, when the perturbations are the same,
73   the rate of learning increases due to savings[28–32]. 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 error[17–19]. Notably, this target error (Fig. 1C, target error) is altered by
100   both implicit (x_i) and explicit (x_e) adaptation:

3

101
$$e^{(n)}_{target} = r^{(n)} - (x^{(n)}_i + x^{(n)}_e) \qquad (1)$$

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
$$e^{(n)}_{SPE} = r^{(n)} - x^{(n)}_i \qquad (2)$$

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
$$x^{(n+1)}_i = a_i x^{(n)}_i + b_i e^{(n)} \qquad (3)$$

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
$$x^{ss}_i = \frac{b_i}{1 - a_i + b_i}(r - x^{ss}_e) \qquad (4)$$

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

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
$$x^{ss}_i = \frac{b_i}{1 - a_i + b_i}r \qquad (5)$$

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 Cressman[15].
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 removed[34] (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 Cressman[15] 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.

6

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 colleagues[41]
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; $\rho=0.87$, 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   ρ=0.709) and also appeared to require greater movement preparation time (Fig. S4B, ρ=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; ρ=-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°.

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 Cressman[15] (Fig. 1) and Saijo and Gomi[42] (Fig. 2).
304   Namely, participants that compensated most for the perturbation utilized large explicit strategies (Fig. 3K;
305   ρ=0.79, p<0.001). But enhancements in overall learning came at the cost of reductions in implicit

306 adaptation (Fig. 3L; ρ=-0.68, p=0.003), due to a competition between implicit and explicit learning (Fig.
307 3M, ρ=-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, ρ=-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 work[28], 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 experiment[28]
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

11

430   suggested that impaired learning in *B* is caused by a change in error sensitivity[26]. 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 imposed[26] (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 Krakauer[12], 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 study[12]. 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 $$x_{i,1}^{(n+1)} = a_i x_{i,1}^{(n)} + b_i e_1^{(n)}$$
$$x_{i,2}^{(n+1)} = a_i x_{i,2}^{(n)} + b_i e_2^{(n)} \tag{6}$$

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

13

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 & Ivry[21] 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 adaptation[62]. 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 reports[34], 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 errors[17], 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 colleagues[33], 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 perturbations[36], 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 colleagues[28] 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 time[26].
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 time[26], 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 colleagues[17] 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 work[26] (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*

16

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 adaptation[66–68]. 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 Cressman[15], 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 colleagues[14] 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 colleagues[41] 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   learning[41]. 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 (≈5°; see Fig. S5B for aim-target displacement[71] of 22.5° and S3A for aim-target displacement[72]
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 Cressman[15] 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 adaptation[75] (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 Krakauer[12] 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 5-20° (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))

18

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 landmark[21]
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 may have learning deficits[20,54,56,83,84] specific to one error but not
754 the other. These possibilities remain to be tested.

755
756

Methods

Here we describe the experiments and corresponding analysis reported in the main text. Much of this work involves reevaluation of earlier literature; this includes data from Haith and colleagues[28] in Figs. 4&6, data from Lerner and Albert et al.[26] in Fig. 7, data from Neville and Cressman[15] in Fig. 1, data from Saijo and Gomi[42] in Fig. 2, data from Fernandez-Ruiz et al.[41] in Fig. 3, data from Mazzoni and Krakauer[12] in Fig. 8, and data from Taylor and Ivry[21] in Fig. 8. Furthermore, some generalization data[71,72] was considered in Fig. S5. The relevant details of these studies are summarized in the sections below alongside the new data collected for this work (Experiments 1-4).

Participants

A detailed description of participants in Haith and colleagues[28] (n=14), Lerner and Albert et al.[26] (n=34 for 5 min and 24 hr groups), Neville and Cressman[15] (n=63), and Mazzoni and Krakauer[12] (n=18), Saijo and Gomi[42] (n=9 for abrupt, n=9 for gradual), Fernandez-Ruiz et al.[41] (n=9), and Taylor and Ivry[21] (n=10 for instruction with visual target, n=10 for instruction without visual target) are described in their respective papers. All volunteers (ages 18-62) in Experiments 1-4 were neurologically healthy and right-handed. Experiment 1 include n=9 participants (5 Male, 4 Female) in the No PT limit group and included n=13 participants (6 Male, 7 Female) in the PT Limit group. Experiment 2 included n=17 participants (10 Male, 7 Female). Experiment 3 included n=10 participants (6 Male, 4 Female). Experiment 4 included n=20 participants (10 Male, 10 Female). Experiments 1-4 were approved by the Institutional Review Board at the Johns Hopkins School of Medicine.

Apparatus

In Experiments 1, 3, and 4 participants held the handle of a planar robotic arm and made reaching movements to different target locations in the horizontal plane. The forearm was obscured from view by an opaque screen. An overhead projector displayed a small white cursor (diameter = 3mm) on the screen that tracked the motion of the hand. Throughout testing we recorded the position of the handle at submillimeter precision with a differential encoder. Data were recorded at 200 Hz. Protocol details were similar for Haith and colleagues[28], Neville and Cressman[15], Saijo and Gomi[42], and Fernandez-Ruiz et al.[41] in that participants gripped a two-link robotic manipulandum, were prevented from viewing their arm, and received visual feedback of their hand position in the form of a visual cursor. In Lerner and Albert et al.[26], participants performed pointing movements with their thumb and index finger while gripping a joystick with their right hand. In Mazzoni and Krakauer[12], participants rotated their hand to displace an infrared marker placed on the index finger. In Taylor and Ivry[21], hand position was tracked via a sensor attached to the index finger while participants made horizontal reaching movements along the surface of a table. In Experiment 2, participants were tested remotely on their personal computer. They moved a cursor on the screen by sliding their index finger along the track pad.

Visuomotor rotation

Experiments 1-4 followed a similar protocol. At the start of each trial, the participant brought their hand to a center starting position (circle with 1 cm diameter). After maintaining the hand within the start circle, a target circle (1 cm diameter) appeared in 1 of 4 positions (0°, 90°, 180°, and 270°) at a displacement of 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 colleagues[28], Lerner and Albert et al.[26], Neville and Cressman[15], Taylor
821 and Ivry[21], Saijo and Gomi[42], Fernandez-Ruiz et al.[41], and Mazzoni and Krakauer[12] 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]:

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

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

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

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 Cressman[15]. Here the authors tested how awareness of a visuomotor rotation altered the

22

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 Cressman[15] 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
$$\theta_{fit} = \underset{\theta}{\arg\min} \sum_{n=1}^{6} (x_{i_n}^{ss} - \hat{x}_{i_n}^{ss})^2 \tag{9}$$

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

23

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 Gomi[42]. 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 rotation[38], 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 Cressman[15] 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 faction (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
$$\theta_{fit} = \arg\min_{\theta} \sum_{n} (e_{abrupt}^{(n)} - \hat{e}_{abrupt}^{(n)})^2 + \sum (e_{gradual}^{(n)} - \hat{e}_{gradual}^{(n)})^2 \tag{10}$$

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 Cressman[15]. For the implicit state, we used
971   20% of the explicit variability, given that aiming strategies are more variable than implicit corrections[14].
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 ± 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 colleagues[41]. 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

25

1003   through the entire rotation period. These data were extracted directly from the primary figures reported
1004   by Fernandez-Ruiz and colleagues[41] 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 colleagues[28]. 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

26

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 screen[24]. 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 direction[47] (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 ≤ 30°, 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 colleagues[28] 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 colleagues[28]; 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

28

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

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 colleagues[28].
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 work[26], 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

31

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
$$\theta_{fit} = \underset{\theta}{\arg\min} \sum_{n=1}^{N} (y_{strategy}^{(n)} - \hat{y}_{strategy}^{(n)})^2 + (y_{no\text{-}strategy}^{(n)} - \hat{y}_{no\text{-}strategy}^{(n)})^2 \tag{12}$$

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 Ivry[21]. 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 Krakauer[12], 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 Krakauer[12]. However, both groups exhibited an implicit aftereffect (Fig. 8H, aftereffect;

1299   first cycle of washout period as reported in Fig. 4C of the original manuscript[21]).

1300   These data were extracted directly from the primary figures reported by Taylor and Ivry[21] 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.

33

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:

1346
$$y^{(n)} = a_i^n y_{ss} \tag{13}$$

1347　Here $y^{(n)}$ refers to the reach angle on the n-th no feedback trial, and y_{ss} corresponds to the asymptotic
1348　behavior prior to the no feedback period. We used *fmincon* in MATLAB R2018a to identify the retention
1349　factor which minimized the difference between the decay predicted by Eq. (13) and that measured during
1350　the no feedback period. We obtained an epoch-by-epoch retention factor of 0.943 ± 0.011 (mean ± SEM).
1351　Note that an epoch consisted of 4 trials, so this corresponded to a trial-by-trial retention factor of 0.985.
1352　When modeling Neville and Cressman[15] (Fig. 1), we cubed this trial-by-trial term because each cycle
1353　consisted of 3 different targets (final retention factor of 0.9565).

1354　　　Next, we measured implicit error sensitivity in the Limit PT group during rotation period trials. To
1355　measure implicit error sensitivity on each trial, we used its empirical definition:

1356
$$b^{(n_1)} = \frac{y^{(n_2)} - a^{n_2-n_1} y^{(n_1)}}{e^{(n_1)}} \tag{14}$$

1357　Eq. (14) determines the sensitivity to an error experienced on trial n_1 when the participant visited a
1358　particular target T. This error sensitivity is equal to the change in behavior between two consecutive visits
1359　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,
1360　we account for decay in the behavior by multiplying the behavior on trial n_1 by a decay factor that
1361　accounted for the number of intervening trials between trials n_1 and n_2. For each target, we used the
1362　specific retention factor estimated for that target with Eq. (13).

1363　　　Using this procedure, we calculated implicit error sensitivity as a function of trial in Experiment 2.
1364　To remove any potential outliers, we identified error sensitivity estimates that deviated from the
1365　population median by over 3 median absolute deviations within windows of 10 epochs. As reported by
1366　Albert and colleagues[37], implicit error sensitivity increased over trials. Eqs. (4) and (5) require the steady-
1367　state implicit error sensitivity observed during asymptotic performance. To estimate this value, we
1368　averaged our trial-by-trial error sensitivity measurements over the last 5 epochs of the perturbation. This
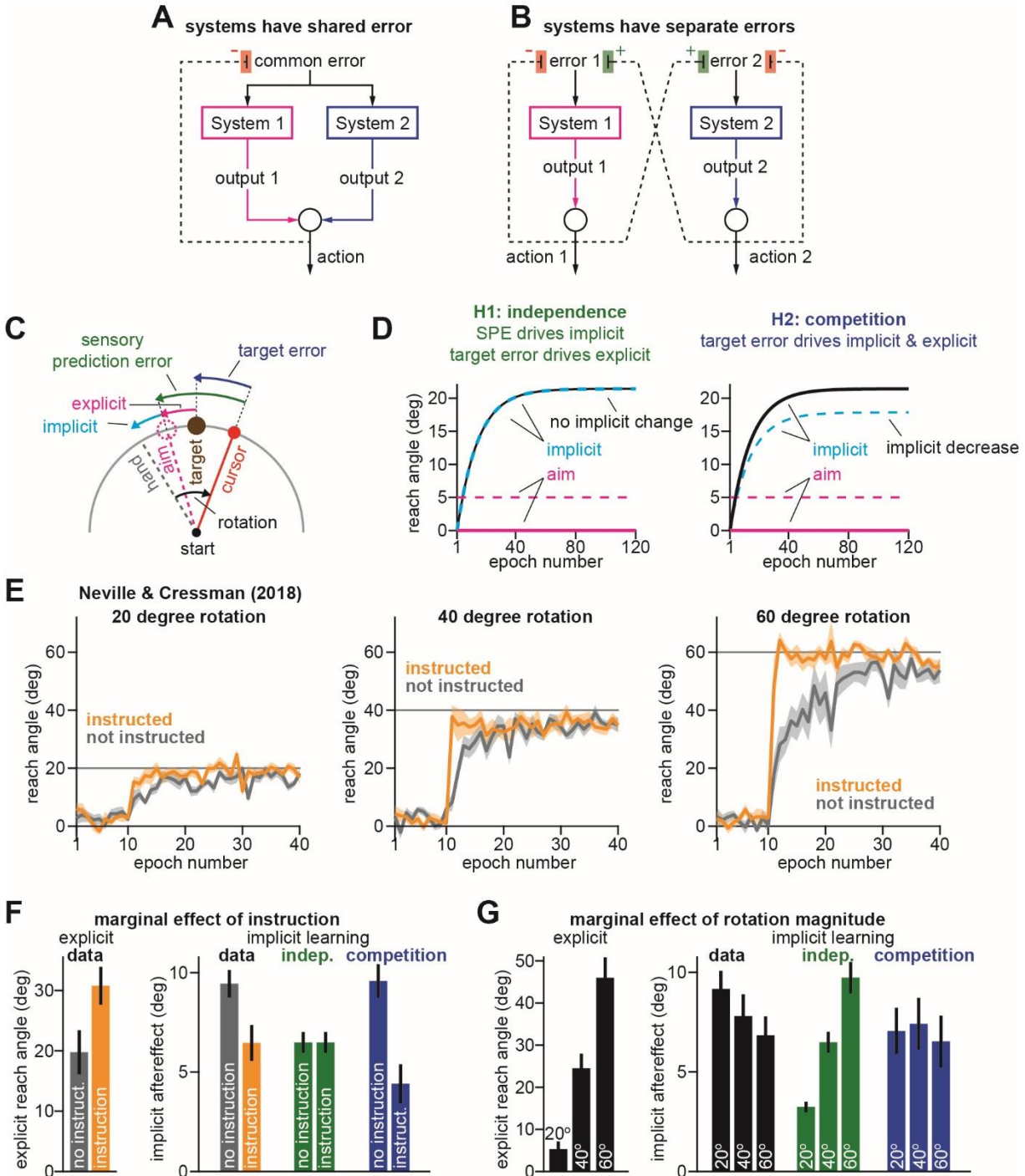1369　yielded an implicit error sensitivity of 0.346 ± 0.071 (mean ± SEM).

34

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 Cressman[15]. 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 ± SEM. Error bars for model predictions refer to mean and standard deviation across 10,000 bootstrapped samples.
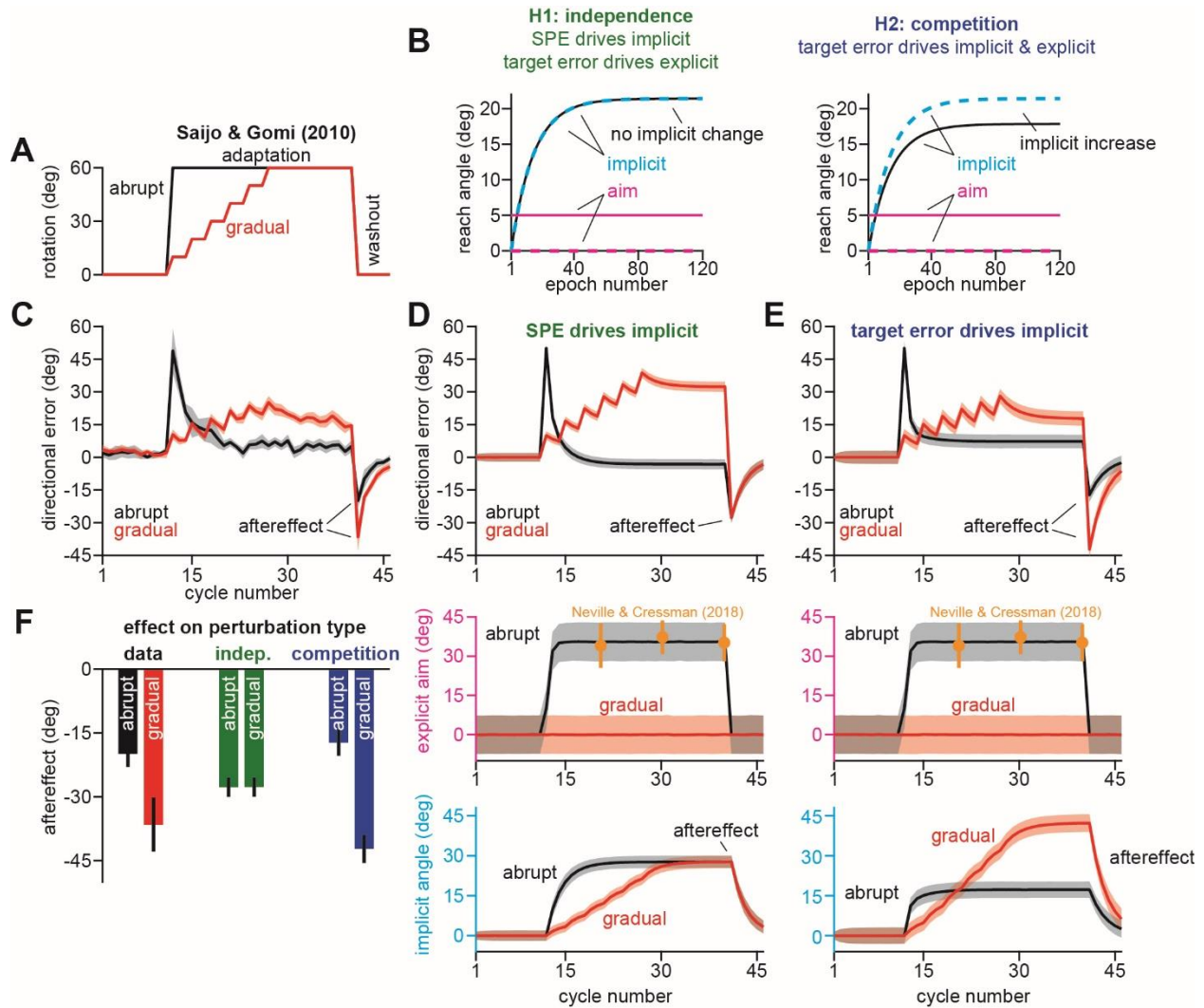
Figure 2. Suppressing explicit strategy increases the total amount of implicit adaptation. Data reported from Saijo and Gomi[42]. **A.** Participants adapted to either an abrupt or gradual 60° rotation followed by a washout period. **B.** We explored two hypotheses: prediction error (H1, aim vs. cursor) vs. target error (H2, target vs. cursor) drives implicit learning. Prediction error hypothesis predicts that suppressing aiming (dashed magenta) through gradual perturbation onset will not change implicit learning (black vs. dashed cyan). Target error hypothesis predicts that suppressing aiming (dashed magenta) will increase implicit adaptation (black vs. dashed cyan). **C.** Directional error during adaptation. Note that while the abrupt group exhibited greater adaptation during the rotation, they also showed a smaller aftereffect suggesting less implicit adaptation. **D.** We simulated a state-space model where the implicit system learned from SPE. The model parameters were selected to best fit the data in **C**. In the middle row, hypothetical abrupt explicit strategy was simulated based on data reported by Neville and Cressman[15] (yellow points). The gradual explicit strategy was assumed to be zero because participants were less aware. At bottom, we show implicit learning predicted by an SPE error source. Note the identical saturation levels. **E.** Same as in **D**, but for implicit adaptation based on target error. Note greater implicit learning in gradual condition at the bottom row. Models in **D** and **E** were fit assuming that implicit error sensitivity and retention are identical across abrupt and gradual conditions. **F.** Here we show the implicit aftereffect on the first washout cycle (12 total trials). Model predictions for SPE learning (indep.) and target error learning (competition) are shown. Data show mean ± SEM across participants. Error bars for model are mean and standard deviation across 20,000 bootstrapped samples.

37

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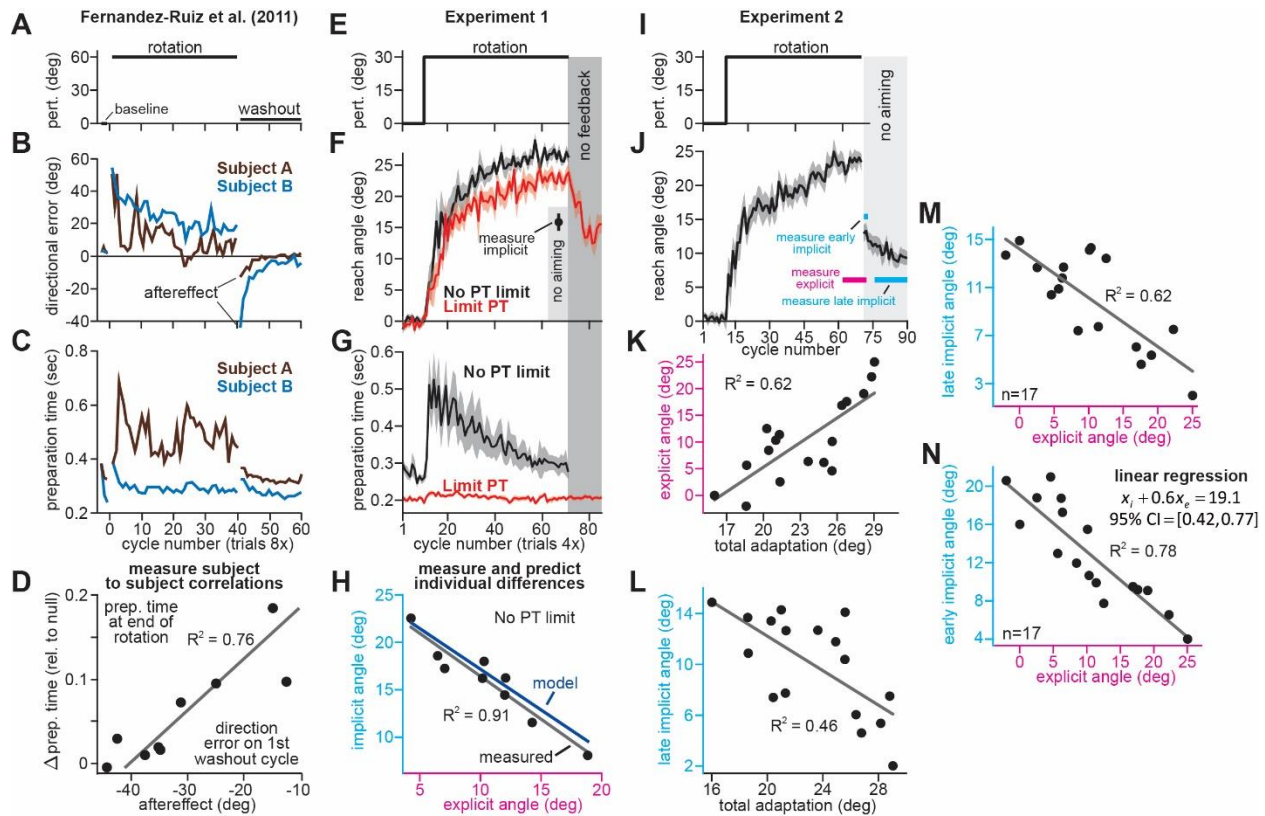
Figure 3. Strategy suppresses implicit learning across individual participants. **A-D.** Data are shown from Fernandez-Ruiz et al.[41]. Participants were exposed to a 60° visuomotor rotation followed by a washout period. Paradigm shown in **A**. Two learning curves for individual participants shown in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

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 ± SEM across participants.

46
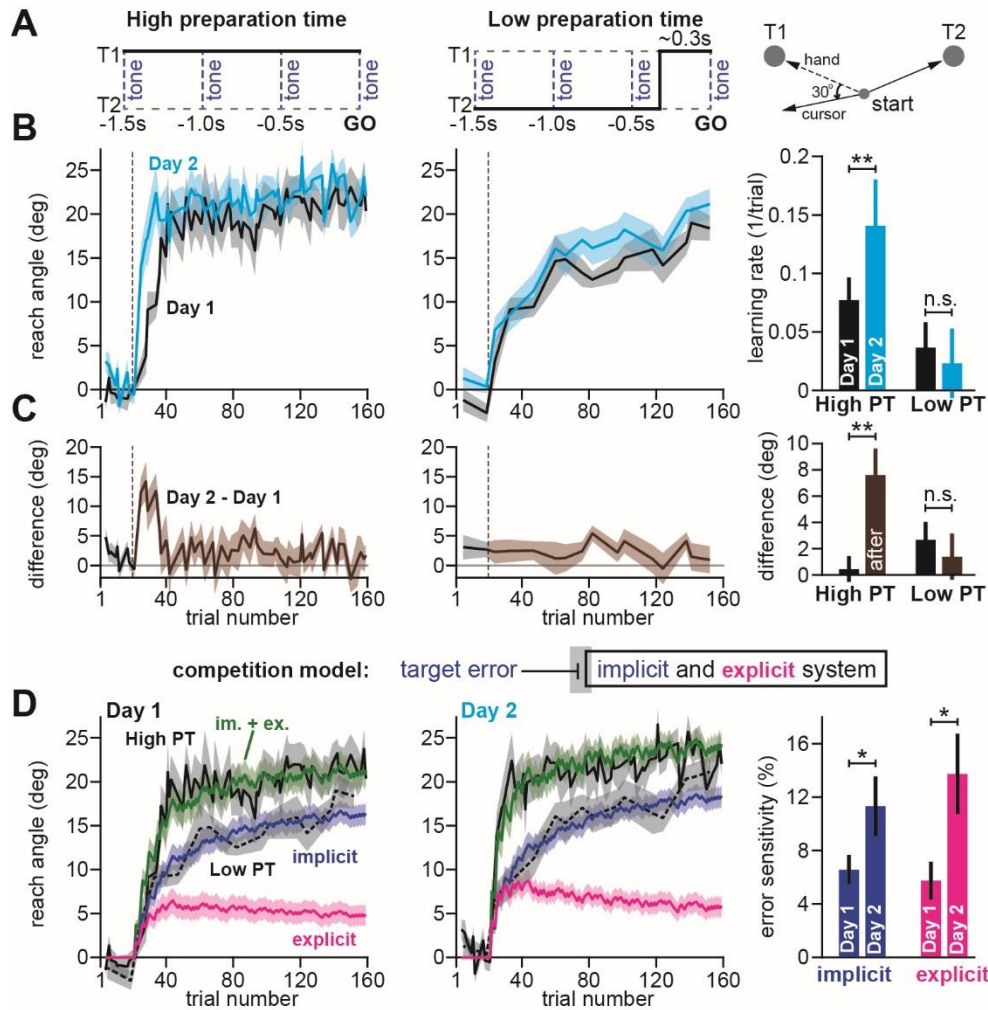
Figure 4. Model predicts increase in implicit error sensitivity without any change in implicit learning rate. **A.** Haith and colleagues[28] instructed participants to reach to Targets T1 and T2 (right). Participants were exposed to a 30° visuomotor rotation at Target T1 only. Participants reached to the target coincident with a tone. Four tones were played with a 500 ms inter-tone-interval. On most trials (80%) the same target was displayed during all four tones (left, High preparation time or High PT). On some trials (20%) the target switched approximately 300 ms prior to the fourth tone (middle, Low preparation time or Low PT). **B.** On Day 1, participants adapted to a 30° visuomotor 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 ± 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.

40

66
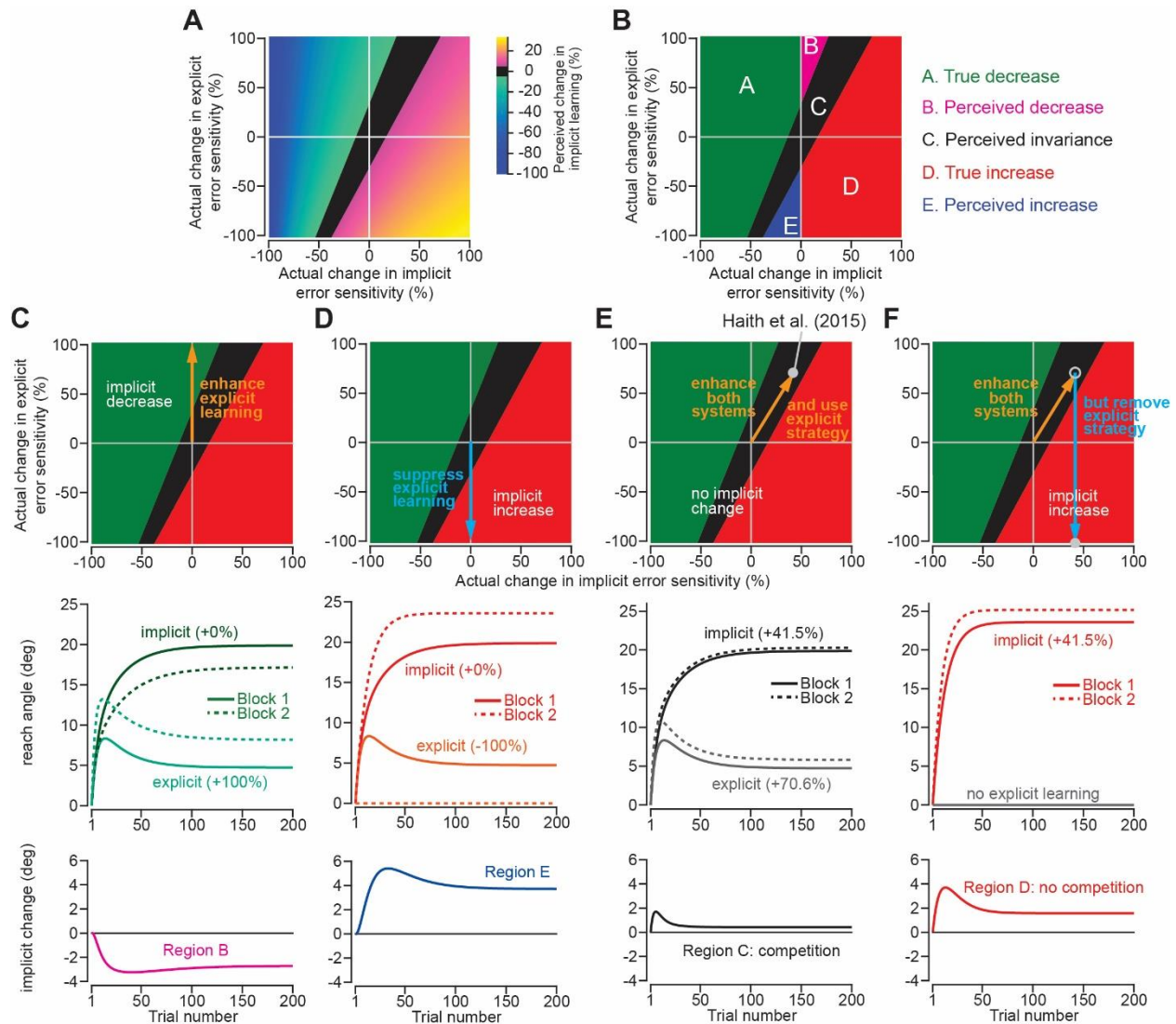
Figure 5. Changes in implicit adaptation depend on both implicit and explicit error sensitivity. **A.** Here we depict the competition map. The x-axis shows change in implicit error sensitivity between reference and test conditions. The y-axis shows change in explicit error sensitivity. Colors indicate the percent change in implicit adaptation (measured at steady-state) from the reference to test conditions. Black region denotes an absolute change less than 5%. The map was constructed with Eq. (8). **B.** The map can be described in terms of 5 different regions. In Region A (true increase), implicit error sensitivity and total implicit adaption both increase in test condition. Region D is same, but for decreases in error sensitivity and total adaptation. In Region B (perceived decrease) implicit adaption decreases though its error sensitivity is higher or same. In Region E (perceived increase), implicit adaptation increases though its error sensitivity is lower or same. Region C shows a perceived invariance where implicit adaptation changes less than 5%. **C.** Top: effect of suppressing explicit learning. Middle: implicit and explicit learning shown in Blocks 1 and 2, where explicit error sensitivity increases 100%. Bottom: implicit learning change (Block 1 to 2). **D.** Top: effect of enhancing explicit learning. Middle: implicit and explicit learning shown in Blocks 1 and 2, where only difference is 100% increase in explicit error sensitivity. Bottom: change in implicit learning (Block 1 to 2). **E.** Top: model simulation for Haith et al.[28]. Middle: implicit and explicit learning during Blocks 1 and 2 where implicit error sensitivity increases by 41.5% and explicit error sensitivity increases by 70.6%. Bottom: negligible change in implicit learning (Block 1 to 2). **F.** Same as in **E** except here explicit strategy is suppressed during Blocks 1 and 2.

83
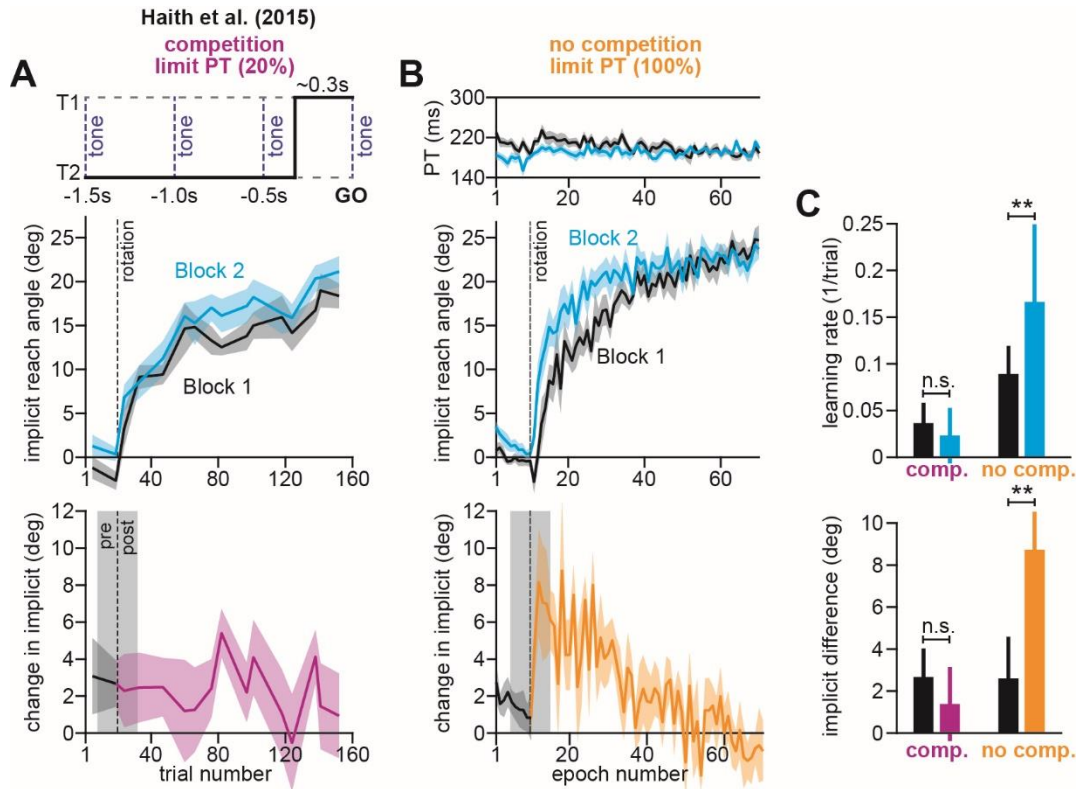
Figure 6. Removing explicit strategy reveals savings in implicit adaptation. **A**. Top: Low preparation time (Low PT) trials in Haith and colleagues[28] used to isolate implicit learning. Middle: learning during Low PT in Blocks 1 and 2. Bottom: difference in Low PT learning between Blocks 1 and 2. **B.** Similar to **A**, but here (Experiment 3) explicit learning was suppressed on every trial, as opposed to only 20% of trials. To suppress explicit strategy, we restricted reaction time on every trial. The reaction time during Blocks 1 and 2 is shown at top. At middle, we show how participants adapted to the rotation under constrained reaction time. At bottom, we show the difference between the learning curves in Blocks 1 and 2. **C.** Here we measured savings in Haith et al. (20% of trials had reaction time limit) and Experiment 3 (100% of trials had reaction time limit). At top, we quantify savings by fitting an exponential curve to each learning curve. Bars show the rate parameter associated with the exponential. At bottom, we quantify savings by comparing how Blocks 1 and 2 differed before perturbation onset (black), and after perturbation onset (purple and yellow). Error bars show mean ± SEM, except for the learning rate at the top of **C** which shows the median. Paired t-tests are used at the bottom of **C**. Wilcoxon signed rank tests are used at the top of **C**. Statistics: n.s. means no significant difference, **p<0.01.
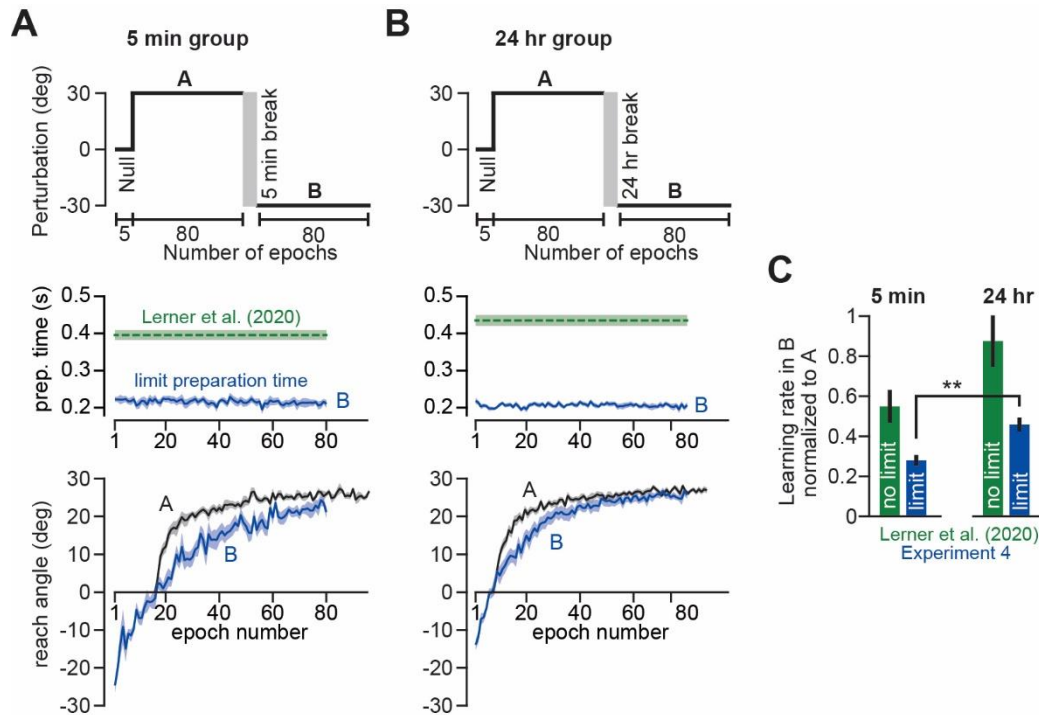
Figure 7. Removing explicit strategy reveals anterograde interference in implicit adaptation. **A.** Top: participants were adapted to a 30° rotation (A). Following a 5-minute break, participants were then exposed to a -30° rotation (B). This A-B paradigm was similar to that of Lerner & Albert et al.[26]. Middle: to isolate implicit adaptation, we imposed strict reaction time constraints on every trial. Under these constraints, reaction time (blue) was reduced by approximately 50% over that observed in the self-paced condition (green) studied by Lerner & Albert et al.[26] Bottom: learning curves during A and B in Experiment 4; under reaction time constraints, the interference paradigm produced a strong impairment in the rate of implicit adaptation. To compare learning during A and B, B period learning was reflected across y-axis. Furthermore, the curves were temporally aligned such that an exponential fit to the A period and exponential fit to the B period intersected when the reach angle crossed 0°. This alignment visually highlights differences in the learning rate during the A and B periods. **B.** Here we show the same analysis as in **A** but when exposures A and B were separated by 24 hours. **C.** To measure the amount of anterograde interference on the implicit learning system, we fit an exponential to the A and B period behavior. Here we show the B period exponential rate parameter divided by the A period rate parameter (values less than 1 indicate a slowing of adaptation). At left 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 from Lerner & Albert et al.[26] where reaction time was unrestricted (no limit). In blue we show our new dataset (Experiment 4) where reaction time was limited to isolate implicit learning. A two-sample t-test was used to test for differences in the implicit impairment at 5 minutes and 24 hours. Error bars show mean ± SEM. Statistics: **p<0.01.
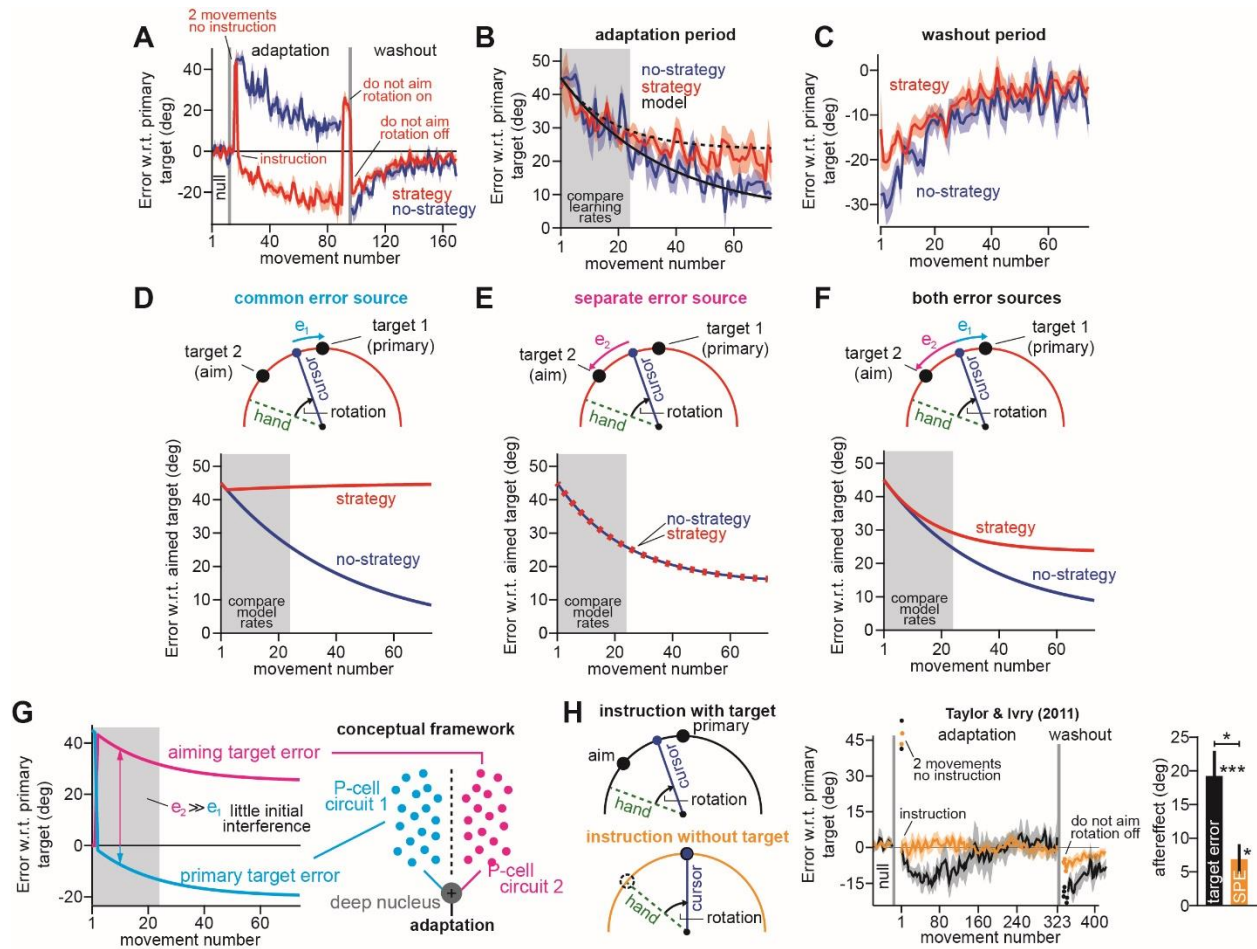
Figure 8. Two visual targets create two implicit error sources. **A.** Figure shows data reported in Mazzoni and Krakauer[12]. Blue shows error between primary target and cursor during adaptation and washout. Red shows the same, but in a strategy group that was instructed to aim to a neighboring target (instruction) to eliminate target errors, once participants experienced two large errors (2 cycles no instruction). **B.** Here we show the error between the cursor and the aimed target during the adaptation period. These curves are the same as in **A** except we use the aimed target rather than primary target, so as to better compare learning curves across groups. **C.** The washout period reported in **A**. Here error is relative to primary target, though in this case aimed and primary targets are the same. **D.** Here we modeled behavior when implicit learning adapts to primary target errors. The primary target error is shown in e_1 at top. Note that no-strategy learning resembles data. However, strategy learning exhibits no drift because the implicit system has zero error. Note here that the primary target error of 0° is a 45° aimed target error in the strategy group. **E.** Similar to **D**, except here the implicit system adapts to errors between the cursor and aimed target. This error is schematized in e_2 at top. Note that this model predicts identical learning in strategy and no-strategy groups. **F.** In this model, the strategy group adapts to both the primary target error and the aimed target error (e_1 and e_2 at top). The no-strategy group adapts only to the primary target error. Learning parameters are identical across groups. **G.** At left, we show how aiming target and primary target errors evolve in the strategy group in **F**. At right, we imagine a potential neural substrate for implicit learning. The primary target error and aiming target error engage two different sub-populations of Purkinje cells in the cerebellar cortex. These two implicit learning modules combine at the deep nucleus. **H.** Figure shows data reported in Taylor and Ivry[21]. Participants performed a task similar to **A**. Before adaptation, participants were taught how to re-aim their reach angles. In the "instruction with target" group, participants re-aimed during adaptation with the aide of neighboring aiming targets (top-left).

44

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 ± SEM. Statistics: *p<0.05, ***p<0.001.

145
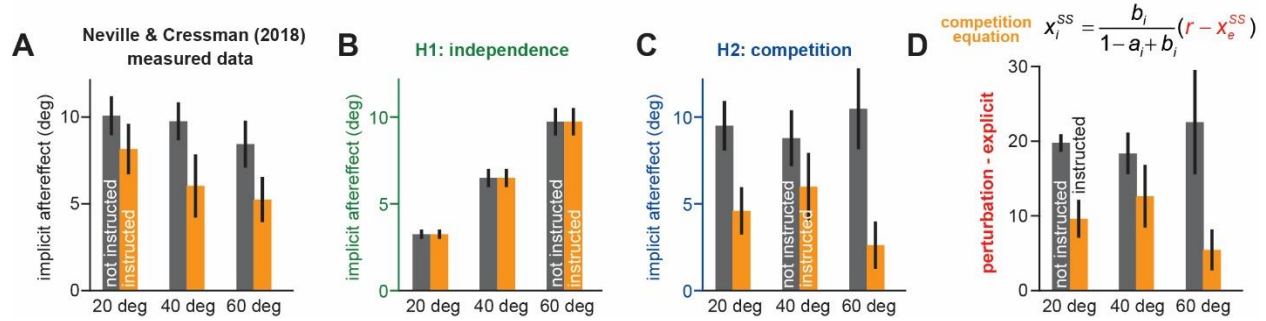
Figure S1. Changes in implicit adaptation in response to awareness and rotation size. Data reported from Neville and Cressman (2018)[15]. **A.** Participants were separated into 1 of 6 groups. Groups differed based on verbal instruction (instructed yellow; non-instructed gray) and rotation magnitude (20° left; 40° middle; 60° right). Here we show implicit learning measured using exclusion trials (reach without re-aiming) at the end of adaptation. **B.** Here we show implicit aftereffects predicted by a model where implicit system learns from SPE only. **C.** Here we show implicit aftereffects predicted by a model where implicit system learns from target error only. **D**. The competition model (target error learning) predicts that implicit learning will be proportional to the difference between the rotation size and the total explicit strategy. Here we show this quantity for all 6 experimental groups. Note that model predictions in **B** and **C** assume that implicit error sensitivity and retention factor are the same across all 6 experimental groups. Error bars for data show mean ± SEM. Error bars for model predictions refer to mean and standard deviation across 10,000 bootstrapped samples.
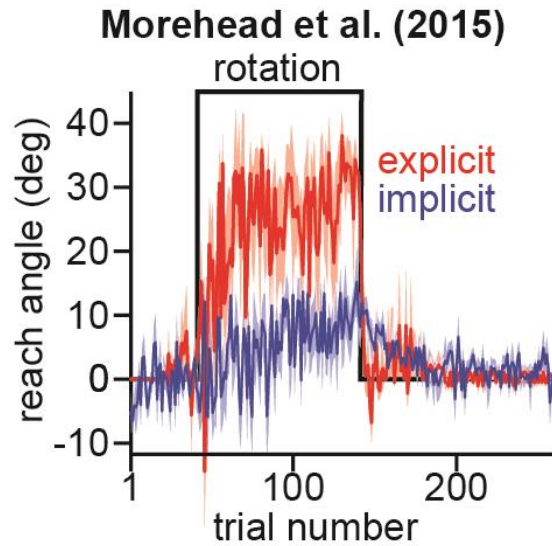
Morehead et al. (2015)

Figure S2. Explicit strategies are rapidly disengaged during washout. Data are reported from Morehead et al. (2015)[34]. Here participants adapted to a 45° rotation, followed by an extended washout period. Explicit learning was measured by asking subjects to report their aiming angle using a ring of visual landmarks. Implicit learning was measured as the difference between the observed reach angle and the direction of reported aim. In this task, participants reached on each trial to 1 of 4 targets. Note the sharp change in explicit angle to zero at the start of the washout period. The aftereffect during a washout period is thought to reflect implicit adaptation. This requires that explicit strategies are rapidly disengaged during washout, consistent with these data. Error bars show mean ± SEM.
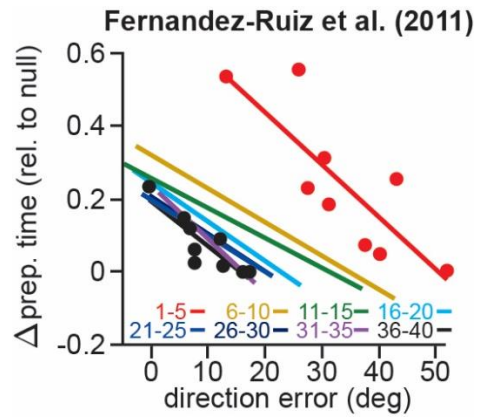
168

169   **Figure S3.** Participants that increase their preparation time exhibit greater total adaptation. Data are reported from

170   Fernandez-Ruiz and colleagues[41]. 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
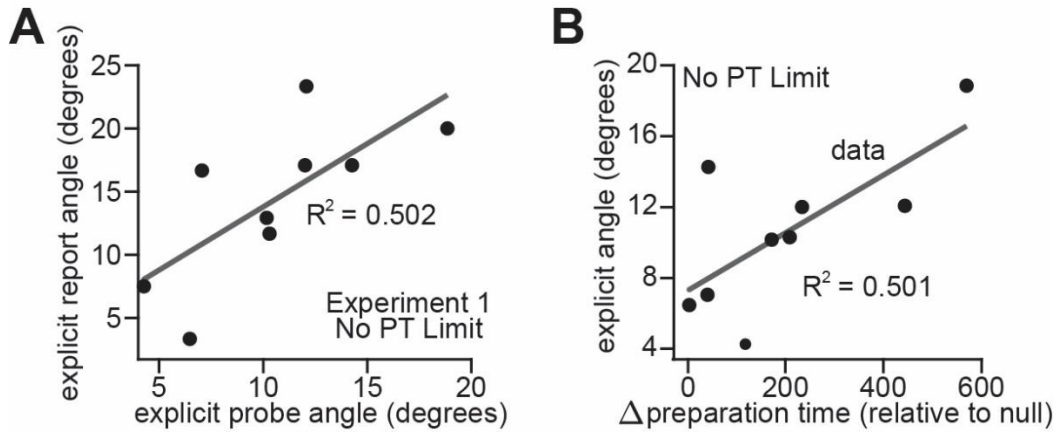
Figure S4. Alternate measures of explicit strategy. **A.** In the No PT limit participants in Experiment 1, we empirically measured explicit re-aiming at the end of adaptation. To do this, we instructed participants to move their hand through the target without any re-aiming. Reach angle precipitously dropped after this instruction. The total change in reach angle (averaged across all 4 targets) represented each participant's strategic re-aiming (x-axis). To validate this empirical measure, we also asked participants to report their explicit strategies after the probe period. Participants were shown a ring of circles surrounding each target and asked to indicate which circle best represented their aiming during at the end of the experiment. This reported explicit measure averaged across all 4 targets is shown on the y-axis. Each dot represents one participant. **B.** Explicit strategies have also been shown to correlate with increases in movement preparation time. Here we show the total explicit strategy measured (via the no aiming probe trial in No PT limit in Experiment 1) as a function of change in preparation time for each individual participant. The change in preparation time was calculated as the difference between the mean preparation time over the first 20 rotation cycles and the last 3 null period cycles. The solid lines in **A** and **B** show a linear regression across individual participants.

49
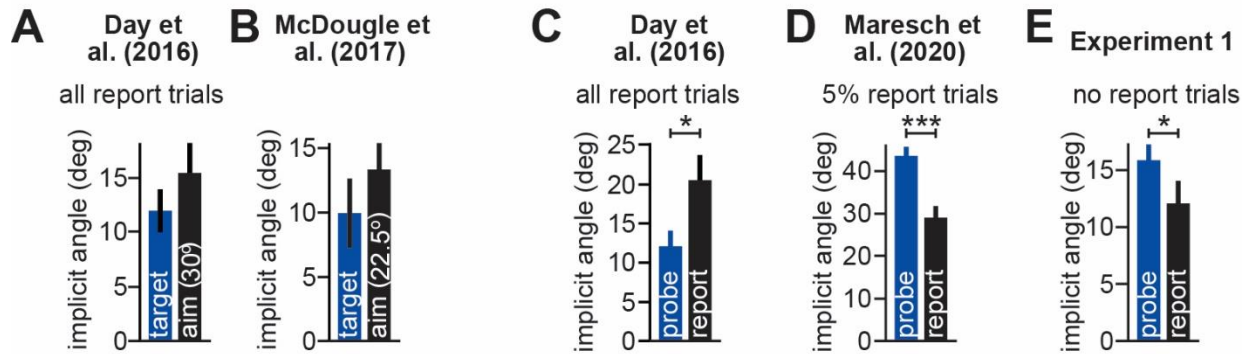
Figure S5. Differences in generalization across visuomotor rotation tasks. **A.** Data collected by Day et al.[72], reported in Fig. 2 of the original manuscript. Here, participants were exposed to a 45° rotation while reaching to a single target. On each trial they were asked to report their aiming direction, using a ring of visual landmarks. In the "target" group, implicit aftereffects were measured at the trained target location. In the "aim" group, implicit aftereffects were probed at a target location 30° away from the trained target, consistent with the direction of the most frequently reported aim. Here we show data from the first aftereffect cycle after the rotation period. **B.** Similar to **A** except for data reported by McDougle et al.[71] (Fig. 3A of the original manuscript). Participants were also exposed to a 45° rotation while reaching to a single target. At the end of the experiment, participants were exposed to an aftereffect block where participants were told to move straight to the target without re-aiming. Here we take two relevant points from the generalization curve measured at the end of learning. The "target" condition represents aftereffects probed at the training target. The "aim" condition shows the aftereffect measured at 22.5° away from the primary target, which was the target closest to the mean reported explicit re-aiming strategy of 26.2°. **C.** Data again from Day et al.[72]. The "probe" implicit learning measure is the same as **A**. The "report" condition shows the amount of implicit learning estimated by subtracting the reported explicit strategy from the reported reach angle on the last cycle of the rotation. **D.** Similar to **C**, but for the intermittent reporting (IR-E) group reported by Maresch et al.[75] (Fig. 4b of the original manuscript). In this group aim was only intermittently reported (4 trials for every 80 normal adaptation trials). Thus, in most cases, participants only had to attend to a single target when reaching. The authors also used 8 training targets (as opposed to 1 in **A**-**C**). The "probe" condition corresponds to the total implicit learning measured at the end of adaptation by telling participants to reach without re-aiming. The "report" condition corresponds to the total implicit learning estimated at the end of adaptation by subtracting the reported aim direction from the measured reach angle. **E.** Here we report implicit learning measured using the "probe" and "report" conditions in Experiment 1, analogous to the measures described in **D**. Error bars show mean ± SEM.

References

1.   Milner, T. E. & Franklin, D. W. Impedance control and internal model use during the initial stage of adaptation to novel dynamics in humans. *J. Physiol.* **567**, 651–664 (2005).

2.   Franklin, D. W. *et al.* CNS learns stable, accurate, and efficient movements using a simple algorithm. *J. Neurosci.* **28**, 11165–11173 (2008).

3.   Albert, S. T. & Shadmehr, R. The Neural Feedback Response to Error As a Teaching Signal for the Motor Learning System. *J. Neurosci.* **36**, 4832–4845 (2016).

4.   Kawato, M. Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* **9**, 718–727 (1999).

5.   Wolpert, D. M., Diedrichsen, J. & Flanagan, J. R. Principles of sensorimotor learning. *Nat. Rev. Neurosci.* **12**, 739–751 (2011).

6.   Thoroughman, K. A. & Shadmehr, R. Electromyographic correlates of learning an internal model of reaching movements. *J. Neurosci.* **19**, 8573–8588 (1999).

7.   Donchin, O. *et al.* Cerebellar regions involved in adaptation to force field and visuomotor perturbation. *J. Neurophysiol.* **107**, 134–147 (2012).

8.   Krakauer, J. W., Ghilardi, M.-F. & Ghez, C. Independent learning of internal models for kinematic and dynamic control of reaching. *Nat. Neurosci.* **2**, 1026–1031 (1999).

9.   Smith, M. A., Ghazizadeh, A. & Shadmehr, R. Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol.* **4**, e179 (2006).

10.   Kim, S., Ogawa, K., Lv, J., Schweighofer, N. & Imamizu, H. Neural Substrates Related to Motor Memory with Multiple Timescales in Sensorimotor Adaptation. *PLoS Biol.* **13**, e1002312 (2015).

11.   Taylor, J. A., Krakauer, J. W. & Ivry, R. B. Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *J. Neurosci.* **34**, 3023–3032 (2014).

12.   Mazzoni, P. & Krakauer, J. W. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J. Neurosci.* **26**, 3642–3645 (2006).

13.   Morehead, J. R., Taylor, J. A., Parvin, D. E. & Ivry, R. B. Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *J. Cogn. Neurosci.* **29**, 1061–1074 (2017).

14.   Miyamoto, Y. R., Wang, S. & Smith, M. A. Implicit adaptation compensates for erratic explicit strategy in human motor learning. *Nat. Neurosci.* **23**, 443–455 (2020).

15.   Neville, K.-M. & Cressman, E. K. The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Exp. Brain Res.* **236**, 2047–2059 (2018).

16.   Benson, B. L., Anguera, J. A. & Seidler, R. D. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J. Neurophysiol.* **105**, 2843–2851 (2011).

17.   Leow, L.-A., Marinovic, W., de Rugy, A. & Carroll, T. J. Task errors drive memories that improve sensorimotor adaptation. *J. Neurosci.* (2020). doi:10.1523/JNEUROSCI.1506-19.2020

18.   Langsdorf, L., Maresch, J., Hegele, M., McDougle, S. D. & Schween, R. Prolonged reaction times eliminate residual errors in visuomotor adaptation. *bioRxiv* (2019). doi:10.1101/2019.12.26.888941

19.   Körding, K. P. & Wolpert, D. M. The loss function of sensorimotor learning. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 9839 LP – 9842 (2004).

20.   Tseng, Y.-W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R. & Bastian, A. J. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J. Neurophysiol.* **98**, 54–62 (2007).

21.   Taylor, J. A. & Ivry, R. B. Flexible cognitive strategies during motor learning. *PLoS Comput. Biol.* **7**, e1001096 (2011).

22.   Wong, A. L. & Shelhamer, M. Using prediction errors to drive saccade adaptation: the implicit double-step task. *Exp. brain Res.* **222**, 55–64 (2012).

23.   Kim, H. E., Parvin, D. E. & Ivry, R. B. The influence of task outcome on implicit motor learning.

Elife **8**, e39882 (2019).

24. McDougle, S. D., Bond, K. M. & Taylor, J. A. Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *J. Neurosci.* **35**, 9568–9579 (2015).

25. Sing, G. C. & Smith, M. A. Reduction in learning rates associated with anterograde interference results from interactions between different timescales in motor adaptation. *PLoS Comput. Biol.* **6**, e1000893 (2010).

26. Lerner, G. *et al.* The Origins of Anterograde Interference in Visuomotor Adaptation. *Cereb. Cortex* **30**, 4000–4010 (2020).

27. Caithness, G. *et al.* Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *J. Neurosci.* **24**, 8662–8671 (2004).

28. Haith, A. M., Huberdeau, D. M. & Krakauer, J. W. The Influence of Movement Preparation Time on the Expression of Visuomotor Learning and Savings. *J. Neurosci.* **35**, 5109–5117 (2015).

29. Coltman, S. K., Cashaback, J. G. A. & Gribble, P. L. Both fast and slow learning processes contribute to savings following sensorimotor adaptation. *J. Neurophysiol.* **121**, 1575–1583 (2019).

30. Kojima, Y., Iwamoto, Y. & Yoshida, K. Memory of Learning Facilitates Saccadic Adaptation in the Monkey. *J. Neurosci.* **24**, 7531–7539 (2004).

31. Medina, J. F., Garcia, K. S. & Mauk, M. D. A mechanism for savings in the cerebellum. *J. Neurosci.* **21**, 4081–4089 (2001).

32. Mawase, F., Shmuelof, L., Bar-Haim, S. & Karniel, A. Savings in locomotor adaptation explained by changes in learning parameters following initial adaptation. *J. Neurophysiol.* **111**, 1444–1454 (2014).

33. Huberdeau, D. M., Krakauer, J. W. & Haith, A. M. Practice induces a qualitative change in the memory representation for visuomotor learning. *J. Neurophysiol.* **122**, 1050–1059 (2019).

34. Morehead, J. R., Qasim, S. E., Crossley, M. J. & Ivry, R. Savings upon Re-Aiming in Visuomotor Adaptation. *J. Neurosci.* **35**, 14386–14396 (2015).

35. Avraham, G., Keizman, M. & Shmuelof, L. Environmental Consistency Modulation of Error Sensitivity During Motor Adaptation is Explicitly Controlled. *J. Neurophysiol.* (2019). doi:10.1152/jn.00080.2019

36. Avraham, G., Morehead, J. R., Kim, H. E. & Ivry, R. B. Re-exposure to a sensorimotor perturbation produces opposite effects on explicit and implicit learning processes. *bioRxiv* 2020.07.16.205609 (2020). doi:10.1101/2020.07.16.205609

37. Albert, S. T. *et al.* An implicit memory of errors limits human sensorimotor adaptation. *bioRxiv* 868406 (2020). doi:10.1101/868406

38. Yin, C. & Wei, K. Savings in sensorimotor adaptation without an explicit strategy. *J. Neurophysiol.* **123**, 1180–1192 (2020).

39. Albert, S. T. & Shadmehr, R. Estimating properties of the fast and slow adaptive processes during sensorimotor adaptation. *J. Neurophysiol.* **119**, 1367–1393 (2018).

40. Thoroughman, K. & Shadmehr, R. Learning of action through adaptive combination of motor primitives. *Nature* **407**, 742–7 (2000).

41. Fernandez-Ruiz, J., Wong, W., Armstrong, I. T. & Flanagan, J. R. Relation between reaction time and reach errors during visuomotor adaptation. *Behav. Brain Res.* **219**, 8–14 (2011).

42. Saijo, N. & Gomi, H. Multiple Motor Learning Strategies in Visuomotor Rotation. *PLoS One* **5**, e9399 (2010).

43. Shadmehr, R., Brandt, J. & Corkin, S. Time-dependent motor memory processes in amnesic subjects. *J. Neurophysiol.* **80**, 1590–1597 (1998).

44. Vaswani, P. A. *et al.* Persistent Residual Errors in Motor Adaptation Tasks: Reversion to Baseline and Exploratory Escape. *J. Neurosci.* **35**, 6969–6977 (2015).

45. Kim, H. E., Morehead, J. R., Parvin, D. E., Moazzezi, R. & Ivry, R. B. Invariant errors reveal

limitations in motor correction rather than constraints on error sensitivity. *Commun. Biol.* **1**, 19 (2018).

46. Werner, S. *et al.* Awareness of Sensorimotor Adaptation to Visual Rotations of Different Size. *PLoS One* **10**, e0123321 (2015).

47. McDougle, S. D. & Taylor, J. A. Dissociable cognitive strategies for sensorimotor learning. *Nat. Commun.* **10**, 40 (2019).

48. Herzfeld, D. J., Vaswani, P. A., Marko, M. K. & Shadmehr, R. A memory of errors in sensorimotor learning. *Science (80-.).* **345**, 1349–1353 (2014).

49. Zarahn, E., Weston, G. D., Liang, J., Mazzoni, P. & Krakauer, J. W. Explaining Savings for Visuomotor Adaptation: Linear Time-Invariant State-Space Models Are Not Sufficient. *J. Neurophysiol.* **100**, 2537–2548 (2008).

50. Huberdeau, D. M., Haith, A. M. & Krakauer, J. W. Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *J. Neurophysiol.* **114**, 969–977 (2015).

51. Hwang, E. J., Smith, M. A. & Shadmehr, R. Dissociable effects of the implicit and explicit memory systems on learning control of reaching. *Exp. brain Res.* **173**, 425–437 (2006).

52. Milner, B. *Les troubles de la memoire accompagnant des lesions hippocampiques bilaterales*. *Physiologie de hippocampe* (1962).

53. Gabrieli, J. D., Corkin, S., Mickel, S. F. & Growdon, J. H. Intact acquisition and long-term retention of mirror-tracing skill in Alzheimer's disease and in global amnesia. *Behav. Neurosci.* **107**, 899–910 (1993).

54. Smith, M. A. & Shadmehr, R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J. Neurophysiol.* **93**, 2809–2821 (2005).

55. Izawa, J., Criscimagna-Hemminger, S. E. & Shadmehr, R. Cerebellar Contributions to Reach Adaptation and Learning Sensory Consequences of Action. *J. Neurosci.* **32**, 4230–4239 (2012).

56. Wong, A. L., Marvel, C. L., Taylor, J. A. & Krakauer, J. W. Can patients with cerebellar disease switch learning mechanisms to reduce their adaptation deficits? *Brain* **142**, 662–673 (2019).

57. Becker, M. I. & Person, A. L. Cerebellar Control of Reach Kinematics for Endpoint Precision. *Neuron* **103**, 335-348.e5 (2019).

58. Morton, S. M. & Bastian, A. J. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J. Neurosci.* **26**, 9107–9116 (2006).

59. Kording, K. P., Tenenbaum, J. B. & Shadmehr, R. The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nat. Neurosci.* **10**, 779–786 (2007).

60. MacLeod, C. M. Forgotten but Not Gone: Savings for Pictures and Words in Long-Term Memory. *J. Exp. Psychol.* **14**, 195–212 (1988).

61. Ebbinghaus, H. *Uber das Gedachtnis*. (Dunacker and Humblot, 1885).

62. Kitago, T., Ryan, S. L., Mazzoni, P., Krakauer, J. W. & Haith, A. M. Unlearning versus savings in visuomotor adaptation: comparing effects of washout, passage of time, and removal of errors on motor memory. *Front. Hum. Neurosci.* **7**, 307 (2013).

63. Leow, L.-A., de Rugy, A., Marinovic, W., Riek, S. & Carroll, T. J. Savings for visuomotor adaptation require prior history of error, not prior repetition of successful actions. *J. Neurophysiol.* **116**, 1603–1614 (2016).

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

65. Miall, R. C., Jenkinson, N. & Kulkarni, K. Adaptation to rotated visual feedback: a re-examination of motor interference. *Exp. Brain Res.* **154**, 201–210 (2004).

66. de Brouwer, A. J., Albaghdadi, M., Flanagan, J. R. & Gallivan, J. P. Using gaze behavior to parcellate the explicit and implicit contributions to visuomotor learning. *J. Neurophysiol.* **120**,

1602–1615 (2018).

67. Maresch, J. & Donchin, O. Reporting affects explicit knowledge in visuomotor rotations in ways not measured by reporting. *bioRxiv* (2019). doi:10.1101/702290

68. Bromberg, Z., Donchin, O. & Haar, S. Eye Movements during Visuomotor Adaptation Represent Only Part of the Explicit Learning. *eNeuro* **6**, ENEURO.0308-19.2019 (2019).

69. Bond, K. M. & Taylor, J. A. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J. Neurophysiol.* **113**, 3836–3849 (2015).

70. Kagerer, F. A., Contreras-Vidal, J. L. & Stelmach, G. E. Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp. brain Res.* **115**, 557–561 (1997).

71. McDougle, S. D., Bond, K. M. & Taylor, J. A. Implications of plan-based generalization in sensorimotor adaptation. *J. Neurophysiol.* **118**, 383–393 (2017).

72. Day, K. A., Roemmich, R. T., Taylor, J. A. & Bastian, A. J. Visuomotor Learning Generalizes Around the Intended Movement. *eNeuro* **3**, ENEURO.0005-16.2016 (2016).

73. Krakauer, J. W., Pine, Z. M., Ghilardi, M. F. & Ghez, C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J. Neurosci.* **20**, 8916–8924 (2000).

74. Tanaka, H., Sejnowski, T. J. & Krakauer, J. W. Adaptation to Visuomotor Rotation Through Interaction Between Posterior Parietal and Motor Cortical Areas. *J. Neurophysiol.* **102**, 2921–2932 (2009).

75. Maresch, J., Werner, S. & Donchin, O. Methods matter: your measures of explicit and implicit processes in visuomotor adaptation affect your results. *bioRxiv* (2020). doi:10.1101/702290

76. Shadmehr, R., Smith, M. A. & Krakauer, J. W. Error correction, sensory prediction, and adaptation in motor control. *Annu Rev Neurosci* **33**, 89–108 (2010).

77. Leow, L.-A., Marinovic, W., de Rugy, A. & Carroll, T. J. Task errors contribute to implicit aftereffects in sensorimotor adaptation. *Eur. J. Neurosci.* **48**, 3397–3409 (2018).

78. Hanajima, R. *et al.* Modulation of error-sensitivity during a prism adaptation task in people with cerebellar degeneration. *J. Neurophysiol.* **114**, 2460–2471 (2015).

79. Kojima, Y. & Soetedjo, R. Elimination of the error signal in the superior colliculus impairs saccade motor learning. *Proc. Natl. Acad. Sci.* **115**, E8987--E8995 (2018).

80. Bastian, A. J., Martin, T. A., Keating, J. G. & Thach, W. T. Cerebellar ataxia: abnormal control of interaction torques across multiple joints. *J. Neurophysiol.* **76**, 492–509 (1996).

81. Herzfeld, D. J., Kojima, Y., Soetedjo, R. & Shadmehr, R. Encoding of error and learning to correct that error by the Purkinje cells of the cerebellum. *Nat. Neurosci.* **21**, 736–743 (2018).

82. Herzfeld, D. J., Kojima, Y., Soetedjo, R. & Shadmehr, R. Encoding of action by the Purkinje cells of the cerebellum. *Nature* **526**, 439–442 (2015).

83. Maschke, M., Gomez, C. M., Ebner, T. J. & Konczak, J. Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. *J. Neurophysiol.* **91**, 230–238 (2004).

84. Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J. & Thach, W. T. Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* **119 (Pt 4**, 1183–1198 (1996).