Interference underlies attenuation upon relearning in sensorimotor adaptation

Short title: Interference of sensorimotor memories

Guy Avraham* and Richard B Ivry

Department of Psychology and Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA 94720, USA

* Corresponding author

E-mail: guyavraham@berkeley.edu

1 **Abstract**

2 Savings refers to the gain in performance upon relearning a task. In sensorimotor adaptation,

3 savings is tested by having participants adapt to perturbed feedback and, following a washout

4 block during which the system resets to baseline, presenting the same perturbation again. While

5 savings has been observed with these tasks, we have shown that the contribution from implicit

6 sensorimotor adaptation, a process that uses sensory prediction errors to recalibrate the

7 sensorimotor map, is actually attenuated upon relearning (Avraham et al., 2021). In the present

8 study, we test the hypothesis that this attenuation is due to interference arising from the

9 washout block, and more generally, from experience with a different relationship between the

10 movement and the feedback. In standard adaptation studies, removing the perturbation at the

11 start of the washout block results in a salient error signal in the opposite direction to that

12 observed during learning. As a starting point, we replicated the finding that implicit adaptation is

13 attenuated following a washout period in which the feedback now signals a salient opposite

14 error. When we eliminated visual feedback during washout, implicit adaptation was no longer

15 attenuated upon relearning, consistent with the interference hypothesis. Next, we eliminated the

16 salient error during washout by gradually decreasing the perturbation, creating a scenario in

17 which the perceived errors fell within the range associated with motor noise. Nonetheless,

18 attenuation was still prominent. Inspired by this observation, we tested participants with an

19 extended experience with veridical feedback during an initial baseline phase and found that this

20 was sufficient to cause robust attenuation of implicit adaptation during the first exposure to the

21 perturbation. This effect was context-specific: It did not generalize to movements that were not

22 associated with the interfering feedback. Taken together, these results show that the implicit

23 sensorimotor adaptation system is highly sensitive to memory interference from a recent

24 experience with a discrepant action-outcome contingency.

Introduction

People exhibit a remarkable ability to retain motor skills. The skier finds herself performing close to her previous level of competence after an 8-month layoff and, while the mind might be wary, our bodies are able to readily recall how to ride a bike even if they have not done so for many years. Indeed, laboratory studies of retention have highlighted the phenomenon of savings, the benefit in performance observed when relearning a previously acquired skill. Originally described in the verbal learning domain (Ebbinghaus, 1913), savings has since come to be recognized as a rather ubiquitous phenomenon, including many examples in the motor learning literature (Coltman et al., 2019; Doyon et al., 2009; Kojima et al., 2004; Mawase et al., 2014; Medina et al., 2001; Milner, 1962; Walker et al., 2002).

Sensorimotor adaptation tasks have provided an interesting testbed for exploring savings in motor learning. In visuomotor adaptation, feedback indicating the participant's hand position is perturbed, usually by imposing an angular rotation. Participants learn to compensate, reaching in the opposite direction of the perturbation. Savings is tested by presenting the same perturbation over two learning blocks, separated by a washout phase with non-perturbed feedback (Albert et al., 2022; Herzfeld et al., 2014; Huang et al., 2011; Krakauer, 2009; Krakauer et al., 2005; Zarahn et al., 2008). With this design, participants often exhibit savings, showing a higher rate of adaptation during the second learning block.

In line with the common conception about the procedural nature of motor skills, this form of savings has been hypothesized to reflect changes in an implicit system that serves to keep the sensorimotor system well-calibrated (Albert et al., 2022, 2021; Coltman et al., 2019; Hadjiosif et al., 2023; Yin and Wei, 2020). For example, it has been proposed that the sensitivity of this system is enhanced when participants are exposed to errors during initial learning, resulting in faster learning upon re-exposure to similar errors (Albert et al., 2021; Herzfeld et al., 2014).

However, by using methods that isolate the contribution of this recalibration process, we have found that implicit sensorimotor adaptation is actually attenuated during relearning (Avraham et al., 2021; see also Hamel et al., 2022, 2021; Leow et al., 2020; Stark-Inbar et al., 2016; Tsay et al., 2021b; Wang and Ivry, 2023; Yin and Wei, 2020). Savings, when observed in adaptation tasks, appears to largely reflect the operation of other learning processes such as the recall of a successful explicit strategy (Avraham et al., 2021; Haith et al., 2015; Huberdeau et al., 2019; Morehead et al., 2015).

Why does implicit sensorimotor adaptation show attenuated relearning rather than savings? We can consider two hypotheses. The first hypothesis is also based on the idea that exposure to a given error changes the sensitivity of the system in response to that error when re-encountered. However, rather than increasing with familiarity, sensitivity may decrease with familiarity. That is, the adaptation system becomes less responsive after prolonged exposure to an error. Mechanistically, desensitization could arise from a saturation of recently activated synapses (Hamel et al., 2022, 2021; Nguyen-Vu et al., 2017).

An alternative hypothesis is based on the idea of interference, a classical concept in the psychological memory literature (Underwood, 1957). In the typical design of a savings study, the first block with perturbed feedback is followed by a washout block with veridical feedback to reset the behavior back to baseline. When exposed to veridical feedback in the adapted state, the participant experiences an error in the opposite direction of that experienced during the initial learning block. Thus, at the end of the washout block, the participant has been exposed to two error signals of opposite signs, one associated with the initial perturbation and a second associated with the washout. When the perturbation is re-introduced, memories associated with these two error signals may compete with one another (Bouton, 1986), especially given that the context is similar (reaching to the same target). As such, the response to the re-introduced
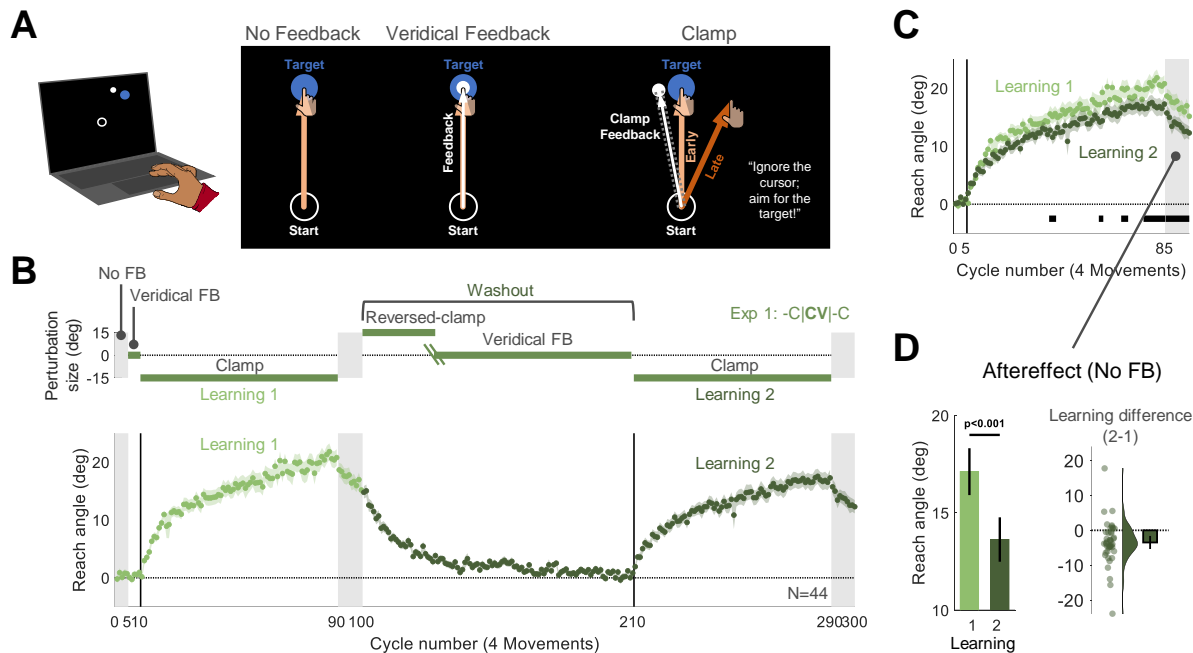
74   perturbation may be attenuated due to interference from the association established during the

75   washout block.

76   We evaluate these two hypotheses in a series of behavioral experiments.

77

78   **Results**

79   We employed a visuomotor task in which task-irrelevant clamped feedback was used to isolate

80   implicit adaptation (Morehead et al., 2017) (Fig. 1A). In this task, participants reach to a visual

81   target while the cursor follows a path with a fixed angular offset from the target (e.g., by 15°).

82   Despite instructions to ignore the cursor, participants show robust implicit adaptation to this type

83   of perturbation, with the direction of the hand movement (reach angle) gradually shifting away

84   from the target (and cursor). In our previous study, we used this manipulation over two learning

85   blocks that were separated by a washout block and found that the implicit change in reach angle

86   during the second learning block was attenuated with respect to the first learning block

87   (Avraham et al., 2021).

88   In Experiment 1, we aimed to replicate this attenuation effect using a similar relearning

89   protocol (abbreviated as -C|**CV**|-C, Fig. 1B). There were two learning blocks with -15° clamped

90   feedback (-C), separated by a washout block. The washout block started with reversed clamped

91   feedback, with the cursor now shifted in the opposite direction (15°, **C**). This was expected to

92   implicitly drive the adapted hand movements back towards the target. Once the participant's

93   reaches were near the target, we transitioned to veridical feedback (V) for the remainder of the

94   washout block. In this manner, the average reach angle at the start of the two clamp blocks

95   should be similar. We also included a short no-feedback block after each learning block to

96   assess the aftereffect. During all phases of the experiment, the instructions remained the same:

97   Reach directly to the target.

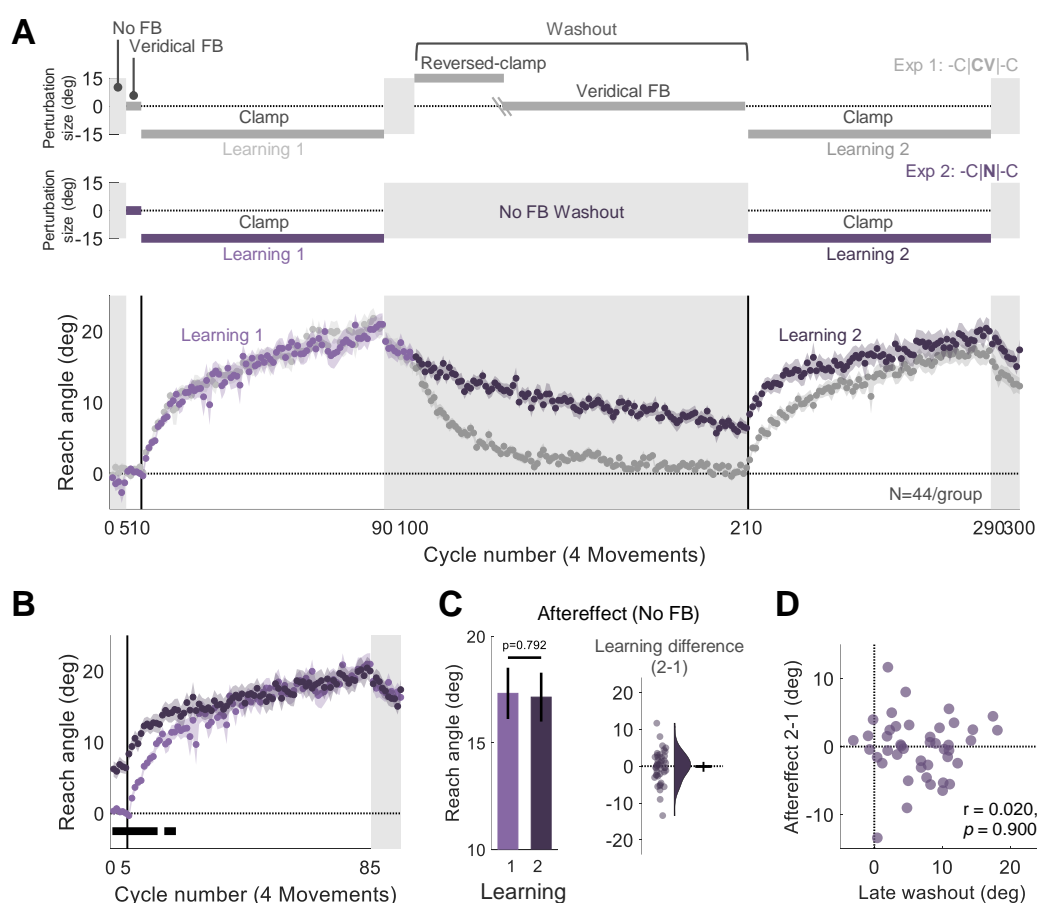**Fig 1. Experiment 1: Upon relearning a visuomotor rotation, implicit adaptation is attenuated.**

(**A**) Task design and schematics of all trial types in Experiment 1. Using a trackpad or mouse, participants (N=44) moved a cursor from the start location (white circle) to a target (blue disk), with the target appearing at one of four locations (one representative location is depicted). There were 3 types of trials: 1) No feedback, with the cursor disappearing at movement onset; 2) Veridical feedback, in which the direction of the cursor (small white disk) was veridical with respect to the direction of the movement; 3) Clamped feedback, in which the cursor followed an invariant path with respect to the target. (**B**) Top: Experimental protocol. The -C|**CV**|-C abbreviation indicates the main block-level structure of the experiment. There were two learning blocks with clamped feedback (-C), each followed by an aftereffect block with no feedback. To reset the sensorimotor map following the first learning block, we used a washout block composed of a reversed-clamp feedback phase (C) and a veridical feedback phase (V). The green oblique lines in the washout block mark the transition between the two phases, with the length of the reversed clamp phase determined on an individual basis (see Methods). Bottom: Time course of mean reach angle, with the data averaged within each cycle of four movements. Light and dark shading signify learning blocks 1 and 2, respectively, with the onset of the clamped feedback marked by the vertical solid lines. (**C**) Overlaid reach angle functions for the two learning blocks and two aftereffect

115   blocks. Horizontal thick black lines denote clusters that show a significant difference between blocks 1

116   and 2 ($p < 0.05$). (**D**) The left panel (pair of bars) presents the aftereffect data (mean ± SEM) for each

117   learning block, measured as the averaged reach angle across all cycles in each aftereffect block. The

118   right panel shows the within-participant difference (Aftereffect 2 – Aftereffect 1; dots and violin plot-

119   distribution of individual difference scores, bar- mean difference and 95% CI). SEM, standard error of the

120   mean. CI, Confidence Interval.

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122   Participants exhibited robust adaptation during the first learning block, and their behavior

123   reverted back to baseline during the washout block. Consistent with our previous findings, the

124   overall implicit change in reach angle during the second learning block was smaller than during

125   the first learning block (Figs. 1B, 1C). To evaluate this effect statistically, we compared the

126   reach angle between the first and second learning blocks, averaging the data over cycles of four

127   reaches (one reach per target). We used a non-parametric cluster-based permutation test to

128   identify clusters of cycles that differed between the two learning blocks (Avraham et al., 2021;

129   Labruna et al., 2019; Maris and Oostenveld, 2007). This analysis revealed multiple clusters in

130   which there was a decrease in reach angle during the second learning block. In line with the

131   cluster-based results, attenuation was also significant when the analysis was restricted to the

132   aftereffect measure of adaptation, namely the mean reach angle during the aftereffect blocks

133   ([mean difference, 95% CI], −3.48°, [-5.36° -1.61°], t(43) = −3.75, $p = 5.20 \times 10^{-4}$, $BF_{10} = 53.2$, d =

134   −0.57, Fig. 1E).

135   In Experiment 1, relearning was tested after a washout block in which participants had

136   performed 110 reaches to each target in the presence of feedback – either reversed-clamp or

137   veridical – that was different than the error signal that drove initial learning. It is unclear if the

138   attenuation is due to the exposure to these alternative and potentially interfering forms of

139   feedback or reflects desensitization to the original error. Experiment 2 was designed to address

140   this question. As in Experiment 1, participants experienced two learning blocks that were

141   separated by a washout block (Fig. 2A). However, no feedback was presented during the entire

142   110-cycle washout block (-C|**N**|-C design). If attenuation upon relearning is due to interference

143   from the feedback experienced during washout, removing this feedback should rescue

144   attenuated learning. In contrast, if attenuation is driven by desensitization to a familiar error, we

145   should again observe attenuation in the second learning block following the no-feedback

146   washout block.

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Fig 2. Experiment 2: Implicit adaptation is not attenuated upon relearning when feedback is

eliminated during the washout block.

151   (**A**) Experimental protocol and learning functions. Top: Participants (N=44) experienced 110 cycles of

152   trials without feedback (N) during a washout block that separated the two learning blocks (-C|**N**|-C design,

153   purple). Bottom: Time course of mean reach angle averaged over cycles. Light and dark shading signify

154   learning blocks 1 and 2, respectively, with the onset of the clamped feedback marked by the vertical solid

155   lines. The design and learning functions from Experiment 1 are reproduced here to provide a visual point

156   of comparison (gray). (**B**) Overlaid reach angle functions for the two learning blocks and two aftereffect

157   blocks in Experiment 2 (significant clusters based on p<0.05) (**C**) The left panel presents the aftereffect

158   (mean ± SEM) for each learning block and the right panel the within-participant difference (Aftereffect 2 –

159   Aftereffect 1; dots and violin plot- distribution of individual difference scores, bar- mean and 95% CI). (**D**)

160   Scatter plot showing no relationship between the reach angle at late washout and change in relearning

161   (Aftereffect 2 – Aftereffect 1). SEM, standard error of the mean. CI, Confidence Interval.
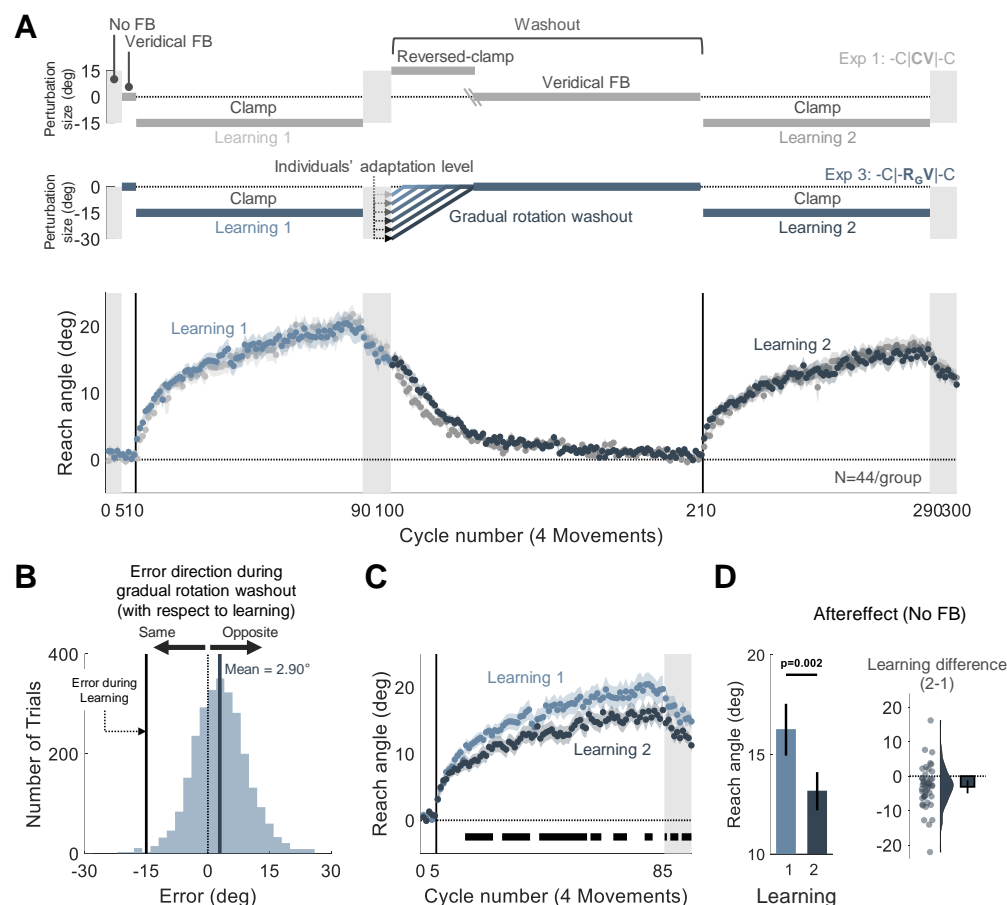
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163   Despite the absence of feedback, adaptation slowly decayed throughout the washout

164   block, presumably due to some form of forgetting or attraction to the original state of the

165   sensorimotor system (Fig. 2A). The decay was, on average, incomplete by the end of the

166   washout block. Thus, the mean reach angle at the beginning of the second learning block was

167   higher than at the start of the first Learning block (Fig 2B). However, after ~20 cycles, the two

168   functions converged and reached a similar state of adaptation by the end of the clamp blocks.

169   Thus, we failed to observe attenuation. This null result was confirmed in the analysis of the

170   aftereffect data (−0.18°, [-1.52° 1.16°], t(43) = −0.266, *p* = 0.792, BF_{10} = 0.169, d = −0.04, Fig.

171   2C). Interestingly, the difference between reach angle in the first and second aftereffect blocks

172   was unrelated to the extent of decay observed during the washout block (r = 0.020, *p* = 0.900,

173   BF_{10} = 0.12). As can be seen in Figure 2D, even those participants who showed complete

174   washout in the absence of feedback did not exhibit attenuated relearning.

175   In summary, the results of Experiment 2 indicate that attenuation upon relearning is not

176   due to desensitization to the error that participants experienced during initial learning. Rather,

177   the results are consistent with the hypothesis that attenuation is due to interference that arises

178   from the feedback experienced during the washout block.

179   What conditions might produce interference during relearning? With the introduction of

180   the reversed clamp at the beginning of the washout block in Experiment 1, participants are

181   exposed to a large error signal that is in the opposite direction to that experienced during the

182   initial learning block. Interference may arise from a competition between the memory traces

183   associated with the two opposing error signals (Heald et al., 2021; Sing and Smith, 2010). This

184   hypothesis can account for the results of Experiment 2 since there was no error presented

185   during the washout block. An even stronger test would be to use feedback during the washout

186   block that did not provide salient error information that was opposite to that observed during the

187   initial learning block.

188   We implemented this test in Experiment 3. Following implicit adaptation with the rotated

189   clamped feedback, participants were told at the start of the washout block that the cursor would

190   now be aligned with their hand. However, we actually applied a visuomotor rotation that was

191   contingent on the movement direction of the hand, setting the size of the rotation so that the

192   cursor would move close to the target (see Methods). The size was determined on an individual

193   basis: For example, if the participant had adapted 19° in the clockwise direction at the end of the

194   rotation block, the rotation was initially set to 19° in the counterclockwise direction. This

195   perturbation was gradually reduced over the washout block (Fig. 3A). Gradual changes in the

196   magnitude of a visuomotor rotation have been shown to result in pronounced implicit adaptation

197   (Christou et al., 2016; Modchalingam et al., 2023). Here, we used this method to nullify an

198   adapted state. When the size of the rotation had decreased to 0°, the feedback was veridical

199   and remained so for the rest of the washout block. We assumed that this method would

200   minimize the participant's experience with salient opposite-signed errors during the early (and

201   all) stages of the washout block despite having adapted during the initial learning block.

Fig 3. Experiment 3: Attenuated adaptation does not require experience with salient, opposite signed error at the beginning of washout.

(**A**) Experimental protocol and learning functions. Top: At the beginning of the washout block in Experiment 3, participants (N=44) experienced a rotated cursor that was contingent on the direction of their hand movement, with the magnitude of the perturbation set to their final adaptation level at the end of the first learning block; in this way, the cursor position would be near the target. The size of the rotation was gradually decreased until reaching 0°, at which point it was veridical and remained so for the rest of the washout block (-C|-R_GV|-C design, blue). Bottom: Time course of mean reach angle averaged over cycles (4 movements). Light and dark shading signify learning blocks 1 and 2, respectively, with the onset of the clamped feedback marked by the solid vertical lines. The design and learning functions from Experiment 1 are reproduced here to provide a visual point of comparison (gray). (**B**) Distribution of errors experienced during the non-zero rotation phase of the washout block. These errors were small in

215   magnitude (mean=2.9°, dark blue solid line) and in the opposite direction of the error experienced during

216   the initial learning block (black solid line). Presumably, these opposite errors are the signals that drive the

217   washout of the initial adaptation. The dotted line represents zero error. (**C**) Overlaid reach angle functions

218   for the two learning blocks. Horizontal thick black lines denote clusters that show a significant difference

219   between blocks 1 and 2 ($p < 0.05$). (**D**) The left panel presents the aftereffect (mean ± SEM) for each

220   learning block and the right panel the within-participant difference (Aftereffect 2 − Aftereffect 1; dots and

221   violin plot- distribution of individual difference scores, bar- mean and 95% CI). SEM, standard error of the

222   mean. CI, Confidence Interval.

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224   After adaptation, participants exhibited a gradual reversion of reach angle back to

225   baseline (Fig. 3A). This washout function was somewhat slower than that observed in

226   Experiment 1 where we had used a salient, reversed clamp to achieve washout (Fig. S1),

227   presumably because the experienced errors during the initial washout trials were much smaller

228   and of variable sign in Experiment 3 ([mean ± standard deviation], 2.90° ± 10.1°, Fig. 3B)

229   (Avraham et al., 2020; Kim et al., 2018; Tsay et al., 2021a; Wei and Körding, 2009).

230   Contrary to our prediction, the elimination of salient, opposite-signed errors did not

231   abolish the attenuation effect. Robust attenuation was observed across the second learning

232   block and during the aftereffect block ([mean aftereffect difference, 95% CI], −3.09°, [-4.99° -

233   1.18°], t(43) = −3.27, p = 0.002, BF$_{10}$ = 15.11, d = −0.49, Figs. 3C, 3D).

234   While the results indicate that attenuation does not require a salient change in the error,

235   an analysis of the feedback provided at the beginning of the washout block shows that

236   participants experienced opposite-signed errors more often than same-signed errors (Fig 3B.

237   Fig S2 provides a comparison with the error distribution experienced with veridical feedback).

238   The small skew in the distribution might be sufficient to produce interference.
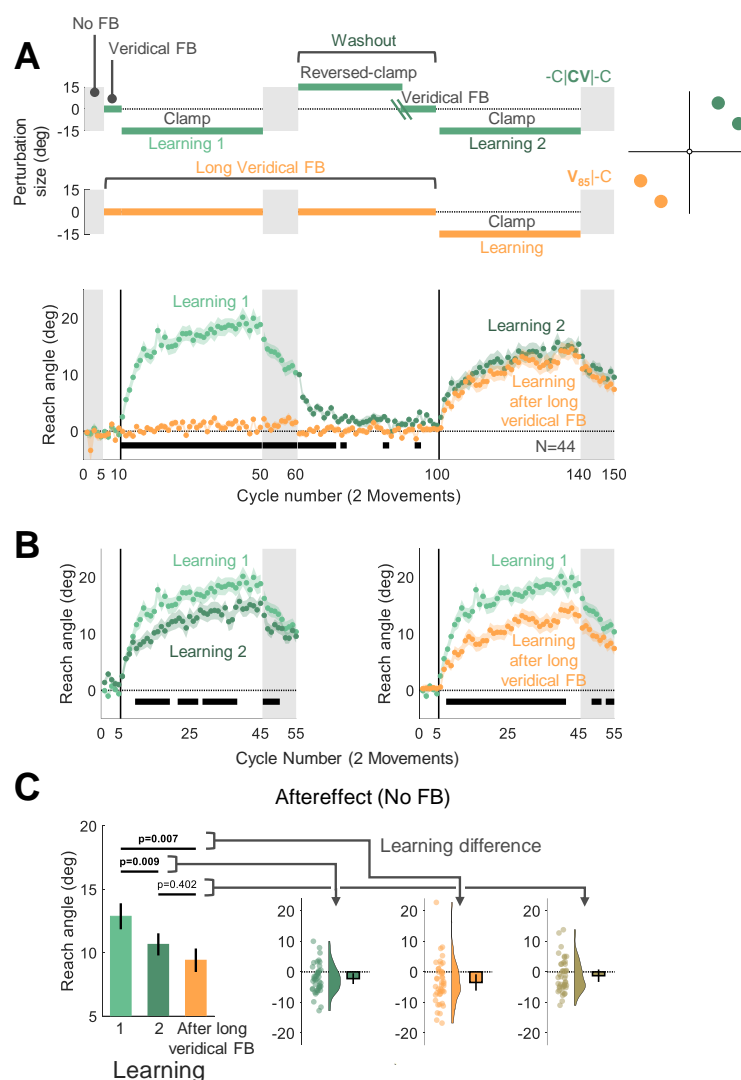
239   Alternatively, interference may arise when multiple associations are linked to the same

240   action. Up to this point, we had assumed that interference would occur when a given action

241   (e.g., moving to a given target location) was associated with two types of perturbations,

242   specifically, opposing visuomotor errors. However, simply experiencing a change in the

243   feedback, even from one that is not perturbed, may be sufficient to elicit interference.

244   We tested this hypothesis in Experiment 4 using a protracted block with veridical

245   feedback, asking if this would attenuate subsequent adaptation to a perturbation. On each trial,

246   the target appeared within one of two 30°-wide wedges located at opposite poles of the

247   workspace (~180° separation, Fig. 4A). When the target appeared in one of the wedges, the

248   perturbation followed a similar schedule to Experiment 1: Two learning blocks with clamped

249   feedback were separated by a washout block -C|**CV**|-C). When the target appeared in the other

250   wedge, the feedback was veridical for the first 85 cycles, followed by a single learning block with

251   clamped feedback (**V₈₅**|-C). Previous work has shown negligible generalization of adaptation for

252   locations separated by more than 45° (Krakauer et al., 2000; McDougle et al., 2017; Morehead

253   et al., 2017). As such, this within-participant design allowed us to ask if extended exposure to

254   veridical feedback was sufficient to attenuate adaptation. Specifically, we asked if adaptation to

255   targets in the **V₈₅**|-C location would be attenuated with respect to the first learning block in the -

256   C|**CV**|-C location.

257   For the -C|**CV**|-C location, adaptation in the second learning block was attenuated with

258   respect to the first learning block, consistent with the results of Experiment 1 (Fig. 4A, 4B).

259   Critically, adaptation in the **V₈₅**|-C location was also attenuated relative to the first learning block

260   in the -C|**CV**|-C location, and it was comparable to the second learning block in the -C|**CV**|-C

261   location. This pattern was also evident in the aftereffect data ($F[1.59, 68.5] = 7.96$, $p = 0.002$,

262    $BF_{10}=40.95$, and $\eta_p^2=0.16$, mean difference Aftereffect 2 – Aftereffect 1: -2.21°, 95% CI: [-3.97° -

263   0.45°], p_B {Bonferroni corrected p value} = 0.009, mean difference Aftereffect after long baseline

264   – Aftereffect 1: -3.46°, 95% CI: [-6.14° -0.79°], p_B = 0.007, mean difference Aftereffect after long

265   baseline – Aftereffect 2: -1.25°, 95% CI: [-3.29° 0.79°], p_B = 0.402, Fig. 4C). Thus, attenuation of

266   implicit adaptation does not require experience with an opposing perturbation; rather, it can also

267   arise following extended experience with veridical feedback.
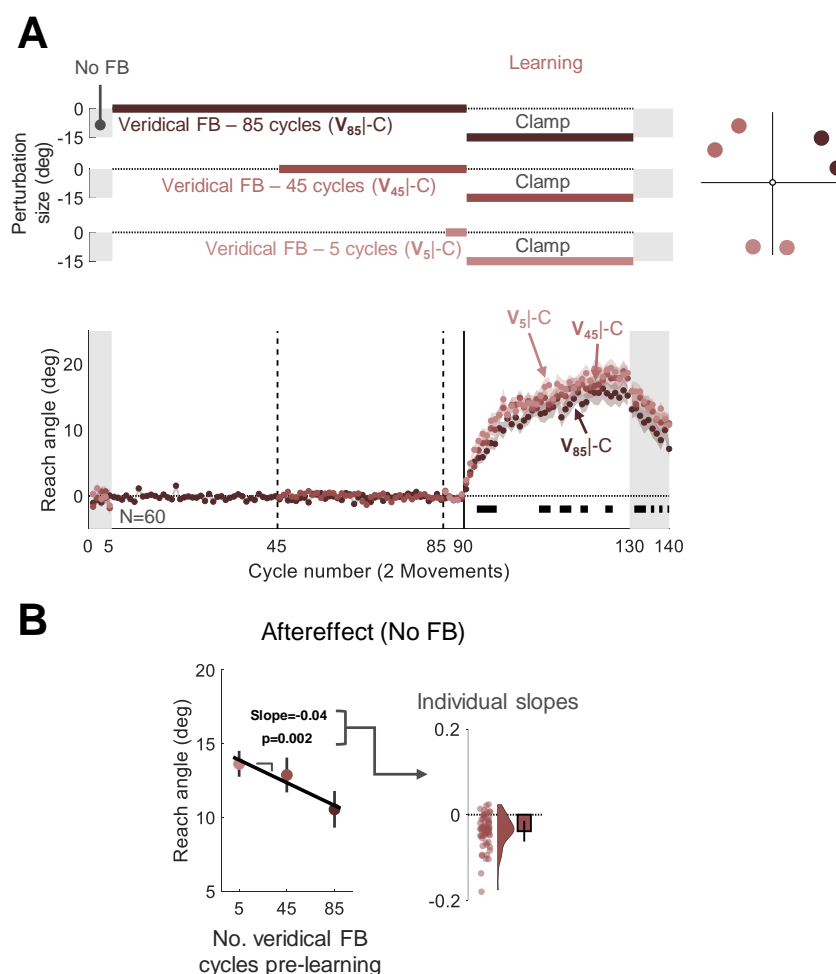
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269

270   **Fig 4. Experiment 4: Adaptation is attenuated for movements that were previously associated with**

271   **either washout after learning or an extended baseline experience with veridical feedback.**

272   (**A**) Experimental protocol and learning functions. Top: The target appeared at one of four locations, with

273   two locations falling within one 30°-wedge and the other two falling within a same-size wedge on the

274   opposite side of the workspace. Participants (N=44) experienced a -C|**CV**|-C schedule (cyan) in one

275   wedge and a **V$_{85}$**|-C design schedule in the other wedge (orange). For the latter, the number of veridical

276   feedback cycles (85) matched the total number of cycles before relearning at the other wedge (excluding

277   the no-feedback trials). Bottom: Time course of mean reach angle averaged over cycles, with each cycle

278   consisting of 2 movements for each wedge. Light and dark cyan signify learning blocks 1 and 2 in the -

279   C|**CV**|-C condition. (**B**) Overlaid reach angle functions comparing the first learning block in -C|**CV**|-C to

280   that of the second learning block in the same wedge (left panel) and to the post long-baseline learning

281   block at the other wedge (right panel). Horizontal thick black lines (B) and (C) denote clusters that show a

282   significant difference between the functions (with $p < 0.017$ as a significance criterion, see Methods). (**C**)

283   Left panel (bars) presents the aftereffect data (mean ± SEM) for each learning block and the right panel

284   shows the within-participant differences for three contrasts: 1) Aftereffect 2 – Aftereffect 1; 2) Aftereffect

285   after long baseline – Aftereffect 1; 3) Aftereffect after long baseline – Aftereffect 2. Dots and violin plots

286   show the distribution of individual difference scores; bar- mean and 95% CI. SEM, standard error of the

287   mean. CI, Confidence Interval.

288

289   Experiment 4 was designed based on the assumption that the mechanisms underlying

290   attenuation do not generalize across the workplace. Although it is well-established that implicit

291   adaptation shows minimal generalization between regions separated by more than 45°

292   (Krakauer et al., 2000; McDougle et al., 2017; Morehead et al., 2017), generalization rules may

293   be different for attenuation. For example, if attenuation generalizes broadly, the reduced rate of

294   learning following extended exposure to veridical feedback at one wedge could be due to

295   interference arising from exposure to the reversed clamp at the other wedge.

296   Given this concern, we used an alternative design in Experiment 5 to assess the effect

297   of extended experience with veridical feedback on attenuation. The target appeared in one of

298   three wedges, with each wedge separated by at least 90° from the other two (Fig. 5A). In all

299   three wedges, there was a single learning block with clamped feedback, with the direction of the

300   perturbation the same across wedges. We varied the number of veridical feedback cycles that

301   preceded the clamped feedback block, using 5 cycles for one wedge (V_5|-C), 45 cycles for a

302   second wedge (V_{45}|-C), and 85 cycles for the third wedge (V_{85}|-C). If experience with veridical

303   feedback is sufficient to cause interference in a context-specific manner, we expect that the

304   level of adaptation will be inversely related to the number of veridical cycles.

305

307   **Fig 5. Experiment 5: Interference from veridical feedback is context-specific.**

308   (**A**) Experimental protocol and learning functions. Top: During the learning block, participants (N=60)

309   experienced rotated clamped feedback while reaching to six targets, with two targets falling within each of

310   three wedges distributed across the workspace. For each wedge, participants experienced a different

311   number of cycles with veridical feedback prior to the learning block: 5 (V_5|-C, light red); 45 (V_{45}|-C,

312   medium red); 85 (V_{85}|-C, dark red). Bottom: Time course of mean reach angle averaged over cycles (2

313   movements) for each wedge. The vertical solid lines at cycles 45 and 85 mark the onset of movements to

314   an additional location, and the vertical solid lines at cycles 90 mark the onset of the task-irrelevant

315   clamped feedback. Horizontal thick black lines denote clusters of cycles that show a significant

316   relationship between the reach angle and the number of veridical cycles ($p < 0.05$). (**B**) Left panel

317   presents the aftereffect results (mean ± SEM) for each learning condition with the fixed effect regression

318   line obtained using a linear mixed model. Right panel shows the distribution (dots and violin plots) of

319   individuals' slopes (random effect); bar- mean slope and 95% CI. SEM, standard error of the mean. CI,

320   Confidence Interval.

321

322   The results were consistent with this prediction. A nonparametric permutation test

323   identified significant cycles during the learning and aftereffect blocks for which the reach angle

324   was negatively associated with the number of veridical cycles (Fig. 5A). This was also evident in

325   a linear mixed-effect analysis assessing the change in aftereffect across the three conditions

326   (Fixed effect slope: −0.04, [-0.06 -0.01], t(178) = −3.14, $p = 0.002$, Fig. 5B). Overall, the results

327   of Experiment 5 provide strong evidence that extended experience with veridical feedback can

328   interfere with implicit adaptation in a context-specific manner.

329

330   **Discussion**

331   Relearning paradigms have offered an important approach to studying learning and memory.

332   While many studies have demonstrated savings, indicative of latent retention of information that

333   was acquired in the past, implicit sensorimotor adaptation exhibits attenuation upon re-exposure

334   to a previously learned perturbation (Avraham et al., 2021; Hamel et al., 2022, 2021; Leow et

335   al., 2020; Stark-Inbar et al., 2016; Tsay et al., 2021b; Yin and Wei, 2020). The goal of this paper

336   was to identify the mechanisms underlying this attenuation. The results indicate that attenuation

337   is observed when an action has been associated with discrepant forms of visual feedback,

338   creating interference between two sensorimotor memories.

339

340   *Implicit adaptation is subject to interference from discrepant feedback signals*

341   In the adaptation literature, studies of relearning have typically used a design in which a

342   washout, perturbation-free block is employed between two learning blocks (Herzfeld et al.,

343   2014; Huang et al., 2011; Leow et al., 2012). The purpose of the washout block is to bring

344   behavior back to baseline (i.e., the hand movement is directed to the visual target) before the

345   re-introduction of the perturbation. As such, one can compare two learning functions that start,

346   at least superficially, from a common state. When considering overall performance, savings is

347   typically observed: Learning in the second perturbation block is faster than during the initial

348   perturbation block.

349   However, the observed behavior likely reflects the operation of multiple learning

350   processes. In particular, in addition to an implicit recalibration process, participants may employ

351   an explicit strategy to compensate for the perturbation (Bond and Taylor, 2015; Kim et al., 2021;

352   Taylor et al., 2014). Savings upon re-exposure to a perturbation appears to reflect the recall of a

353   strategy that had proven to be successful in the initial perturbation block (Avraham et al., 2021;

354   Haith et al., 2015; Morehead et al., 2015). By using non-contingent, clamped feedback, we were

355   able to eliminate strategy use and thus, by inference, isolate learning to just that produced by

356   implicit adaptation (Morehead et al., 2017; Tsay et al., 2020b). Under such conditions,

357   relearning is attenuated rather than facilitated. Critically, this attenuation has also been

358   observed in tasks that used other methods to isolate implicit sensorimotor adaptation (Avraham

359   et al., 2021; Hamel et al., 2021; Huberdeau et al., 2019; Leow et al., 2020; Yin and Wei, 2020).

360   Our initial hypothesis was that this attenuation reflects interference that arises when a

361   movement is associated with conflicting error signals. When veridical feedback is re-introduced

362   in the washout block, a salient error is experienced, one that is in the opposite direction of that

363   experienced during the initial perturbation block. Similarly, conflicting error signals are

364   associated with the same movement when reversed clamped feedback is used to drive

365   washout. Consistent with the interference hypothesis, relearning was not attenuated when

366   feedback was omitted from the washout block. However, subsequent experiments showed that

367   interference does not require conflicting error signals: We also observed attenuation when we

368   used a procedure to wash out adaptation in the absence of a salient opposite error signal and,

369   more dramatically, during an initial perturbation block that followed an extended baseline block

370   with veridical feedback. Thus, interference appears to be between discrepant feedback signals

371   and not competing error signals.

372   The attenuating effect from a prolonged baseline period with veridical feedback also

373   helps clarify that the effect is due to anterograde interference rather than retrograde interference

374   (see also Hinder et al., 2007; Krakauer et al., 2005; Miall et al., 2004; Villalta et al., 2015).

375   Anterograde interference refers to the disruptive effect of one memory on the ability to either

376   acquire or recall another memory. In contrast, retrograde interference refers to the disruptive

377   effect of a new memory on the consolidation of a previously learned memory. The fact that

378   attenuation is seen in the initial exposure to a perturbation is consistent with an anterograde

379   interference account. We recognize that retrograde interference may also be operative in the

380   experiments that included two learning blocks (Experiments 1-4). To assess this, future

381   experiments with clamped feedback could adopt classic manipulations used to evaluate the

382 relative contribution of anterograde and retrograde interference such as varying the delay

383 between the initial learning block, washout block, and re-learning block. These manipulations

384 would also be important to ask how interference effects are modulated when there is greater

385 time for consolidation of the memory associated with the initial perturbation (Bock et al., 2001;

386 Brashers-Krug et al., 1996; Caithness et al., 2004; Criscimagna-Hemminger and Shadmehr,

387 2008; Goedert and Willingham, 2002; Krakauer et al., 1999; Shadmehr and Holcomb, 1999,

388 1997).

389

390 *Interference or desensitization?*

391 We have proposed that the difference observed between the two learning blocks reflects the

392 interference of two competing memories, one associated with the feedback experienced during

393 learning and another with the feedback experienced during washout (or from a long baseline

394 block). By this view, the output of the system reflects the contribution from two memories,

395 yielding a change in behavior even if the parameters of the system (e.g., learning rate) remain

396 invariant.

397 An alternative perspective centers on the idea that the adaptation system retains a

398 memory of error history and uses this information to adjust its sensitivity to the error. For

399 example, in the Memory of Error model, the system upregulates the learning rate in response to

400 experienced or stable errors and downregulates the learning rate in response to unfamiliar or

401 variable errors (Albert et al., 2022, 2021; Coltman et al., 2019; Herzfeld et al., 2014; Yin and

402 Wei, 2020). The failure to observe savings in the implicit adaptation system, together with the

403 findings that the implicit response is the same for stable or variable errors, support the notion

404 that an increase in learning rate (i.e., savings) is likely a property of explicit processes (Avraham

405 et al., 2020; Hutter and Taylor, 2018; Wang et al., 2024a).

406   Nonetheless, attenuation upon relearning could be taken to reflect a flexible implicit

407   system, one in which the sensitivity to error decreases over learning sessions rather than

408   increases. For example, learning might become weaker due to the saturation or depletion of

409   neuroplasticity mechanisms (Hamel et al., 2022, 2021). Consistent with this hypothesis, a recent

410   study showed that attenuation was observed when there were 320 trials in the first perturbation

411   block, but not when this number was reduced to 40 trials (De La Fontaine et al., 2023).

412   However, to match the overall number of trials between the two conditions, the authors

413   extended the baseline block for participants in the short learning condition. As shown in

414   Experiments 4 and 5 above, an extended baseline block with veridical feedback attenuates

415   learning in the first block. Indeed, in De La Fontaine's study, the aftereffect of the first

416   perturbation block was smaller for the long baseline/short learning group compared to the short

417   baseline/long learning group. Thus, the absence of attenuation for the former group may be due

418   to interference in both learning blocks.

419   Nonetheless, the interference and desensitization hypotheses are not mutually

420   exclusive. Attenuation in the second learning block could be driven by a contribution from both

421   interference and desensitization (Hamel et al., 2022, 2021). However, attenuation is neither

422   observed when visual feedback is eliminated in the washout block (Experiment 2) nor during a

423   prolonged perturbation block with the same error (Avraham et al., 2021; Kim et al., 2018;

424   Morehead and Smith, 2017). Both results would appear at odds with a desensitization account,

425   at least one in which desensitization occurs as a function of the amount of experience or time

426   responding to a given perturbation. At present, we assume that interference is the primary

427   mechanism underlying attenuation upon relearning, at least in visuomotor adaptation.

428   Hadjiosif et al. (Hadjiosif et al., 2023) have suggested that the behavior during relearning

429   depends on the time-dependent decay characteristics of distinct memory components. One

430   component is a temporally volatile process that can rapidly respond to a perturbation but results

431   in a change in state that is quickly forgotten; this system is hypothesized to show heightened

432   sensitivity to experienced errors and thus drive savings. The second component is a temporally

433   stable process that exhibits slow learning but shows high retention over time; this system is

434   hypothesized to exhibit attenuation upon relearning. Our results are inconsistent with the view

435   that attenuation is restricted to a temporally stable implicit process. Given the number of target

436   locations and short inter-trial intervals in our experiments, and based on the parameters in

437   Hadjiosif et al.'s model, a temporally volatile process would still be making a significant

438   contribution to behavior in some of our conditions (e.g., in Experiment 4, the median time

439   between reaches to a given target = 1.92 s, interquartile range: [1.65 s 2.33 s], corresponding to

440   a decay of only ~5% (Hadjiosif et al., 2014)). Thus, we should have observed savings rather

441   than attenuation. We hypothesize that given the methods used in their study, the behavioral

442   changes they attribute to an implicit temporally volatile process are actually due to strategic

443   adjustments in aiming. In particular, probing implicit learning on a small subset of trials tends to

444   overestimate the implicit component (Maresch et al., 2021) as participants may fail to

445   completely dispense with an aiming strategy used in most trials (Avraham et al., 2021).

446

447   *Interference as an example of viewing adaptation from the perspective of associative learning*

448   The interference effect we observe in visuomotor adaptation is similar to a well-established

449   phenomenon in associative learning, latent inhibition (Solomon and Moore, 1975). For example,

450   in fear conditioning, pairing a neutral stimulus (conditioned stimulus, CS, e.g., a tone) with an

451   aversive electric shock (unconditioned stimulus, US) leads to a predictive fear response

452   (conditioned response, CR) to the CS. Latent inhibition refers to the finding that conditioning of a

453   CS-US pair is weaker following prolonged exposure to the CS in the absence of the US (CS-

454   alone) (Solomon and Moore, 1975). Thus, if an extended CS-alone block is used to extinguish a

455   conditioned response, reacquisition of this CR will be attenuated when the CS is again paired

456   with the US (Bouton, 1986).

457   This paradigm is structurally similar to the conditions in which we find attenuation in

458   relearning for sensorimotor adaptation: The pairing of movement with the initial feedback

459   perturbation is broken during the washout block with the introduction of discrepant feedback.

460   Furthermore, both latent inhibition and attenuation upon re-learning in adaptation exhibit context

461   specificity. An attenuated fear response was only evident in the context in which extinction was

462   experienced; when the rats were moved to a different cage between extinction and

463   reacquisition, reacquisition was not attenuated (Bouton, 2002; Bouton and Swartzentruber,

464   1989). Similarly, adaptation in Experiment 5 was attenuated in a wedge previously associated

465   with a long experience with non-perturbed feedback, but it was spared when tested in a new

466   wedge.

467   The parallels between these two types of learning may not be incidental (Calame et al.,

468   2023; Raymond et al., 1996; Villalta et al., 2015). Some forms of associative learning, like delay

469   eyeblink conditioning, share important features with implicit sensorimotor adaptation, including

470   strict constraints on the timing of the sensory feedback (Kitazawa et al., 1995; Schneiderman

471   and Gormezano, 1964; Smith et al., 1969; Wang et al., 2024b) and a strong dependency on the

472   integrity of the cerebellum (Donchin et al., 2011; Gao et al., 2016; Izawa et al., 2012; Medina et

473   al., 2000). We have recently considered the utility of a unified framework, viewing implicit

474   sensorimotor adaptation as an associative learning process (Avraham et al., 2022). In a series

475   of experiments, we demonstrated how neutral cues (tone and light) can modulate reach

476   adaptation in a manner that follows the principles of associative learning.

477   A critical issue in considering a unified framework is to examine the mechanistic overlap

478   between the components of the two processes. We have proposed that the onset of a target,

479   the typical cue for movement initiation in adaptation studies, serves as the CS, one that

480 becomes associated with the perturbed feedback (US). The repeated pairing of the CS and US

481 will increase their associated strength, resulting in an adapted movement (CR) to that target

482 even when the feedback is removed (aftereffect). When viewed in this framework, we see that

483 the target (or the movement plan associated with that target, see Avraham et al., 2022), has

484 CS-like features. For example, adaptation to nearby targets exhibits a generalization pattern

485 similar to that observed in the conditioned eyeblink response to variations in the CS (e.g., tone

486 frequency) (Krakauer et al., 2000; Siegel et al., 1968). Viewing anterograde interference in

487 adaptation as a form of latent inhibition also emphasizes that the target can be viewed as a CS.

488 Repeated movement to a target with veridical feedback will result in attenuated adaptation when

489 the target (CS) is subsequently paired with the perturbed feedback (US); this attenuation is not

490 observed for movements to distant targets.

491 One problem with the latent inhibition analogy is that we found no attenuation after a

492 long washout block in which feedback was eliminated (Experiment 2) whereas fear conditioning

493 is attenuated following a block of trials in which the CS is presented alone. Eliminating the

494 feedback in sensorimotor adaptation may not be equivalent to eliminating the US in a classical

495 conditioning study, at least when the no-feedback phase is introduced immediately after the

496 learning block. In this condition, the adaptation system may operate as if it is still in the most

497 recent context. As such, when the perturbation is re-introduced, there is no interference. By this

498 hypothesis, we would predict that using an extended block of no-feedback trials at the start of

499 an experiment, where the system is in a non-adapted, baseline state, would result in attenuation

500 in a subsequent learning block.

501 In summary, a unified framework for associative learning and sensorimotor adaptation

502 helps explain the mechanism underlying memory interference in adaptation. Prolonged

503 experience with non-perturbed feedback (e.g., during baseline or a washout block) produces a

504 strong association, perhaps in a Hebbian-like manner, between the movement plan and that

505   form of feedback (Della-Maggiore et al., 2017). From a Bayesian perspective, the participant

506   forms an inference about the causal structure of the environment, with the non-perturbed

507   feedback being linked to a specific target (the context) (Gershman et al., 2015, 2010). When

508   perturbed feedback is subsequently presented in the same context, the old association

509   interferes with the formation of a new association.

510

511   *Relevance of interference to the retention of real-world motor skills*

512   It seems paradoxical that a task as simple as implicit sensorimotor adaptation is so sensitive to

513   interference, even from veridical feedback, whereas complex skills such as bike riding or skiing

514   can be retained over many years, even without practice. However, as shown in the current

515   study, interference requires experience with discrepant feedback within a similar context. The

516   striking retention of complex motor skills may arise because they lack contextual overlap with

517   other behaviors in our motor repertoire. We preserve our ability to ride a bike because we do not

518   perform other skills sufficiently similar to produce interference.

519   The difference in complexity between simple reaching movements and skilled actions

520   may also limit how well the principles of interference identified in this study extend to more

521   complex movements. We have emphasized that interference is a feature of implicit

522   sensorimotor adaptation, a system designed to ensure that the sensorimotor system remains

523   exquisitely calibrated. While this process is surely operative in the learning and performance of

524   skilled actions, other learning processes will also be relevant to performance; it remains to be

525   seen how they are subject to interference effects. We have noted that explicit strategy use can

526   support savings. However, strategy use could also be prone to interference if a previously

527   learned strategy gets in the way of discovering a new approach (Adamson, 1952). Similarly,

528   other implicit processes essential for highly skilled behavior such as pattern identification and

529   response selection can be subject to pronounced interference effects when the task goal

530   changes (Logan, 1982; Shiffrin and Schneider, 1977).

531   In the present study, we have used a very restrictive and contrived experimental setup to

532   isolate a particular learning system and characterize one way in which the operation of this

533   system changes as a function of experience. It will be interesting to apply a similar strategy in

534   looking at other learning processes and examining more ecological tasks, with an eye on

535   identifying the conditions that support or interfere with memory consolidation.

536

537   **Methods**

538   *Ethics Statement*

539   The study was approved by the Institutional Review Board at the University of California,

540   Berkeley. All participants provided written informed consent to participate in the study and were

541   paid based on a rate of $9.44/hr.

542

543   *Participants and experimental setup*

544   236 healthy volunteers (aged 19-38 years; 130 females, 97 males, and 9 identified as 'other' or

545   opted not to disclose their sex/gender identity) were tested in six experiments: 44 in each of

546   Experiments 1, 2, 3, and 4, and 60 in Experiment 5. The sample size for each experiment was

547   determined based on the effect size (d=0.6) observed in our previous study showing attenuation

548   of implicit adaptation upon relearning (Avraham et al., 2021), with a significance level of α=0.05

549   and power of 0.95. The actual number allowed us to counterbalance the direction of the

550   visuomotor perturbation and, where appropriate, the target locations (detailed below).

551   We used an online platform created within the lab for conducting sensorimotor learning

552   experiments (Tsay et al., 2021a, 2020a). The platform was developed using JavaScript and

553   HTML. Participants were recruited using the crowdsourcing website Prolific (www.prolific.co)

554   and performed the experiment remotely with their personal computers. They were asked to

555   provide information concerning the size of the monitor and the device used (optical mouse or

556   trackpad), as well as their dominant hand (left, right, or ambidextrous). The program was written

557   to adjust the size of the stimuli based on a participant's monitor size. Due to an error, the data

558   from the questionnaire was not saved. However, our analysis of nearly 2,000 individuals using

559   this platform has shown that implicit visuomotor adaptation does not vary systematically

560   between response devices or handedness (Tsay et al., 2023, 2021a).

561

562   *Task*

563   At the beginning of each trial, a white circle (radius: 1% of screen height) appeared at the center

564   of the screen, indicating the start location (Fig. 1A). The participant moved a white cursor

565   (radius: 0.8% of screen height) to the start location. We refer to the body part controlling the

566   cursor — the wrist for mouse users or finger for trackpad users — as the "hand". After the

567   cursor was maintained in the start location for 500 ms, a blue target (radius: 1% of screen

568   height) appeared at one of four or six locations (see detailed experimental protocols below)

569   positioned along a virtual circle around the start location (radial distance: 25% of screen height).

570   The participant was instructed to rapidly "reach" towards the target, attempting to slice

571   through the target with their hand. Movement time was calculated as the interval between the

572   time the center of the cursor exceeded the radius of the start location to the time at which the

573   movement amplitude reached the radial distance of the target. To encourage the participants to

574   move fast, the auditory message "too slow" was played if the movement time exceeded 300 ms.

575   After crossing the target distance, the cursor, when displayed, disappeared and the participant

576   moved back to the start location. The cursor reappeared when the hand was within 25% of the

577   radial distance from the start-to-target distance.

578   In each experiment, there were three types of feedback conditions (Fig. 1A). On no

579   feedback trials, the cursor was blanked when the hand left the start circle. On veridical feedback

580   trials, the cursor was visible and aligned with the movement direction of the hand; that is, its

581   position corresponded to the standard mapping between the mouse/trackpad and the screen

582   cursor. For the third type of trials, we used task-irrelevant clamped feedback, a visuomotor

583   perturbation that has been shown to drive implicit adaptation with minimal contamination from

584   explicit learning processes (Morehead et al., 2017). Here, the cursor moved along a fixed path,

585   displaced 15° from the target (clockwise or counterclockwise, counterbalanced across

586   participants). We opted to use a 15° clamp as a perturbation of this magnitude is within the

587   range of error sizes (~6°-60°) shown to induce the maximum rate and extent of adaptation (Kim

588   et al., 2018). The radial position of the cursor corresponded to the participant's hand position.

589   Thus, the radial position is contingent on the participant's movement, but the angular position is

590   independent of the participant's reaching direction. The participant was instructed to ignore the

591   feedback and always reach directly to the target.

592   To emphasize these instructions, three demonstration trials were performed prior to

593   each clamp block. The target location was fixed for all three trials and chosen to be at least 45°

594   from the two locations on the horizontal meridian (0° and 180°) and 45° from the nearest target

595   used for learning. In all three demonstration trials, 15° clamped feedback was provided. For the

596   first demonstration trial, the participant was instructed to "Reach straight to the left" (180°), and

597   for the second, "Reach straight to the right" (0°). Following each of these trials, a message

598   appeared to highlight that the cursor was moving away from their hand and target. For the third

599   demonstration trial, the participant was instructed to "Aim directly for the target", emphasizing

600   again that they should ignore the cursor.

601

602   *Experimental protocol*

603   The main aim of this study was to examine the mechanisms underlying attenuation of implicit

604   sensorimotor adaptation upon relearning. The experiments described below include either one

605   or two blocks with clamped feedback to drive implicit adaptation. The learning blocks were

606   surrounded by blocks with various types of feedback depending on the design of each

607   experiment. Throughout the paper, we use the following convention to describe the

608   experimental protocols. -C refers to a learning block with clamped feedback. The minus (-) sign

609   indicates a perturbation direction that is opposite from the expected direction of adaptation. C

610   (without the minus sign) refers to blocks using a clamp that is rotated in the opposite direction of

611   the clamp used during the learning blocks. V refers to blocks with veridical feedback. N refers to

612   blocks with no feedback. The non-learning blocks, which constitute the main manipulations

613   across our experiments, are highlighted in bold fonts and are separated from the learning blocks

614   using the | sign.

615   <u>Experiment 1: Readaptation following standard washout (-C|**CV**|-C design)</u>

616   Experiment 1 was designed to provide a replication of our previous finding that implicit

617   adaptation is attenuated upon relearning (Avraham et al., 2021). The main protocol included two

618   learning blocks separated by a washout block (-C|**CV**|-C). The experimental session consisted

619   of 300 movement cycles, each involving one movement to each of four target locations: 45°,

620   135°, 225°, 335° (1200 movements in total). The four targets appeared in a pseudorandom and

621   predetermined order within a cycle. The session was composed of the following blocks (Fig.

622   1B): No Feedback (5 cycles), Veridical Feedback (5 cycles), Learning 1 (80 cycles), Aftereffect

623   1 (10 cycles), Washout (110 cycles), Learning 2 (80 cycles) and Aftereffect 2 (10 cycles).

624   The two initial blocks (No Feedback and Veridical Feedback) were included to familiarize

625   the participants with the experimental setup. For these trials, participants were instructed to

626   move their hand directly to the target. By providing veridical feedback in the second block, we

627   expected to minimize idiosyncratic reaching biases. The two learning blocks are the blocks in

628   which we expected to observe implicit adaptation. The aftereffect blocks provided an additional

629   assessment of adaptation. These occurred immediately after the learning blocks, and visual

630   feedback was absent in these trials. Just before the start of the aftereffect block, an instruction

631   screen informed the participant that the cursor would no longer be visible and reminded them

632   that their task was to move directly to the target. The participant pressed a key to start the

633   aftereffect block. While some forgetting might occur during this break, we anticipate that the

634   delay was short. Indeed, the reach angle during the first cycle of the aftereffect block closely

635   matched the reach angle during the last 10 cycles of the learning block ([mean Aftereffect (1st

636   cycle) / Late learning, 95% confidence interval, CI], Learning 1: 0.92, [0.81 1.04], Learning 2:

637   0.99, [0.85 1.14]).

638   The washout block was used to bring behavior back to baseline. Typically in studies of

639   relearning in sensorimotor adaptation, washout is administered by removing the perturbation

640   (e.g., the rotation of the cursor) and providing veridical feedback (Albert et al., 2022; Herzfeld et

641   al., 2014; Huang et al., 2011; Krakauer et al., 2005; Morehead et al., 2015; Yin and Wei, 2020;

642   Zarahn et al., 2008). However, assuming adaptation has occurred, the introduction of veridical

643   feedback after adaptation results in a relatively large discrepancy between the expected and

644   observed feedback. We were concerned that this would make participants aware of the change

645   in behavior induced by the clamp, and that this might alter their behavior in the second learning

646   block (e.g., invoke a strategy to offset the anticipated effects of adaptation). To minimize

647 awareness of adaptation, the washout block consisted of two phases (Fig. 1B) (Avraham et al.,

648 2021). In the first phase, we reversed the direction of the clamp. The participant was informed

649 that they would again not have control over the movement direction of the feedback, and they

650 were reminded to ignore the feedback and aim directly for the target. The reversed clamp will

651 reverse adaptation, driving the direction of the hand back towards the target. When the median

652 reach direction was within 5° of the targets for five consecutive cycles, the second phase was

653 implemented with the feedback now veridical.

654 Demonstration trials were provided at the start of each phase of the washout block, three

655 for the reversed clamp and three for veridical feedback. The demonstration trials were similar to

656 those presented before the learning blocks (same target location and same instructions for

657 where to reach). Note that the demonstration trials for the phase with veridical feedback

658 appeared when the participant's reaches were relatively close to the target. As such, we

659 expected that participants would be unaware of any residual adaptation at the start of this

660 phase. We did not assess participants' awareness about their change in behavior during

661 learning. However, when surveyed in a previous study that used the same procedure, none of

662 the participants reported awareness of any learning-related changes in their behavior (Avraham

663 et al., 2021).

664 We opted to keep the total number of washout cycles fixed. Thus, the number of cycles

665 in each phase of the washout block was determined on an individual basis using the

666 performance criterion described above. All participants experienced at least 70 cycles (mean ±

667 standard deviation, 91.3±13.4) of veridical feedback before the second clamp block, ensuring

668 they had sufficient exposure to unperturbed feedback before the onset of the second learning

669 block.

670 <u>Experiment 2: Readaptation following no feedback washout (-C|**N**|-C design)</u>

671 Experiment 2 was designed to test if the attenuation of implicit adaptation upon relearning is due

672 to interference from the feedback experienced during washout. To this end, we tested a

673 condition in which feedback was withheld during the entire washout block (Fig. 2A). The

674 protocol was similar to Experiment 1 with one change: We eliminated the feedback in the 110-

675 cycle washout block (-C|**N**|-C design). As such, the washout block was identical to the preceding

676 aftereffect block.

677 <u>Experiment 3: Readaptation following gradual rotation washout (-C|**-R$_G$V**|-C design)</u>

678 Experiment 3 was designed to test if experience with salient, opposite-signed errors at the

679 beginning of the washout block (e.g., the reversed-clamped feedback in Experiment 1) is

680 required to attenuate adaptation upon relearning. The protocol was similar to that used in

681 Experiment 1 with the difference being the procedure used in the washout block. To minimize

682 exposure to large opposite errors, we used rotated feedback that was contingent on the

683 movement of the hand and tailored on an individual basis. For each participant, we calculated

684 the mean reach angle during the first aftereffect block and, for the first cycle of the washout

685 block, rotated the cursor from the actual hand position by that angle multiplied by -1 (Fig. 3A, -

686 C|**-R$_G$V**|-C design). In this way, the rotated visual feedback should counteract the effects of

687 adaptation, with the net effect that the cursor would cross relatively close to the target. On each

688 successive cycle, the size of the rotation was decreased by 1° until it reached zero (veridical

689 feedback). For the remainder of the washout block, the feedback was veridical.

690 At the beginning of the washout block, participants were told that the cursor would now

691 be aligned with their hand position. We added three demonstration trials to reinforce these

692 instructions. These trials were similar to the demonstration trials used to illustrate the clamped

693 feedback (same target location and instructions of aiming direction). Since the target location

694 used for the demonstration trials (270°) was 45° from the nearest target locations used for

695 adaptation (225° and 315°), we expected a generalization of ~25% adaptation for reaches to the

696   demonstration locations (Morehead et al., 2017). Thus, the rotation size during these

697   demonstration trials was set to be 25% of the magnitude of the participant's aftereffect. We

698   assumed this would give the impression that the cursor was aligned with the participant's

699   movement.

700   <u>Experiment 4: Adaptation following extended veridical feedback (V_{85}|-C)</u>

701   Experiment 4 was designed to test if extended exposure to veridical feedback was sufficient to

702   produce attenuation of subsequent adaptation. The experimental session consisted of 150

703   cycles, each consisting of one movement to each of four targets: 30°, 60°, 210°, 240° (Fig. 4A).

704   The four targets appeared in a pseudorandom and predetermined order within a cycle. Adjacent

705   targets were paired [(30°, 60°) and (210°, 240°)] to define a wedge.

706   For one wedge, we used a -C|**CV**|-C design, consisting of No Feedback (5 cycles),

707   Veridical Feedback (5 cycles), Learning 1 (40 cycles), Aftereffect 1 (10 cycles), Washout (40

708   cycles), Learning 2 (40 cycles), and Aftereffect 2 (10 cycles). As in Experiment 1, the washout

709   block consisted of a reversed clamp phase and a veridical feedback phase, with the transition

710   between the two phases adjusted on an individual basis (see above). For the second wedge, we

711   used a V_{85}|-C design, consisting of No Feedback (5 cycles), Veridical Feedback (85 cycles, with

712   an additional 10 cycle block of No Feedback inserted between cycles 50 and 61), Learning (40

713   cycles), and Aftereffect (10 cycles). Before each learning block, the participant was provided

714   with a full description of the nature of the feedback for each wedge. In addition, six

715   demonstration trials (three for each wedge) were provided to emphasize the instructions. The

716   association between the wedge location and protocol was counterbalanced across participants.

717   <u>Experiment 5: Adaptation following varying experiences with veridical feedback at distinct</u>

718   <u>contexts (V_5|-C / V_{45}|-C / V_{85}|-C design)</u>

719   Experiment 5 examined if the interference effect from veridical feedback is context specific. The

720   target could appear at one of six locations: 10°, 40°, 130°, 160°, 250°, 280° (Fig. 5A). Pairs of

721   adjacent targets defined three wedges [(10°, 40°), (130°, 160°) and (250°, 280°)], and the

722   number of veridical feedback cycles prior to adaptation varied across the three wedges. The

723   session started with a 5-cycle No Feedback block in which participants moved to each of the six

724   targets, with the locations selected in a random order (within a cycle). This was followed by a

725   Veridical Feedback block (85 cycles). However, the number of wedges included in each cycle

726   changed over the course of the block. In the first phase (40 cycles), the target only appeared in

727   the two locations that defined one wedge; in the second phase (40 cycles), a second wedge

728   was added; and in the third phase (5 cycles), the remaining wedge was included. In this

729   manner, each wedge (counterbalanced across participants) was associated with a different

730   number of veridical feedback trials prior to learning: 5 (V_5|-C), 45 (V_{45}|-C) or 85 (V_{85}|-C) cycles.

731   This was followed by a Learning block (40 cycles) and an Aftereffect block (10 cycles); within

732   each of these, all six targets were included in each cycle.

733

734   *Data analysis*

735   The kinematic data recorded from the mouse/trackpad were temporarily stored on the Google

736   Firebase database and downloaded for offline analyses using custom-written MATLAB codes.

737   The primary dependent variable was the direction of hand movement (reach angle). Reach

738   angle was defined by two lines, one from the start position to the target and the other from the

739   start position to the hand position at the moment it crossed the radial distance of the target. For

740   participants who experienced a counterclockwise clamp during the learning blocks, the sign of

741   the reach angle was flipped. In this manner, a positive reach angle indicates movement in the

742   opposite direction of the perturbed feedback, the expected change due to adaptation. The reach

743   angle for each movement cycle was calculated by averaging the reach angle of all reaches

744   within a cycle, one to each of the different target locations.

745   We excluded trials in which the reach angle deviated from the target location by more

746   than 100° and trials in which the absolute trial-to-trial change in reach angle was larger than 20°

747   (Avraham et al., 2021). Based on these criteria, a total of 1.97% of all trials were excluded.

748   For Experiment 3, we plotted the distribution of errors participants experienced during

749   the non-zero rotation trials of the washout block (Fig. 3B). To evaluate this distribution with

750   respect to an error distribution for veridical feedback (Fig. S2), we used data from another group

751   of participants (N=44). This group experienced an extended, 195-cycle block with veridical

752   feedback. To plot the distribution, we used the data from cycles 100-116, matching the phase of

753   the experiment and the mean number of trials used for calculating the distribution in Experiment

754   3.

755

756   *Statistical analysis*

757   Two statistical approaches were used to analyze the changes in reach angle that occurred in

758   response to the clamped feedback. For the first approach, we used a nonparametric

759   permutation test to identify clusters of cycles in which the reach angle differed between

760   conditions (Avraham et al., 2021; Labruna et al., 2019; Maris and Oostenveld, 2007). For

761   example, to examine within-participant changes in adaptation between the first and the second

762   learning in Experiment 1 (Fig. 1C), a two-tailed paired-sample t test was performed for each

763   cycle within the learning and aftereffect blocks.

764   We defined consecutive cycles in which the difference was significant (p<0.05) as a

765   'cluster' and calculated for each cluster the sum of the t-values that were obtained for the cycles

766   in that cluster (referred to as a t-sum statistic). A null distribution of the t-sum statistic was

767   constructed by performing 10,000 random permutations with the data: For each permutation,

768   the data for a given participant was randomly assigned to "block 1" or "block 2". For each

769   permuted data set, we performed the same cluster-identification procedure as was done with

770   the actual data and calculated the t-sum statistic for each cluster. In cases where several

771   clusters were found for a given null set permutation, we recorded the t-sum statistic of the

772   cluster with the largest t-sum value. Thus, the generated null distribution is composed of the

773   maximal t-sum values achieved by chance, a method that controls for the multiple comparisons

774   involved in this analysis (Maris and Oostenveld, 2007). Each of the clusters identified in the non-

775   permuted data were considered statistically significant if its t-sum was larger than 95% of the t-

776   sums in the null distribution, corresponding to a *p*-value of 0.05.

777   The same analysis was used to assess within-participants changes in reach angle

778   between two learning and aftereffect blocks in Experiments 1, 2, 3, and 4. For Experiment 4, we

779   did this procedure three times, for the following comparisons: Learning 2 in the -C|**CV**|-C

780   location vs Learning 2 in the **V$_{85}$**|-C location, Learning 1 vs Learning 2 in the -C|**CV**|-C location,

781   and Learning 1 in the -C|**CV**|-C location vs Learning 2 in the **V$_{85}$**|-C location. Therefore, we

782   increased the threshold to identify significant clusters against the null distribution to 98.3%,

783   corresponding to *p*-value of 0.05/3=0.017.

784   In Experiment 5, we had three conditions that varied in the number of cycles of veridical

785   feedback before learning (85, 45 and 5 cycles). We hypothesized that the extent of adaptation

786   would decrease with the increased experience with veridical feedback. Therefore, we used a

787   linear regression analysis, with the response variable (y) being the mean cycle reach angle and

788   the predictor variable (X) being the number of veridical feedback cycles. We included a constant

789   intercept. We extracted the slope of the regression line for each cycle, and submitted that to the

790   non-parametric, cluster-based permutation analysis. Thus, significant clusters in Figure 5A

791   represent clusters of cycles in which the slope of the regression is significantly different than

792   zero (and negative, representing a decrease in adaptation with increasing experience with

793   veridical feedback) against a null distribution.

794   The second approach focused on the aftereffect measure of adaptation. This was

795   defined as the mean reach angle over all ten cycles of the aftereffect block. To examine

796   changes in adaptation between the two blocks in Experiments 1, 2, and 3, we used two-tailed

797   paired-sample t tests. For the within-participant comparisons of the aftereffect across conditions

798   in Experiments 4, we used a one-way repeated measures ANOVA. The sphericity assumption

799   was violated in Experiment 4, and thus, the F-test degrees of freedom was adjusted using the

800   Greenhouse–Geisser correction. For Experiment 5, we used a linear mixed-effect model to fit

801   the aftereffect data, including fixed-effect slope and intercept for the number of veridical cycles

802   before learning (4, 45, and 85) and random-effect slope and intercept for the individual

803   participants. For all of the experiments, the statistical significance threshold was set at the

804   p<0.05. p_B denotes the Bonferroni corrected p-value. In addition, we report the Bayes factor

805   BF_{10}, the ratio of the likelihood of the alternative hypothesis (H_1) over the null hypothesis (H_0)

806   (Kass and Raftery, 1995). For t-tests, we report the Cohen's d effect size (Cohen, 2013), and for

807   the repeated-measures ANOVAs, we report effect sizes using partial eta-squared (η_p^2). We

808   followed the assumption of normality based on the central limit theorem as the sample size for

809   all experiments was larger than N=30.

810

811   *Data and code availability*

812   All raw data files and codes for data analysis are available from the GitHub repository:

813   https://github.com/guyavr/InterferenceRelearningMotorAdaptation.git

814

815   **Acknowledgments**

818

Competing interests

820   RBI is a co-founder with equity in Magnetic Tides, Inc.

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Figure captions

Fig 1. Experiment 1: Upon relearning a visuomotor rotation, implicit adaptation is attenuated.

(**A**) Task design and schematics of all trial types in Experiment 1. Using a trackpad or mouse, participants (N=44) moved a cursor from the start location (white circle) to a target (blue disk), with the target appearing at one of four locations (one representative location is depicted). There were 3 types of trials: 1) No feedback, with the cursor disappearing at movement onset; 2) Veridical feedback, in which the direction of the cursor (small white disk) was veridical with respect to the direction of the movement; 3) Clamped feedback, in which the cursor followed an invariant path with respect to the target. (**B**) Top: Experimental protocol. The -C|**CV**|-C abbreviation indicates the main block-level structure of the experiment. There were two learning blocks with clamped feedback (-C), each followed by an aftereffect block with no feedback. To reset the sensorimotor map following the first learning block, we used a washout block composed of a reversed-clamp feedback phase (C) and a veridical feedback phase (V). The green oblique lines in the washout block mark the transition between the two phases, with the length of the reversed clamp phase determined on an individual basis (see Methods). Bottom: Time course of mean reach angle, with the data averaged within each cycle of four movements. Light and dark shading signify learning blocks 1 and 2, respectively, with the onset of the clamped feedback marked by the vertical solid lines. (**C**) Overlaid reach angle functions for the two learning blocks and two aftereffect blocks. Horizontal thick black lines denote clusters that show a significant difference between blocks 1 and 2 ($p < 0.05$). (**D**) The left panel (pair of bars) presents the aftereffect data (mean ± SEM) for each learning block, measured as the averaged reach angle across all cycles in each aftereffect block. The right panel shows the within-participant difference (Aftereffect 2 – Aftereffect 1; dots and violin plot- distribution of individual

1073   difference scores, bar- mean difference and 95% CI). SEM, standard error of the mean. CI,

1074   Confidence Interval.

1075

1076   **Fig 2. Experiment 2: Implicit adaptation is not attenuated upon relearning when feedback**

1077   **is eliminated during the washout block.**

1078   (**A**) Experimental protocol and learning functions. Top: Participants (N=44) experienced 110

1079   cycles of trials without feedback (N) during a washout block that separated the two learning

1080   blocks (-C|**N**|-C design, purple). Bottom: Time course of mean reach angle averaged over

1081   cycles. Light and dark shading signify learning blocks 1 and 2, respectively, with the onset of the

1082   clamped feedback marked by the vertical solid lines. The design and learning functions from

1083   Experiment 1 are reproduced here to provide a visual point of comparison (gray). (**B**) Overlaid

1084   reach angle functions for the two learning blocks and two aftereffect blocks in Experiment 2

1085   (significant clusters based on p<0.05) (**C**) The left panel presents the aftereffect (mean ± SEM)

1086   for each learning block and the right panel the within-participant difference (Aftereffect 2 –

1087   Aftereffect 1; dots and violin plot- distribution of individual difference scores, bar- mean and 95%

1088   CI). (**D**) Scatter plot showing no relationship between the reach angle at late washout and

1089   change in relearning (Aftereffect 2 – Aftereffect 1). SEM, standard error of the mean. CI,

1090   Confidence Interval.

1091

1092   **Fig 3. Experiment 3: Attenuated adaptation does not require experience with salient,**

1093   **opposite signed error at the beginning of washout.**

1094   (**A**) Experimental protocol and learning functions. Top: At the beginning of the washout block in

1095   Experiment 3, participants (N=44) experienced a rotated cursor that was contingent on the

1096   direction of their hand movement, with the magnitude of the perturbation set to their final

1097   adaptation level at the end of the first learning block; in this way, the cursor position would be

1098   near the target. The size of the rotation was gradually decreased until reaching 0°, at which

1099   point it was veridical and remained so for the rest of the washout block (-C|-R_GV|-C design,

1100   blue). Bottom: Time course of mean reach angle averaged over cycles (4 movements). Light

1101   and dark shading signify learning blocks 1 and 2, respectively, with the onset of the clamped

1102   feedback marked by the solid vertical lines. The design and learning functions from Experiment

1103   1 are reproduced here to provide a visual point of comparison (gray). (**B**) Distribution of errors

1104   experienced during the non-zero rotation phase of the washout block. These errors were small

1105   in magnitude (mean=2.9°, dark blue solid line) and in the opposite direction of the error

1106   experienced during the initial learning block (black solid line). Presumably, these opposite errors

1107   are the signals that drive the washout of the initial adaptation. The dotted line represents zero

1108   error. (**C**) Overlaid reach angle functions for the two learning blocks. Horizontal thick black lines

1109   denote clusters that show a significant difference between blocks 1 and 2 ($p < 0.05$). (**D**) The left

1110   panel presents the aftereffect (mean ± SEM) for each learning block and the right panel the

1111   within-participant difference (Aftereffect 2 – Aftereffect 1; dots and violin plot- distribution of

1112   individual difference scores, bar- mean and 95% CI). SEM, standard error of the mean. CI,

1113   Confidence Interval.

1114

1115   **Fig 4. Experiment 4: Adaptation is attenuated for movements that were previously**

1116   **associated with either washout after learning or an extended baseline experience with**

1117   **veridical feedback.**

1118   (**A**) Experimental protocol and learning functions. Top: The target appeared at one of four

1119   locations, with two locations falling within one 30°-wedge and the other two falling within a

1120   same-size wedge on the opposite side of the workspace. Participants (N=44) experienced a -

1121   C|**C**V|-C schedule (cyan) in one wedge and a **V$_{85}$**|-C design schedule in the other wedge
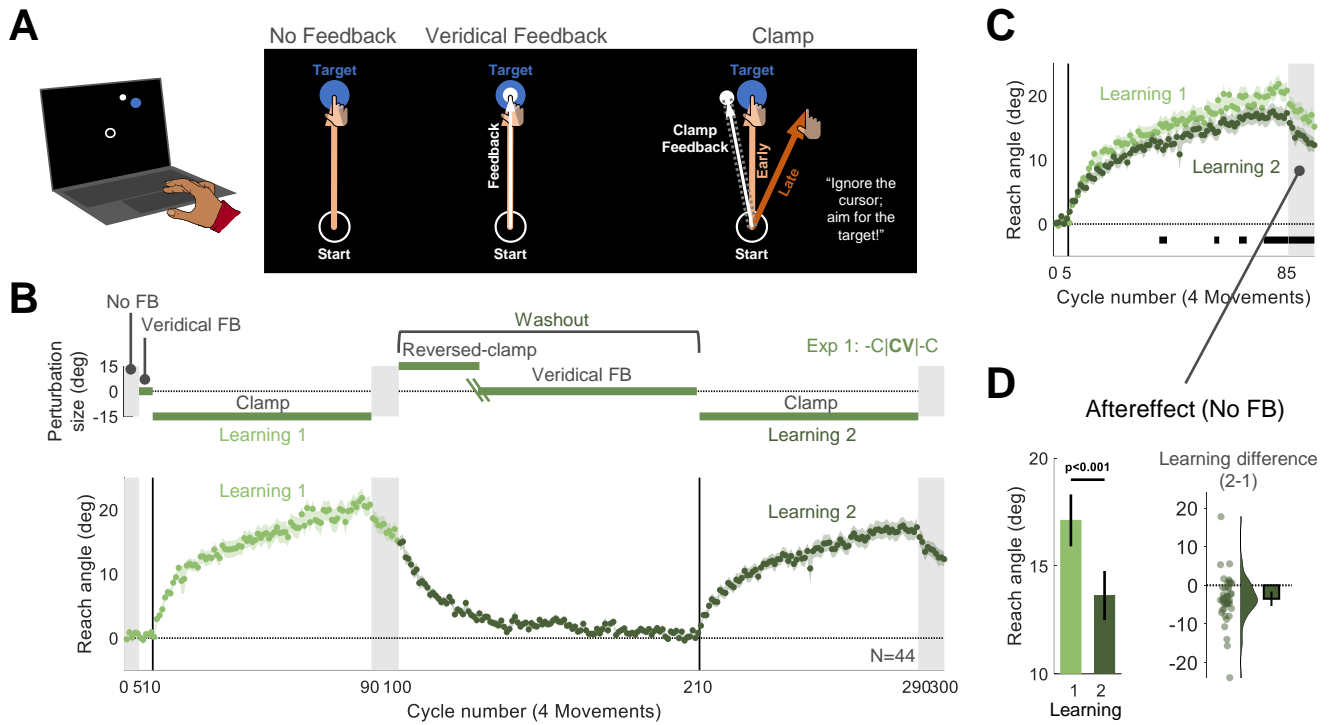
1122   (orange). For the latter, the number of veridical feedback cycles (85) matched the total number

1123   of cycles before relearning at the other wedge (excluding the no-feedback trials). Bottom: Time

1124   course of mean reach angle averaged over cycles, with each cycle consisting of 2 movements

1125   for each wedge. Light and dark cyan signify learning blocks 1 and 2 in the -C|**CV**|-C condition.

1126   (**B**) Overlaid reach angle functions comparing the first learning block in -C|**CV**|-C to that of the

1127   second learning block in the same wedge (left panel) and to the post long-baseline learning

1128   block at the other wedge (right panel). Horizontal thick black lines (B) and (C) denote clusters

1129   that show a significant difference between the functions (with $p < 0.017$ as a significance

1130   criterion, see Methods). (**C**) Left panel (bars) presents the aftereffect data (mean ± SEM) for

1131   each learning block and the right panel shows the within-participant differences for three

1132   contrasts: 1) Aftereffect 2 – Aftereffect 1; 2) Aftereffect after long baseline – Aftereffect 1; 3)

1133   Aftereffect after long baseline – Aftereffect 2. Dots and violin plots show the distribution of

1134   individual difference scores; bar- mean and 95% CI. SEM, standard error of the mean. CI,

1135   Confidence Interval.

1136

1137   **Fig 5. Experiment 5: Interference from veridical feedback is context-specific.**
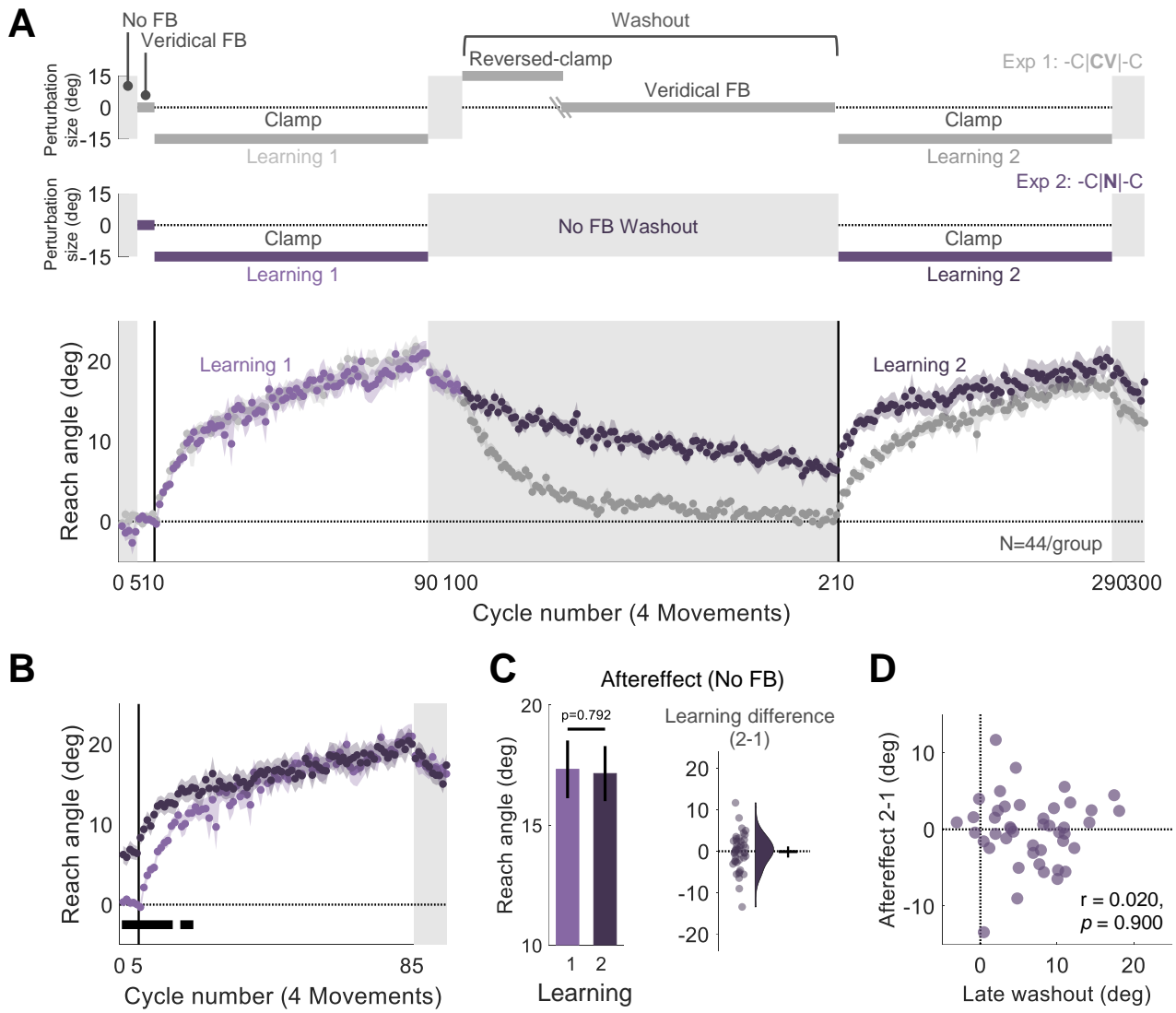
1138   (**A**) Experimental protocol and learning functions. Top: During the learning block, participants

1139   (N=60) experienced rotated clamped feedback while reaching to six targets, with two targets

1140   falling within each of three wedges distributed across the workspace. For each wedge,

1141   participants experienced a different number of cycles with veridical feedback prior to the

1142   learning block: 5 (**V$_5$**|-C, light red); 45 (**V$_{45}$**|-C, medium red); 85 (**V$_{85}$**|-C, dark red). Bottom: Time

1143   course of mean reach angle averaged over cycles (2 movements) for each wedge. The vertical

1144   solid lines at cycles 45 and 85 mark the onset of movements to an additional location, and the

1145   vertical solid lines at cycles 90 mark the onset of the task-irrelevant clamped feedback.

1146   Horizontal thick black lines denote clusters of cycles that show a significant relationship
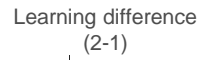
1147   between the reach angle and the number of veridical cycles ($p < 0.05$). (**B**) Left panel presents

1148   the aftereffect results (mean ± SEM) for each learning condition with the fixed effect regression

1149   line obtained using a linear mixed model. Right panel shows the distribution (dots and violin

1150   plots) of individuals' slopes (random effect); bar- mean slope and 95% CI. SEM, standard error

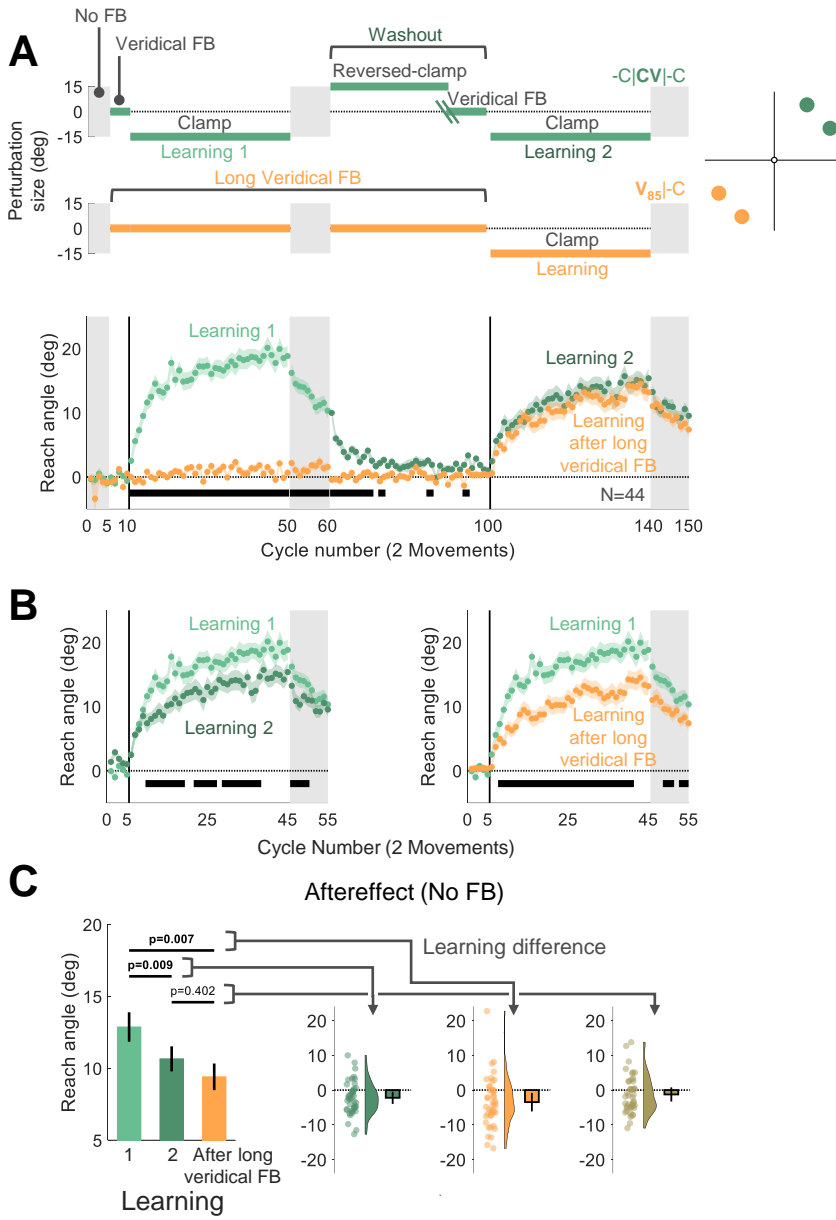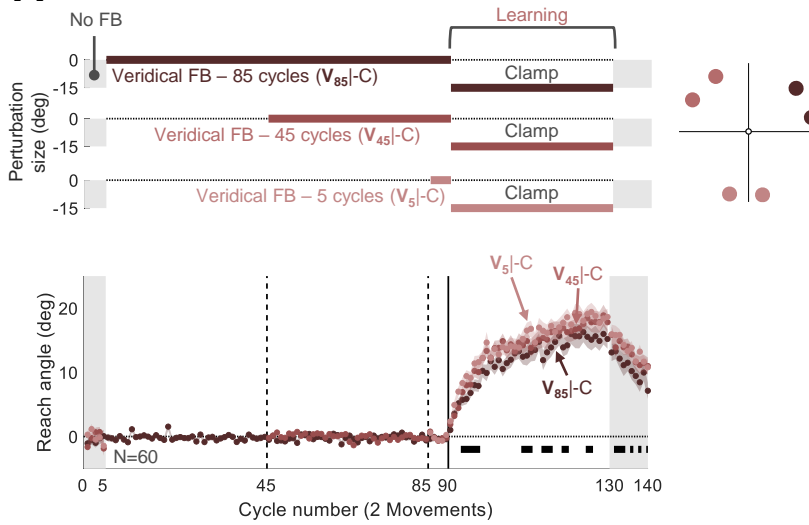1151   of the mean. CI, Confidence Interval.

Figure 1

Figure 2

Figure 3

A

No FB
Veridical FB

Washout
Reversed-clamp
Veridical FB

Exp 1: -C|**CV**|-C

Perturbation size (deg)

Clamp
Learning 1

Clamp
Learning 2

Individuals' adaptation level

Exp 3: -C|-**R$_G$V**|-C

Perturbation size (deg)

Clamp
Learning 1

Gradual rotation washout

Clamp
Learning 2

Reach angle (deg)

Learning 1

Learning 2

N=44/group

Cycle number (4 Movements)

B

Error direction during gradual rotation washout (with respect to learning)

Same   Opposite

Mean = 2.90°

Error during Learning

Number of Trials

Error (deg)

C

Reach angle (deg)

Learning 1

Learning 2

Cycle number (4 Movements)

D

Aftereffect (No FB)

p=0.002

Reach angle (deg)

Learning

Learning difference (2-1)

Figure 4

Figure 5

A

B

Aftereffect (No FB)