1   **Title: Task errors drive memories that improve sensorimotor adaptation.**

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11 **Abstract**

12   Traditional views of sensorimotor adaptation, or adaptation of movements to
13 perturbed sensory feedback, emphasize the role of automatic, implicit correction of
14 sensory prediction errors (differences between predicted and actual sensory
15 outcomes). However, latent memories formed from sensorimotor adaptation,
16 prominently evidenced in improved learning (i.e., savings), have recently been
17 attributed to strategic corrections of task errors (failures to achieve task goals). To
18 dissociate contributions of task errors and sensory prediction errors to latent
19 sensorimotor memories, we perturbed target locations to remove or enforce task
20 errors during learning and/or test. We show that prior learning to correct task errors
21 was sufficient for savings: a history of sensory prediction errors was neither sufficient
22 nor obligatory for savings. Limiting movement preparation time further revealed two
23 distinct components of this learning: 1) time-consuming, flexible strategies, and 2)
24 rapidly expressible, inflexible stimulus-response associations. The results show that
25 adaptive responses to sensorimotor perturbations take many forms.

26 **Introduction**

27   A large body of knowledge created in the last 25 years about motor learning
28 has been drawn from the paradigm of sensorimotor adaptation. Here, a systematic
29 perturbation is applied to the visual representation of movement (Cunningham, 1989;
30 von Helmholtz et al., 1924), or to limb dynamics (Dietz et al., 1994; Shadmehr et al.,
31 1994), such that the sensory consequences of motor commands are changed. This
32 necessitates adaptive motor responses in order to restore effective movement under
33 the new conditions. Given changes in the environment and the body, such adaptive
34 processes are essential to sustain successful movement in the natural world. There
35 are, however, long standing questions over the extent to which principles of
36 sensorimotor adaptation apply to other forms of motor learning; especially to the

37 acquisition of novel motor skills. This issue is important because novel skill

38 acquisition is of considerable practical relevance: during rehabilitation (Krakauer et

39 al., 2017), sport (e.g., learning to serve a tennis ball), and industry (e.g., learning to

40 control a back-hoe).

41   A key piece of evidence pertinent to the question of how sensorimotor

42 adaptation relates to other forms of motor learning is the extent to which exposure to

43 sensorimotor perturbations generates long-lasting memories. Sensorimotor memory

44 is often operationalised as improved adaptation when re-encountering a similar

45 perturbation, and the phenomenon, commonly termed savings, is well documented

46 (Brashers-Krug et al., 1996; Cassady et al., 2018; Day et al., 2018; Flook et al.,

47 1977; Kojima et al., 2004; Mawase et al., 2014; Roemmich et al., 2015; Seidler et al.,

48 2017). Importantly, the sensorimotor memories implied by savings are latent,

49 because the benefit of previous exposure persists even after behaviour is returned to

50 the naïve state by removing the perturbation for many trials (Zarahn et al., 2008),

51 even a year after the initial encounter (Landi et al., 2011; Maeda et al., 2018). A

52 latent form of memory for sensorimotor perturbations is both obligatory for success

53 given the non-stationarity of our environment, and reminiscent of new motor skill

54 memories, which can be flexibly expressed according to context.

55   Although a long history of work has sought to identify the mechanisms that

56 underlie savings (e.g., Hadjiosif et al., 2013; Herzfeld et al., 2014; Huang et al.,

57 2011; Huberdeau et al., 2015a; Mawase et al., 2014; Orban de Xivry et al., 2015;

58 Smith et al., 2006), the topic remains controversial. One influential proposal was the

59 idea that savings occurs because specific actions are associated with task success

60 during initial adaptation to the perturbation, and that these actions are recalled upon

61 task failure when a related perturbation is subsequently encountered (Huang et al.,

62 2011). An alternative idea is that exposure to a new sensorimotor environment

63 induces a form of "meta-learning", in which the structure of the perturbation is

64 encoded in memory to assist subsequent adaptation (Braun et al., 2009). More

65 recently, savings was attributed to changes in the sensitivity to errors (Gonzalez

66 Castro et al., 2014; Herzfeld et al., 2014). According to this idea, experiencing a

67 systematic sequence of errors generates a memory of errors, which increases

68 sensitivity to those errors and the gain of error correction when reencountering

69 similar errors (Gonzalez Castro et al., 2014; Herzfeld et al., 2014).

70   Despite the importance of the phenomenon of savings for the broad field of

71 motor learning, interest in the processes that underlie the effect has declined since

72 the emergence of compelling evidence that savings in standard visuomotor rotation

73 tasks is dominated by volitional, strategic selection of actions that restore task

74 success (Avraham et al., 2019; de Brouwer et al., 2017; Haith et al., 2015; Morehead

75 et al., 2015). For example, if leftward displacement of visual feedback causes a

76 person to miss the target to the left, they tend to deliberately aim to the right of the

77 target to counteract the error (Uhlarik, 1973). Using cues to signal perturbation onset

78 prompted rapid re-selection of the adapted movement on the first trial, even before

79 participants re-experienced the previously encountered error (Morehead et al.,

80 2015). Similarly, suppressing strategy use by limiting movement preparation time

81 prevented the expression of savings (Haith et al., 2015). If savings were solely a

82 manifestation of deliberate strategy use, then "cognitive" functions which determine

83 how successfully one might acquire and implement strategies would be central to

84 acquisition of latent sensorimotor memories: non-strategic "motor" processes would

85 thus be of less importance.

86   But is the conscious awareness of a strategy, to apply a corrective movement

87 that already exists within the participant's motor repertoire, really all that is retained

88 when a person adapts movement to a perturbation? Or are there components of

89 savings that are less amenable to conscious control? Savings is evident in

90 alternative sensorimotor adaptation contexts where the required corrective

91 movement is less obvious, such as force field and split-belt treadmill paradigms

92 (Cassady et al., 2018; Day et al., 2018; Mawase et al., 2014; Roemmich & Bastian,

93 2015) or in saccadic adaptation (Kojima et al., 2004). This suggests the existence of

94 a component to long-term retention of latent sensorimotor memories that is less

95 accessible to conscious awareness. If there are indeed multiple components to long-

96 term sensorimotor memories, then what are the necessary conditions for their

97 encoding and expression? A systematic approach to address this question requires

98 experiments to dissociate the contributions of the different types of errors that drive

99 sensorimotor adaptation, both during the initial exposure to the perturbation and

100 when the putative latent learning is subsequently expressed. Sensorimotor

101 perturbations, by definition, evoke sensory prediction errors (i.e., discrepancies

102 between predicted sensory outcomes of movements and actual sensory outcomes of

103 movements), but can also lead to task errors (i.e., a failure to successfully

104 accomplish a task, such as missing a target). These errors have dissociable neural

105   correlates (Diedrichsen et al., 2005; Palidis et al., 2018; Reuter et al., 2018;

106   Torrecillos et al., 2014) and dissociable behavioural consequences (Izawa et al.,

107   2011; Nikooyan et al., 2015; Therrien et al., 2016). Which of these errors are

108   required for the encoding and expression of long-term sensorimotor memories?

109   Here, we show that correcting for task errors during an initial exposure to

110   visuomotor rotation is necessary for latent retention of visuomotor memory, and that

111   it is not necessary to reexperience task errors in order to subsequently express this

112   learning. Further, we show that a history of correcting for task errors, provoked by

113   perturbing target location rather than sensory feedback of movement, can evoke

114   faster adpatation to a subsequent sensorimotor perturbation, even when participants

115   have no prior experience of this sensorimotor perturbation. This learning appeared at

116   first glance to show hallmarks of a volitionally controlled strategy: it was flexible

117   enough to accommodate a different reach solution at training and at test. However,

118   flexibility disappeared when we limited movement preparation time: performance

119   was worse than naïve as participants continued to re-engage the now-maladaptive

120   reach solution that they had learned previously to associate with restoration of

121   success in the task. Thus, improved adaptation to sensorimotor perturbation requires

122   a history of compensating for task errors, and the latent sensorimotor memories that

123   underlie improved adaptation to subsequent perturbations can take at least two

124   distinct forms, 1) volitionally controlled, flexible strategies and 2) inflexible stimulus-

125   response associations that are less amenable to volitional control.

126   **Methods and Materials**

127   **Participants**

128   There were a total of 132 participants (75 female, age range 17-34 years,

129   mean age 20.6). All participants were naïve to visuomotor rotation and force-field

130   adaptation tasks, and were naïve to the aims of the study. Participants received

131   course credit or monetary reimbursement upon study completion. The study was

132   approved by the Human Research Ethics Committee at The University of

133   Queensland. All participants provided written informed consent. This study conforms

134   with the Declaration of Helsinki.

135   **Apparatus**

136   Participants completed the task using a vBOT planar robotic manipulandum,

137   which has a low-mass, two-link carbon fibre arm and measures position with optical

138 encoders sampled at 1,000 Hz (Howard et al., 2009). Participants were seated on a

139 height-adjustable chair at their ideal height for viewing the screen for the duration of

140 the experiment. Visual feedback was presented on a horizontal plane on a 27" LCD

141 computer monitor (ASUS, VG278H, set at 60Hz refresh rate) mounted above the

142 vBOT and projected to the participant via a mirror in a darkened room, preventing

143 direct vision of her/his hand. The mirror allowed the visual feedback of the targets,

144 the start circle, and hand cursor to be presented in the plane of movement, with a

145 black background. The start was aligned approximately 10cm to the right of the

146 participant's mid-sagittal plane at approximately mid-sternum level. An air-sled was

147 used to support the weight of participants' right forearms, to reduce possible effects

148 of fatigue.

General Trial Structure

150 While grasping the robot arm, participants moved their hand-cursor (0.5cm

151 radius red circle) from the central start circle (0.5cm radius white circle) to the targets

152 (0.5cm radius yellow circles). Targets appeared in random order at one of eight

153 locations (0°, 45°…. 315°) at a radius of 9 cm from a central start circle. At the start

154 of each trial, the central start circle was displayed. If participants failed to move their

155 hand-cursor to within 1cm of the start circle after 1 second, the robotic

156 manipulandum moved the participant's hand to the start circle (using a simulated 2

157 dimensional spring with the spring constant magnitude increasing linearly over time).

158 A trial was initiated when the cursor remained within the home location at a speed

159 below 0.1cm/s for 200ms. Across all experiments, we used a classical timed-

160 response paradigm (e.g., e.g., Schouten et al., 1967) to manipulate movement

161 preparation time during the planar reaching task (Favilla et al., 1996). A sequence of

162 three tones, spaced 500ms apart, was presented at a clearly audible volume via

163 external speakers. Participants were instructed to time the onset of their movements

164 with the onset of the third tone, which was more highly-pitched than the two

165 previous, and slice through the target with their cursor. Movement initiation time was

166 identified online as when hand speed exceeded 2cm/s. Targets appeared at 1000ms

167 minus a monitor display latency (27.6 ± 1.8ms), before the third tone. Thus, target

168 direction information became available 972ms before the desired initiation time.

169 When movements were initiated 50ms later than the third tone, the trial was aborted:

170 the screen went black and the text "Too Late" was displayed on the feedback screen.

171   When movements were initiated more than 100ms before the desired initiation time,

172   the trial was aborted: the screen went black and a "Too Soon" error message was

173   displayed. Thus, movements had to be initiated between 872 and 1022ms of target

174   presentation. We chose this movement preparation time for consistency with our

175   previous work using the timed-response paradigm with visuomotor rotations (Leow et

176   al., 2017). No visual feedback about movements was available when trials were

177   aborted, and so such trials were repeated at the end of the cycle. We enforced long

178   movement preparation times across most conditions to prevent the possibility that

179   the task error manipulation resulted in self-selection of different movement

180   preparation times. Under these conditions, participants had ample opportunity (i.e.

181   time for movement preparation) to use explicit strategies.

182   Across all conditions, cursor feedback was displayed after the hand had

183   moved 4cm from the start to target (located 9cm away from the start). At this point,

184   the direction of cursor velocity was measured to define target movements in some

185   conditions as described below. During **StandardTaskError** conditions, the target

186   remained stationary throughout the trial, such that whether or not participants hit the

187   target was contingent on the participant's reach direction. During **NoTaskError**

188   conditions, the target was shifted to align with the direction of cursor velocity,

189   measured at 4cm into the movement. This is analogous to moving a basketball hoop

190   towards the ball mid-flight; the ball always goes through the hoop regardless of the

191   person's actions. During **EnforcedTaskError** conditions, the target was shifted

192   randomly by 20°–30° (counterclockwise in half of the trials, clockwise in half of the

193   trials) relative to the cursor direction when the hand

194   had moved 4 cm from the start. This is analogous to moving a basketball hoop away

195   from the ball's trajectory; participants can never get the ball through the hoop

196   regardless of where they shoot. In Experiments 3 and 4, we imposed systematic task

197   errors without any perturbation of the hand-cursor relationship: the target was moved

198   during the movement by 30° relative to the original target position, always in the

199   same direction (clockwise for half of all participants, counterclockwise of half of all

200   participants, counterbalanced): no rotation of the visual feedback of movement was

201   imposed when this occurred.

202   To familiarize participants with the equipment and the timed-response

203   paradigm, all participants were first allowed a familiarization block comprising a

204   maximum of 6 cycles. One cycle consisted of 1 trial to each of the 8 targets, and

205 target order was random within each cycle. Participants were explicitly instructed to

206 make shooting movements so that the cursor passed through the targets, rather than

207 to stop on the targets. Cursor feedback terminated as soon as the desired movement

208 extent (the 9cm distance between the start and the target) was achieved. After

209 familiarisation, all participants (regardless of assigned condition) were given the

210 same task instruction, as follows. "Your task in this experiment is to hit the targets.

211 The computer might disturb the cursor and/or the target, this is a normal part of the

212 experiment, just try to hit the target as well as you can". Participants then completed

213 the following blocks. **Baseline** (6 cycles): no rotation of visual feedback. **Training**

214 (60 cycles): For experiments 1 & 2, a 30° rotation of cursor feedback representing

215 the hand position was imposed. Half of all participants encountered a clockwise 30°

216 rotation and half encountered a 30° counterclockwise rotation. For experiments 3-4,

217 no cursor rotation was applied during this training phase, but a 30° rotation of target

218 position relative to the original target position was applied mid-movement. Half of all

219 participants encountered a clockwise 30° rotation and half encountered a 30°

220 counterclockwise rotation. **No feedback** (6 cycles): Upon leaving the start circle, no

221 feedback about movements was available. Before this block, participants received

222 explicit instructions about the rotation removal, as follows: "Any disturbance that the

223 computer has applied is now gone, and the feedback of your movement will now be

224 hidden as soon as it leaves the start circle, so please move straight to the target".

225 **Washout**: Cursor position feedback was restored, but the 30° rotation of cursor was

226 removed. For Experiments 1 and 2, to prevent the experience of washout-related

227 task errors, task errors were removed across all conditions (i.e., the target position

228 shifted mid-movement to ensure that the cursor always hit the target). The length of

229 the washout block was the same as the adaptation block (60 cycles). For

230 Experiments 3 and 4, participants had no prior experience of the cursor rotation, only

231 task errors, and they could volitionally reach straight to the target by the end of the

232 no-feedback block, thus it was unnecessary to employ a long washout with the no-

233 task-error manipulation to avoid exposure to errors related to abrupt removal of the

234 perturbation: we thus provided 12 washout cycles without mid-movement target

235 shifts. **Test** (60 cycles): the 30° rotation of cursor feedback was imposed (half of all

236 participants encountered a clockwise 30° rotation and half encountered a 30°

237 counterclockwise rotation). Between each block, there was a small delay to allow for

238 experimental instructions and loading of the computer code for different experimental

239   blocks.

Data analysis

241   Movement onset time was taken as the time at which hand speed first

242   exceeded 2 cm/s. Reach directions were quantified at 20 percent of the radial

243   distance between the start and the target. Reaches with absolute initial direction

244   errors greater than 60° with respect to the target (movements that were more than

245   60° to the left or the right of the target) were considered outliers, and were removed

246   from analyses. Experiment1: StandardTaskErrors: 0.62%, NoTaskErrors 0.11%,

247   EnforcedTaskErrors: 1.73%; Experiment2: TrainStandardTaskErrors: 0.29%,

248   TrainEnforcedTaskErrors: 0.62%; TrainNoTaskErrors: 0.17%; Experiment 3: Same:

249   0.30%, Different: 0.20%. Experiment 4:ShortDifferent: 3.82%; ShortSame: 4.31%,

250   ShortNaive:4.59%). Excluding these trials did not have any qualitative impact on the

251   results. Trials were averaged in cycles of eight (one trial for each target angle) for

252   conversion to percent adaptation (see below). For graphing purposes, reach

253   directions for participants who experienced counterclockwise rotations (30°) were

254   sign-transformed and pooled with data for participants who experienced

255   counterclockwise (30°) rotations: values closer to 30° indicate more complete

256   adaptation.

257   For all blocks except the test block, we estimated adaptation performance as

258   percent adaptation, which quantifies reach directions relative to the ideal reach

259   direction (as shown in Hadjiosif & Smith, 2013).

260    $$naive\ percent\ adaptation = 100\% \times \frac{reach\ direction - baseline\ bias}{ideal\ reach\ direction - baseline\ bias}.$$

261

262   For the test block, we were interested in savings, which is improved learning

263   at test compared to naïve. Even with exposure to the same number of no-rotation

264   trials at washout as at training (480 trials), washout was often incomplete.

265   Incomplete washout can inadvertently magnify estimates of savings. Estimates of

266   savings thus needs to take into account the extent of washout. We estimated percent

267   adaptation for the test block as follows, where reach biases in the washout phase

268   were estimated as the mean of the final 3 cycles of the washout block, similar to

269   Haith et al. (2015).

270    $$test\ percent\ adaptation = 100\% \times \frac{reach\ direction - washout\ bias}{ideal\ reach\ direction - washout\ bias}$$

271

272   To evaluate savings (improved adaptation compared to naïve), we selected

273   first 5 cycles (i.e., the first 40 trials) of the naïve and test block for comparisons using

274   Welch's t-tests (Delacre et al., 2017)(or Mann-Whitney U-tests if assumptions of

275   normality were violated), as savings tends to be most evident at initial exposure/re-

276   exposure to the rotation in visuomotor rotation paradigms. We note however that this

277   window may miss important effects outside the first 5 cycles, particularly since

278   adaptation is slower when task errors are removed or enforced (Kim et al., 2019;

279   Leow et al., 2018). To avoid missing effects outside the first 5 cycles of the block, we

280   additionally estimated performance in the entire adaptation block by splitting each

281   60-cycle adaptation block into an early phase (estimated as mean percent

282   adaptation from the first 30 cycles) and a late phase (estimated as mean percent

283   adaptation from the last 30 cycles). To compare naïve to test adaptation

284   performance, we used Training (naïve, test) x Phase (early, late) ANOVAs on early

285   and late phase percent adaptation, with greenhouse-geisser corrections applied

286   where appropriate. For Experiment 1, test block adaptation was compared to naïve

287   block adaptation within the same group of participants. For Experiment 2, test block

288   adaptation with a certain task error manipulation was compared to naïve adaptation

289   from a different group with equivalent task error manipulations. Specifically, the

290   TrainStandardTE group and the TrainEnforcedTE group experienced no task errors

291   at test, and thus were compared to the naïve no task error block from the

292   TrainNoTaskErrors group. The TrainNoTaskErrors group experienced standard task

293   errors at test and thus were compared to the naïve standard task error block in the

294   TrainStandardTaskErrors group. Similarly, for Experiment 3, test block adaptation

295   with standard task errors was compared with the naïve standard task error block in

296   the TrainStandardTaskError group from Experiment 2. For Experiment 4, test block

297   adaptation with short preparation time and standard task errors were compared with

298   data from a separate control group who experienced the same short preparation time

299   and standard task error conditions, but who were naïve to any training to reduce task

300   errors or sensory prediction errors.

301   A common alternative measure of savings is to assess for increases in rate

302   constants, obtained by fitting the data to exponential functions. Rate constant

303   analyses were not used here for the following reasons. For datasets where savings

304   is evident as immediate adaptation in the first cycle upon perturbation exposure

305   (Huberdeau et al., 2015a; Landi et al., 2011), rate constants are typically small

306   because the rapid initial adaptation is not captured by the fit. This can give the

307   erroneous impression that savings is absent, and this situation was apparent in

308   some of our data. When we tried to avoid this problem by fixing the fit parameter that

309   reflects the y value when x = 0 as the mean reach direction in the immediately

310   previous no-rotation cycle, the fits poorly characterized the data. These results agree

311   with previous work demonstrating that exponential functions poorly represent

312   individual learning curves, which often show abrupt step-like increases in

313   performance (Gallistel et al., 2004).

314   Statistical analyses were performed with SPSS and JASP. Graphs were

315   plotted with GraphPad Prism version 7.00 for Windows, GraphPad Software, La Jolla

316   California USA, www.graphpad.com.

317   **Results**

318   **Experiment 1: Task errors are important for savings**

319   In Experiment 1, we asked whether savings would be present if adaptation

320   was learnt in the absence of task errors, or with task errors that were enforced

321   regardless of the participants' actions. During training, all participants were exposed

322   to a 30° rotation of cursor feedback. In the StandardTaskError condition, since the

323   target was not moved within a trial, task errors were allowed to vary contingent upon

324   participants' responses to the cursor perturbation (Figure 1B). Task errors were

325   enforced in the EnforcedTaskError condition by moving the target mid-movement so

326   that the cursor always missed the target by 20-30° (Figure 1E). Task errors were

327   removed in the NoTaskError condition by moving the target to align with the cursor

328   trajectory mid-movement (Figure 1H). After initial exposure to the visuomotor

329   rotation, behaviour was returned to the unadapted state by removing the cursor

330   rotation in a washout phase. During this washout, we also employed the

331   NoTaskError manipulation across all groups to prevent experience of task errors

332   upon abrupt removal of the cursor rotation. At the test block (i.e., the second

333   exposure to the visuomotor rotation) we applied the same task error manipulations

334   that each group experienced when they were initially exposed to the perturbation.

335   Reach directions across all cycles for groups are shown in Figure 1A. Both

336   removing task errors and enforcing task errors slowed adaptation compared to

337   experiencing standard task errors that were contingent upon the corrective

338   responses of the participant. One participant from the no task error group did not

339   move towards the presented target in the cycles 41 to 47, which resulted in the

340   variability that is apparent in the group average plot. The analysis outcomes were

341   similar with and without this dataset.

342   With standard task errors, percent adaptation at test tended to improve

343   compared to naive immediately after rotation onset (Figure 1C), similar to Huberdeau

344   et al. (2015a). This improvement was primarily evident in the first 8 trials of exposure

345   to the cursor rotation (i.e., the first cycle), as adaptation in the first cycle improved at

346   test compared to naive (naïve: 8.5+/-6.6%, test: 32.0+/-8.6%, cohen's d=0.74).

347   Improvements compared to naïve were marginal when estimated over the first 5

348   cycles (naïve: 37.5+/- 3.9%; test: 53.4+/-8.6%, p= 0.0554, cohen's d= 0.618). Block x

349   Phase (early adaptation, late adaptation) ANOVA comparing the naïve and the test

350   block showed a non-significant main effect of block and no significant interactions

351   with block.

352   With enforced task errors (Figure 1H), percent adaptation in the first 5 cycles

353   did not differ reliably at test (15.9+/-2.7%) compared to naïve (18.5+/-3.0%),

354   t(11)=0.663, p=.521, cohen's d=0.192. Block x Phase (early adaptation, late

355   adaptation) ANOVA comparing the naïve and the test block showed a non-significant

356   main effect of block, F(1,11)=2.855, p=0.119, partial η-squared=0.2, and no reliable

357   interactions with block.

358   With no task errors (Figure 1I), percent adaptation in the first 5 cycles did not

359   differ reliably from naïve (17.7+/-3.1%) to test (13.1+/-2.8%), t(11)=1.08, p=.303,

360   cohen's d =0.3. Block x Phase ANOVA on the entire adaptation block showed worse

361   adaptation at test (mean of the entire test block: 46.3+/-5.1%) compared to naïve

362   (mean of the entire naïve block, 53.0+/-3.6%, figure 1I), significant main effect of

363   block, F(1,11)=5.95, p=0.033, partial η-squared=0.35.

364
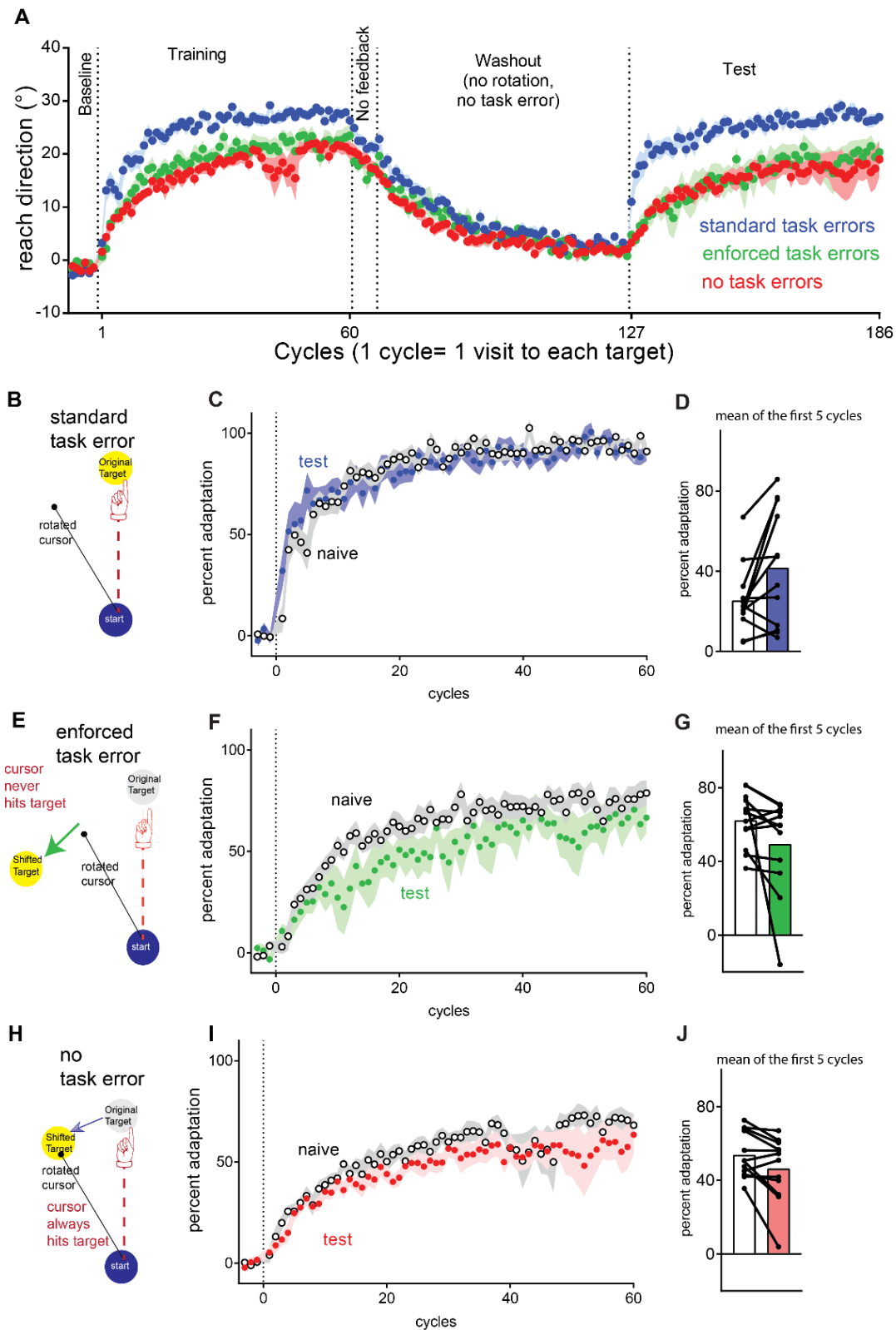
Figure 1. Experiment 1: Despite re-exposure to the same rotation, savings was absent with no task errors or enforced task errors. At both training and test (i.e., during exposure to a 30° cursor rotation, participants were exposed to either standard task errors (B), enforced task errors (E), or no task errors (H). Cycle averaged reach directions across all blocks (A). Cycle averaged percent adaptation compared to naïve white circles) (C, F, I), and mean percent adaptation averaged across cycles (D, F G). Improved adaptation (greater percent adaptation) compared to naïve was evident with standard task errors (C & D), but not with enforced task errors (F&G), and not with no task errors (I & J). For D, F, G, error bars=95% CI. All other error bars are SEM.

374   Thus, despite exposure to the same cursor perturbation, and therefore

375 previous experience of the similar sensory prediction errors, savings was not evident

376 in the groups that did not experience correctable task errors as a result of the cursor

377 perturbation.

378 **Experiment 2: Task errors are required at encoding but not at retrieval.**

379   The absence of savings when perturbation-induced task errors were removed

380 suggests some role of perturbation-induced task errors in savings. A few

381 interpretations are possible. First, task errors might act as a retrieval cue to trigger

382 the memory that is responsible for savings (Huberdeau et al., 2015a). Second, task

383 errors might be necessary to encode a memory that is responsible for savings. Third,

384 task errors might be necessary both at encoding and at retrieval for savings: savings

385 can only occur when previously experienced task errors are revisited. We

386 dissociated these possibilities in Experiment 2. Task errors were manipulated either

387 at training or at test to identify whether savings requires prior experience of task

388 errors during first exposure to a perturbation (when a memory is first "encoded") or

389 when the perturbation is re-encountered (when a memory is "retrieved"). A

390 TrainStandardTaskError group (n=12, 6CW, 6CCW) was deprived of task errors at

391 test (target was shifted mid-movement so that the cursor always hit the target), but

392 were provided standard task errors at training (i.e. no target shifts): absence of

393 savings here would suggest that task errors are necessary as a retrieval cue for

394 savings. A TrainNoTaskError group (n=12, 6CW, 6CCW) was deprived of task errors

395 at training, but experienced standard task errors at test (target did not move mid-

396 movement): absence of savings here would suggest that the task errors are not

397 required as a retrieval cue, but are a necessary component to encoding a memory

398 that results in savings. Does savings result from the experience of task errors alone,

399 or does savings require learning to correct for task errors? To test this, a

400 TrainEnforcedTaskError group (n=12,6CW, 6CCW) were provided with enforced task

401 errors at training (target always moves away from the cursor mid-trial, such that they

402 could never succeed in reducing task errors), and were tested for savings in the

403 absence of task errors. After training, all groups encountered 6 no-feedback cycles

404 and 60 no-rotation washout cycles with no task error, and then re-encountered the

405 same cursor rotation as they experienced at training. To evaluate savings, test

406 performance was compared to the naive adaptation of another group who

407 experienced the same task error conditions. Specifically, the no task error test phase

408 from the TrainStandardTaskError and the TrainEnforcedTaskError groups was

409 compared to the no task error training phase of the TrainNoTaskError group. The

410 standard task error test phase from the TrainNoTaskError group was compared to

411 the standard task error training phase of the TrainStandardTaskError group.

412 Figure 2C shows that in the TrainStandardTaskError group, standard task

413 errors at training resulted in better-than-naïve adaptation at test, even in the absence

414 of task errors at test, as evidenced in better adaptation at the first 5 cycles at test

415 (36.5+/-8.0%) compared to naive (15.2+/-1.5%), t(11.7)= 2.61, p= 0.016, cohen's

416 d=1.065. Similarly, Group (TrainStandardTaskError, Naïve) x Phase (Early

417 Adaptation, Late Adaptation) ANOVA showed a significant main effect of Group:

418 F(1,22)=10.211, p= .004, partial eta-squared =.317. Thus, a history of task errors

419 improved re-adaptation to a cursor rotation even when the perturbation did not cause

420 any task errors upon second exposure.

421 In the TrainEnforcedTaskError group (Figure 2F), adaptation in the first 5

422 cycles did not differ reliably at test (17.6+/-4.1%) compared to naïve (15.2+/-1.4%),

423 t(13.7) = 0.561, p = 0.584, cohen's d = 0.229. Group (TrainEnforcedTaskError,

424 Naïve) x Phase ANOVA showed no reliable main effect of Group, F(1,22) = 1.20,

425 p=.285, partial eta-squared=.052, and a non-significant Phase x Group interaction,

426 F(1,22) = 0.69, p = 0.413, partial η-squared = 0.03. Enforcing task errors at training

427 thus did not appear to improve adaptation compared to naïve when tested without

428 task errors. Thus, merely experiencing task errors, without learning to correct for

429 those task errors, was not sufficient to evoke subsequent savings.

430 In the TrainNoTaskError group (Figure 2I), adaptation in the first 5 cycles did

431 not differ reliably at test (35.9+/-6.3%) compared to naïve (40.3+/-6%), t(21.9) =

432 0.499, p = 0.623, cohen's d = 0.204. This lack of improvement compared to naïve

433 was shown throughout the entire adaptation block (Figure 2I), as Group

434 (TrainNoTaskError, Naïve) x Phase (Early, Late Adaptation) ANOVA showed a non-

435 reliable main effect of group, F(1,22) = 1.38, p = 0.25, partial η-squared = 0.05, and

436 a non-reliable Phase x Group interaction, F(1,22) = 3.47, p = 0.08, partial η-squared

437 = 0.13. Thus, depriving participants of task errors when they were first exposed to

438 the cursor rotation at training resulted in no savings despite the subsequent

439 presence of standard task errors at test.

440   Thus, a history of adapting movements to correct task errors appears

441   necessary to encode learning that improves adaptation to a previously experienced

442   visuomotor rotation. The presence of task errors appears unnecessary to retrieve

443   this learning.

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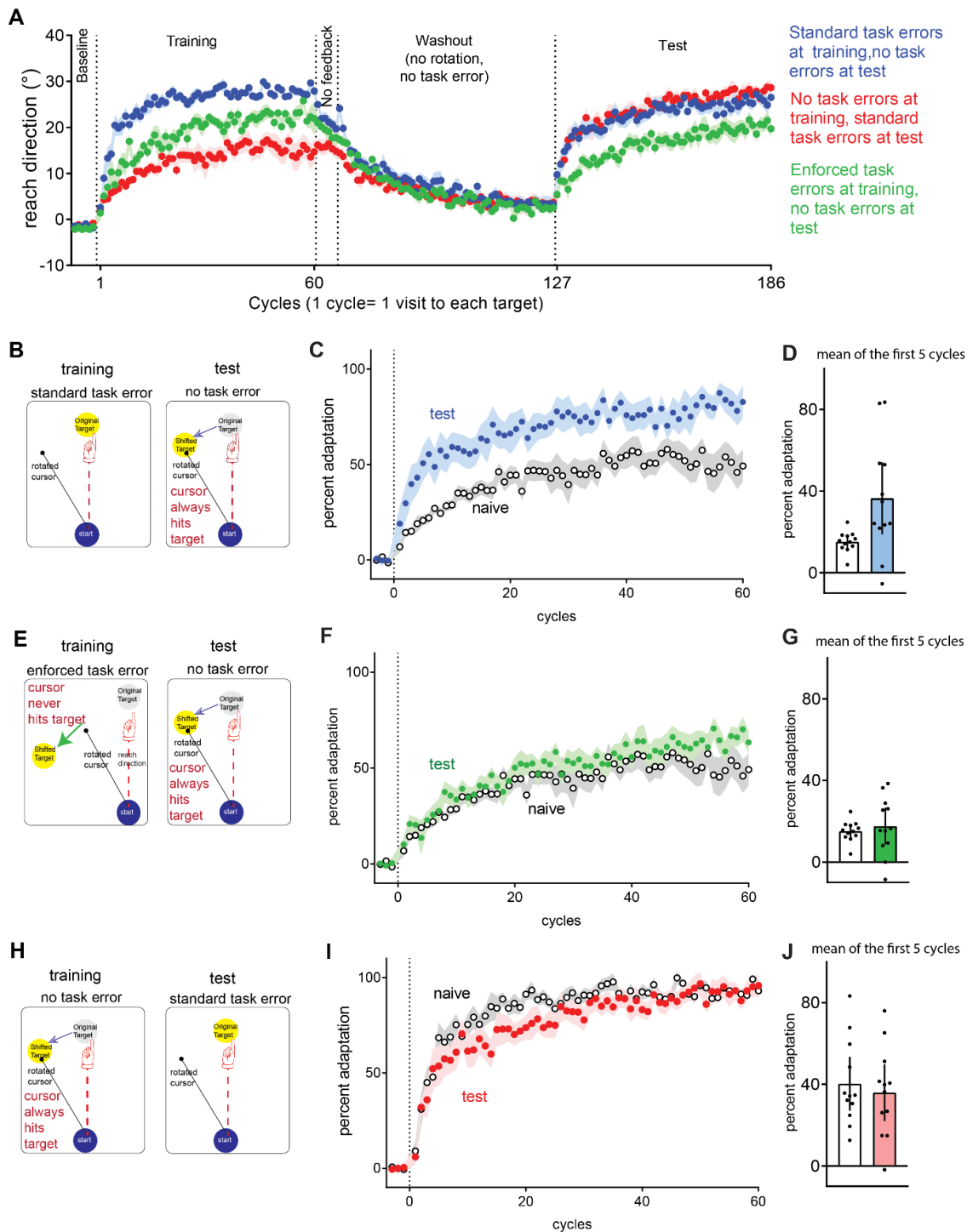
Figure 2. Experiment 2 showed that savings requires a history of adaptation to task errors.
During initial exposure to the cursor rotation (training), participants experienced task errors (either standard task errors **(B)** or enforced task errors **(E)**, or experienced no task errors **(H)**. At re-exposure to the cursor rotation (test), participants who experienced task errors at training were now deprived of task errors **(B & E)** whereas participants who were deprived of task errors at training were now provided task errors. **(A)** Cycle averaged reach directions across all blocks. Note that task errors were removed at washout in all groups to ensure that abrupt removal of the perturbation would not inadvertently evoke task errors. Clear symbols and white bars indicate naïve adaptation. **(B).** Even without task errors at test, a history of standard task errors at training improved subsequent adaptation, (greater percent adaptation in C & D)**.** In contrast, adaptation was not improved in the group who experienced a history of enforced task errors that could not be corrected for (F&G). Adaptation was also unimproved without a history of task errors at training, despite the presence of task errors at test. (I & J). For D, F, G, error bars=95% CI. All other error bars are SEM.

458

Experiment 3: Previous learning to correct for task errors can evoke savings.

Recent work suggests that savings in visuomotor rotation primarily reflects the deliberate application of a strategy, where participants explicitly re-aim to the one side of a target to counteract the rotation of cursor feedback (Haith et al., 2015; Morehead et al., 2015). This view considers the role of implicit adaptation to sensory prediction errors as secondary to the role of strategy in savings, and would interpret the presence/absence of savings with task errors in Experiments 1 and 2 to be because task errors provoke the formation of explicit strategies. An alternative view is that task errors alter the sensitivity to sensory prediction errors (Kim et al., 2019; Leow et al., 2018), and increased sensitivity to these errors produce savings (Herzfeld et al., 2014). We cannot dissociate between the two alternative explanations based on data from Experiments 1 and 2 alone because task errors here were not wholly independent of sensory prediction errors; the task error manipulations were always made in the presence of a perturbation of the hand-cursor relationship (which therefore induced sensory prediction errors). Thus, we next examined how learning to correct for task errors alone, in the absence of sensory prediction errors (i.e., in the absence of any perturbation of the hand-cursor relationship), affected subsequent adaptation to a visuomotor rotation.

In Experiment 3, we did not perturb the cursor at training, but enforced systematic task errors that could be counteracted by a re-aiming strategy: the target always moved away by 30° from the original target location mid-movement: participants could correct these task errors by re-aiming 30° away from the original target (see Figure 3a). For one group of participants, the reach solution needed to hit a given target after it jumped mid-movement was the same reach solution needed to counteract the cursor rotation in the test block (**Same**, n=12, 6 CW, 6 CCW). For example, if the target jump at training was 30° counterclockwise, then the cursor rotation at test was 30° clockwise (thus requiring a counterclockwise compensatory hand movement). To test whether this learning is flexible enough to accommodate a different reach solution, we had another group of naïve participants (**Different**, n=12, 6 CCW, 6CW), where the reach direction required to hit targets at training was opposite to that at test. Pilot testing revealed substantial individual differences in how quickly participants developed a strategy to re-aim at training. Thus, if the experimenter observed that participants had yet to show successful re-aiming by trial

492   180 of the 480-trial training block, the experimenter explicitly instructed participants

493   that a strategy may be needed to hit the target. This explicit instruction was required

494   in 2 of the 12 participants in the Same group, and 6 of the 12 participants in the

495   Different group. Here, the instruction was given without exposure to the cursor

496   perturbation but after exposure to the *task* error. At the test block, no instructions

497   about re-aiming were provided. To quantify savings, we compared percent

498   adaptation at test to naïve controls who experienced similar task error manipulations

499   (i.e., the naïve adaptation block from the group who experienced standard task

500   errors at training in Experiment 2).

501   Figure 3B shows reach directions in all cycles. After instructing participants

502   that the task error manipulation had been removed, reach directions reverted rapidly

503   back to baseline in the no-feedback block. This illustrates that the re-aiming

504   response can be switched off immediately upon instruction.

505   Despite being naïve to the cursor rotation, improved adaptation was evident

506   when the reach solution at test was the same as training (Figure 3C), as better

507   adaptation at test was evident in the first 5 cycles at test (69.1+/-8.7%) compared to

508   naïve (40.3+/-6%), $t(19.5) = 2.722$, $p = 0.013$, cohen's $d = 1.111$. This effect was

509   primarily limited to the first 5 cycles, as analyses on the entire adaptation block via

510   Group x Phase (Early, Late Adaptation) ANOVA showed a unreliable main effect of

511   Group, $F(1,22) = 2.82$, $p = 0.107$, partial η-squared = 0.11, and an unreliable Phase

512   x Group interaction, $F(1,22) = 1.1$, $p = 0.304$, partial η-squared = 0.04. Similarly,

513   improved adaptation was evident when the reach solution at test was opposite to

514   that at training (Figure 3E), as evident in better adaptation in the first 5 cycles at test

515   (72.2+/-6.7%) compared to naïve (40.3+/-6%), $t(21.7) = 3.558$, $p=0.002$, cohen's

516   d=1.453. Group x Phase (Early, Late Adaptation) ANOVA showed a main effect of

517   Group, $F(1,22) = 8.11$, $p = 0.00934$, partial η-squared = 0.26. The Phase x Group

518   interaction was not reliable, $F(1,22) = 1.75$, $p = 0.199$, partial η-squared = 0.07.

519   Hence, previous learning to counteract task errors was sufficient to improve

520   subsequent adaptation to a visuomotor rotation, even when participants were naïve

521   to perturbation-induced sensory prediction errors. This learning was flexible: it

522   elicited savings even when the reach solution required to hit a given target at training

523   was different from the reach solution required to hit that target at test.

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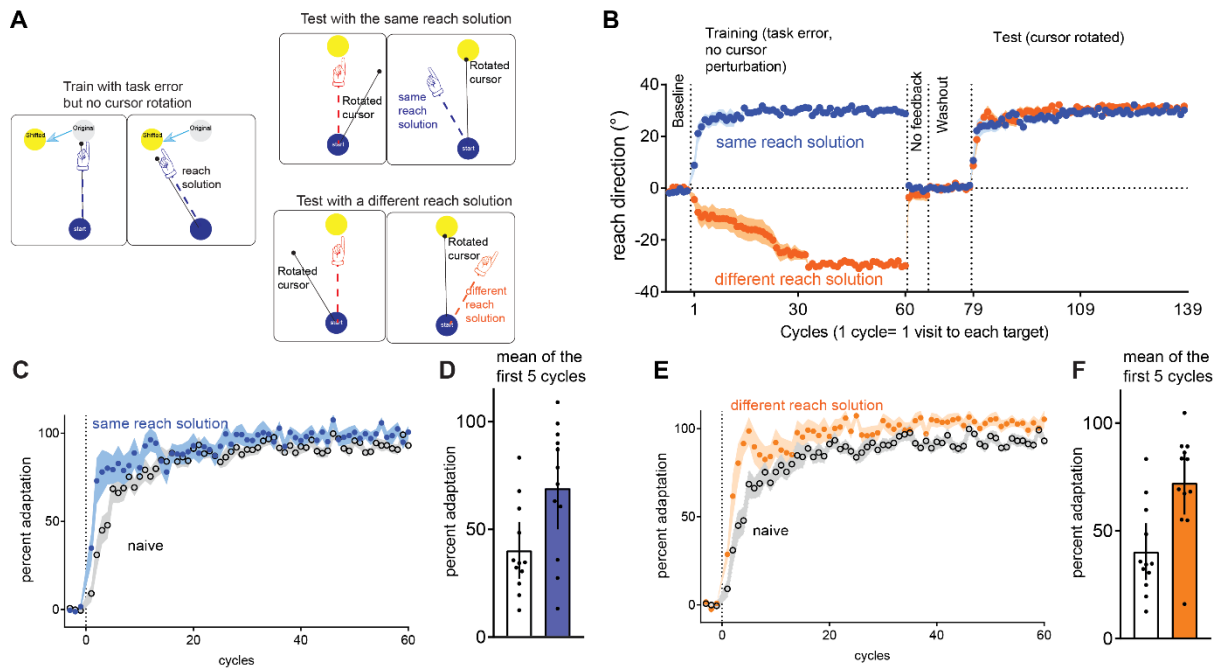
Figure 3. Experiment 3 shows that previous learning to correct for task errors in the absence of sensory prediction errors can evoke savings in visuomotor rotation. To test whether previous learning to counteract task errors could improve naive adaptation (i.e., when participants were naïve to perturbations of sensory feedback), we did not impose a cursor rotation at training, but rather moved the target away from its original position by 30° at mid-movement. To hit the target, participants had to to re-aim by 30°. Participants rapidly reverted to baseline performance after receiving instructions that all disturbances had been removed. At test, participants encountered a 30° cursor rotation for the first time. One group (Same) had the cursor rotation in the opposite direction as the target movement direction during training, such that the participants could use the same reach solution at training and test. The other group (Different) had the cursor rotation in the same direction as the target movement direction during training, such that participants had directionally opposite reach solutions at training and test. (B). Cycle-averaged reach directions throughout the experiment, where each symbol represents 1 cycle (1 visit to each target), and reaches closer to 30° during test represent reaches that more adapted. Cycle-averaged percent adaptation during test (filled circles) compared to naïve (clear circles) for the same reach solution (C) and the different reach solution (E). Mean percent adaptation averaged over the first 5 cycles with the same solution (D) and with a different solution (F) Savings was evident in more adapted reaches compared to naïve (clear symbols) for both the Same group (C & D) and the Different group (E & F). For D & F, error bars=95% CI. All other error bars are SEM.

Experiment 4: Expressing a memory of task errors at short latencies.

We next explored the mechanisms by which learning to compensate for task errors can improve subsequent visuomotor rotation adaptation. Task error correction likely relies on strategic processes that demand cognitive resources, because error compensation is reduced by manipulations that limit cognitive resources, such as time-constraints or a dual task (Anguera et al., 2012; Fernandez-Ruiz et al., 2011; Galea et al., 2010; Haith et al., 2015; Leow et al., 2017; Malone et al.; Taylor et al., 2007, 2008). In visuomotor rotation paradigms, these observations are consistent with the notion that mental rotation of a movement plan at a specified angle away from a target is computationally expensive, and requires time (Bhat et al., 1998;

554   Georgopoulos et al., 1987; Pellizzer et al., 1993). Could savings occur even when

555   these time-consuming cognitive processes were suppressed by limiting preparation

556   time? To explore this, we replicated the design of Experiment 3, except that

557   participants were required to move within a short preparation time of 250ms after the

558   time of target presentation throughout all trials. We used the timed-response

559   paradigm we described previously in the methods for all the previous experiments,

560   but instead of presenting the target at 1000ms before the imperative to move, we

561   now present the target 250ms before the imperative to move (Leow et al., 2017).

562   There were two conditions: **ShortSame** (n=12, 6 CW, 6 CCW), where the reach

563   solution is the same at training and at test, and **ShortDifferent**, (n=12, 6 CW, 6

564   CCW), where the reach solution is opposite at training and at test. Cycle-averaged

565   reach directions are shown in Figure 4. At training, despite the preparation time

566   constraints, participants did learn to compensate for task errors (Figure 4B), as

567   percent adaptation was larger at the late phase of the training block than the early

568   phase, as shown by a significant main effect of Phase, $F(1, 23) = 57.1$, $p=1.1e-7$,

569   partial eta-squared=0.7. However, the extent of compensation (estimated as the last

570   10 cycles) was less complete with short preparation time in Experiment 4

571   (ShortSame: 51.5+/-3.5%, ShortDifferent: 54.4+/-4.9%) than with long preparation

572   time in Experiment 3 (Same 98.9+/-1.8%, Different: 97.4+/-2.5%), as

573   ReachSolutionDirection (Same, Different) x Preparation Time (Short, Long) showed

574   a significant main effect of preparation time $F(1, 44) = 179.3$, $p = 4.0e-17$, partial eta-

575   squared = 0.8.

576   We compared adaptation performance in the test block to a naïve control

577   group tested under similar preparation time and task error conditions (ShortNaive,

578   n=12, 6 CW, 6 CCW). In the ShortSame group who trained with the same reach

579   solution at test and training, adaptation at test was better than naïve (Figure 4C), as

580   mean of the first 5 cycles of the test block, 44.7+/-3.4% was better than naïve,

581   26.9+/-2.9%, $t(21.6)= 3.964$, $p=6.581e -4$, cohen's d=1.618). Improved adaptation

582   compared to naive was primarily concentrated in the first 5 cycles, as examining the

583   entire adaptation block with a Group x Phase (Early, Late adaptation) ANOVA

584   yielded an non-significant effect of Group $F(1,22) = 0.01$, $p = 0.898$, partial η-squared

585   = 0, and a non-significant Phase x Group interaction, $F(1,22) = 0.17$, $p = 0.679$,

586   partial η-squared = 0.

587   When the reach solution at test differed from that at training in the

588   ShortDifferent group, test performance was **worse** than naïve (Figure 4E). Percent

589   adaptation in the first 5 cycles at test (11.8+/-4.4%) was worse than naïve (26.9+/-

590   2.9%), t(19.2)= 2.839, p= 0.010, cohen's d = 1.159. This was despite the fact that

591   participants had already disengaged the previously learnt reach solution in the

592   preceding no-rotation blocks with instruction (Figure 4B). Group x Phase (Early, Late

593   adaptation) on the entire adaptation block showed a Phase x Group interaction,

594    $F(1,22) = 9.59$, p = 0.00524, partial η-squared = 0.3, as worse adaptation tended to

595   occur in the early phase (i.e., the first 30 cycles) but not in the late phase (the final

596   30 cycles) (see Figure 4E).

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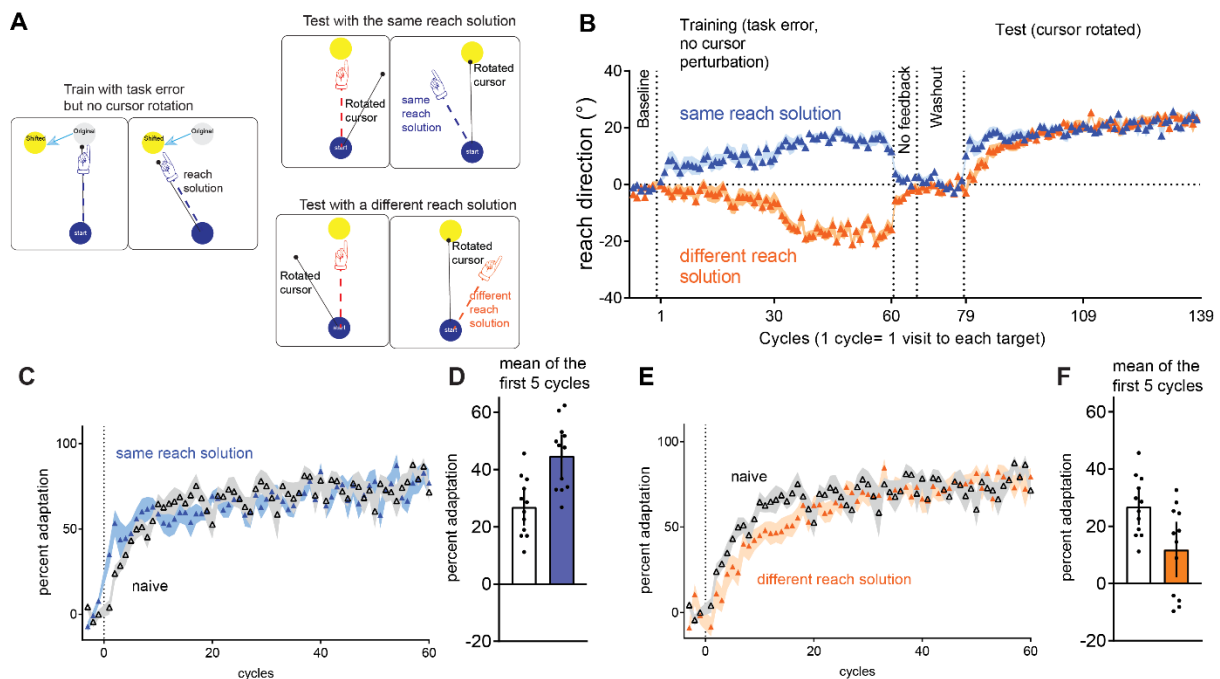
599   **Figure 4.** Experiment 4 replicates the design of Experiment 3, except that participants completed all
600   trials under short preparation time of 250ms (A). Cycle-averaged reach directions, where each circle
601   represents 1 cycle, or 1 visit to each target (B). Cycle-averaged percent adaptation during test (filled
602   triangles) compared to naïve (clear triangles) for the same reach solution (C) and the different reach
603   solution (E). Mean percent adaptation averaged over the first 5 cycles with the same solution (D) and
604   with a different solution (F). Savings was evident in more adapted reaches compared to naïve (clear
605   symbols) for the ShortSame group (C & D). For the ShortDifferent group, adaptation was worse than
606   naive (E & F). For D & F, error bars=95% CI. All other error bars are SEM.

607

608

Discussion

In this work, we demonstrate a fundamental role for task errors in savings for visuomotor rotation adaptation; a phenomenon that is a hallmark of latent sensorimotor memory. We show that savings was absent without prior experience of task errors (Experiments 1 & 2), and that prior correction of task errors, even without prior exposure to sensory prediction errors, is sufficient to elicit savings (Experiments 3 & 4). Thus, systematic task errors that prompt adaptive motor responses can affect subsequent adaptation to never-before encountered sensorimotor perturbations. The results reinforce the notion that adaptive responses to sensorimotor perturbations take multiple forms, and suggest that task errors play a primary role in driving improved performance upon exposure to novel sensorimotor conditions. In particular, we suggest that latent sensorimotor memories, which improve subsequent adaptation, rely on (at least) two distinct components, both of which are driven by the failure to attain movement goals. The first is a strategic component that is flexible enough to facilitate corrective responses in the opposite direction, but that requires substantial preparation time. The second component is a set of inflexible stimulus-response associations between targets and reach directions, that can be expressed under time-pressure.

A history of adaptation to task errors are necessary for savings

An influential model of sensorimotor adaptation suggests that a history of errors increases sensitivity to those errors, resulting in improved learning when familiar errors are re-encountered (Herzfeld et al., 2014). Sensorimotor perturbations typically evoke both sensory prediction errors and task errors, but it was previously unclear how these errors contribute to latent sensorimotor memories that improve learning (Leow et al., 2016; Orban de Xivry & Lefevre, 2015). Here we show that, at least in visuomotor rotation paradigms, a history of adaptation to task errors is crucial to encode latent memories that improve subsequent adaptation. Task errors that could not be corrected (i.e., enforced task errors that occurred regardless of the participants' behaviour) did not improve learning. Furthermore, Experiment 2 showed that task errors need not be present upon re-exposure to the perturbation, contradicting the proposal that task errors act as a retrieval cue to trigger savings (Huberdeau et al., 2015a).

Savings do not require a history of sensory prediction errors

The results of Experiments 1 and 2 are consistent with the idea that savings results from a memory that requires task errors for its encoding. What is the nature of this learning? One possibility is that task errors drive deliberate corrective responses during adaptation (McDougle et al., 2016), and that faster subsequent recognition and/ or selection of actions that correct task errors accounts for savings (Haith et al., 2015; Huberdeau et al., 2015a; Huberdeau et al., 2015b; Morehead et al., 2015). If this is true, then deliberate correction of task errors alone, even when naïve to sensory prediction errors, should be sufficient for savings. To the best of our knowledge, this question was not previously addressed (Haith et al., 2015; Huberdeau et al., 2017; Morehead et al., 2015; Orban de Xivry & Lefevre, 2015). We therefore tested this in Experiment 3, where a systematic task error was imposed at training (targets always jumped mid-movement by 30°) without any perturbation of hand position feedback. Training to correct for these task errors improved subsequent adaptation to the 30° rotation of hand position feedback compared to naïve participants, even though we did not provide any instruction to apply previous learning. Thus, learning to counteract task errors in the absence of a sensorimotor perturbation was enough to improve adaptation to a never-before encountered sensorimotor perturbation.

How might correction of task errors lead to savings?

Exactly what is encoded when task errors are corrected? In Experiment 3, we found that adaptive responses to task errors can be switched off upon instruction that the perturbation has been removed, but that this learning was still retained in latent form to affect subsequent adaptation when a similar context was encountered. This suggests that this form of sensorimotor learning is fundamentally distinct from the adaptive responses to sensory prediction errors, which are expressed in an obligatory manner for many trials after the perturbation is removed. The persistent and obligatory response to sensory prediction error is often conceived as remapping between a desired movement direction (i.e., a motor plan) and the motor commands that are generated to ~~achieve~~ execute the movement. We speculate that the contextually flexible adaptive response to task errors arises from an earlier component of the sensory to motor transformation: a mapping between the behavioural goal and the motor plan selected to achieve it. This would be consistent

674   with a non-obligatory expression of the learning, because we can choose to achieve

675   behavioural goals in many different ways.

676   Given that we can instruct participants to deliberately use re-aiming strategies

677   to reduce errors (Benson et al., 2011; Mazzoni et al., 2006; Savoie et al., 2018;

678   Schween et al., 2014; Taylor et al., 2011), it is possible that a history of deliberately

679   correcting for task errors (induced by target jumps) led to savings (under visuomotor

680   rotation conditions) by prompting acquisition of a re-aiming strategy. Indeed, one

681   view is that savings results solely from deliberate strategy use (Morehead et al.,

682   2015). This view is supported by findings of no savings when cognitive resources are

683   suppressed by shortening movement preparation time during visuomotor adaptation

684   (Haith et al., 2015). Time pressure presumably suppresses time-consuming mental

685   rotation processes required to re-aim at a planned angle away from the presented

686   target (Bhat & Sanes, 1998; Georgopoulos & Massey, 1987; Pellizzer &

687   Georgopoulos, 1993). In contrast, recent findings show savings despite time

688   pressure when participants were allowed repeated episodes of adaptation to

689   opposing visuomotor rotation perturbations (Huberdeau et al., 2017). How might one

690   reconcile these findings? We think that the savings shown in that study might result

691   from residual capacity to re-aim away from a target despite short latencies, as the

692   rotations were only applied to one of two possible targets. It is clear that when there

693   is a small target set size (i.e., a small predictable range of required movements, for

694   example when there were only two targets in McDougle et al. (2019), or when the

695   targets were distributed in a narrow, predictable range in Leow et al. (2017)), time-

696   pressure does not prevent people from aiming at a specified angle away from a

697   target. McDougle and Taylor (2019) showed that small set sizes promotes caching of

698   stimulus-response associations between targets and corresponding required

699   movements. When the required response was less predictable (i.e., with 8 or 12

700   targets randomly presented in a wide spatial array), time pressure resulted in

701   intermediate reaches that only partially compensated for the rotation—increasing

702   time-pressure corresponded with less complete compensation (Leow et al., 2017;

703   McDougle & Taylor, 2019), consistent with analog movement re-planning via mental

704   rotation.

705   What are the contributions of stimulus-response associations and mental

706   rotation to savings? We explored this in Experiment 4 by replicating Experiment 3,

707 but limiting preparation time. Given the 8-target array, the required response was

708 less predictable than in Huberdeau et al. (2017). At training, time pressure resulted

709 in incomplete compensation, as consistent with the results of Leow et al. (2017);

710 McDougle and Taylor (2019), implying a restriction in mental rotation. Despite this,

711 adaptation was better-than-naive when the reach solution at test was the same as at

712 training, and *worse* than naïve when the reach solutions were opposite at training

713 and test. We interpret the findings as follows. Task errors in visuomotor rotation

714 tasks typically provoke both mental rotation and stimulus-response associations.

715 Time-pressure suppresses mental rotation capacity, but might not prevent the

716 formation of stimulus-response associations between target errors and reach

717 solutions. We think such associations were formed in our Experiment 4, and that,

718 after washout, these latent stimulus-response associations were re-expressed when

719 confronted with a similar sensorimotor context (in this case, experiencing errors to

720 the side of targets). This learned association elicits savings when reach solutions for

721 each target are the same at training and test, and interference when the reach

722 solutions differ. This interference is particularly interesting, because it occurred

723 despite participants being obviously able to volitionally disengage recently learned

724 reach solutions in the preceding no-rotation trials with similar time demands.

725 Maladaptive retrieval of an inappropriate reach solution might thus be triggered by

726 task errors (which were absent in the preceding no-feedback, no-rotation trials), and

727 this pre-potent response to the trigger was poorly inhibited under time pressure. An

728 alternative interpretation is that practice of mentally rotating a target in one direction

729 at training makes it more difficult to mentally rotate the target in the opposite

730 direction under time-pressure at test, because prior mental rotation can interfere with

731 subsequent mental rotation in an opposite direction (Sack et al., 2007). An important

732 clue to identify which potential explanation is more likely comes from findings of

733 deficient savings (Bedard et al., 2011; Leow et al., 2013; Leow et al., 2012; Marinelli

734 et al., 2009) and anterograde interference in Parkinson's disease (Leow et al., 2013).

735 Here, the better performance of Parkinson's disease patients when adapting to a

736 rotation opposite to that previously experienced (Leow et al., 2013) seems unlikely to

737 result from superior mental rotation. Parsimony therefore suggests that the more

738 likely culprit is deficient acquisition of stimulus-response associations at initial

739 learning (Foerde et al., 2011; Shohamy et al., 2006; Vo et al., 2014). Our current

740   data therefore suggest that inflexible stimulus-response associations can contribute

741   to latent sensorimotor memories.

742   Athough we demonstrate a role for learning to correct task errors in improving

743   adaptation, we do not yet fully understand *how* task errors affect learning in typical

744   sensorimotor adaptation where task errors and sensory prediction errors co-occur.

745   Several possibilities exist. One possibility is that task errors might modulate the

746   sensitivity to sensory prediction errors, and this increased sensitivity might elicit a

747   gain in adaptation rate (Kim et al., 2019). There is some evidence to support this

748   hypothesis, as task errors can modulate the alteration of sensorimotor maps as a

749   result of exposure to sensory prediction errors (Kim et al., 2019; Leow et al., 2018;

750   Reichenthal et al., 2016; Schaefer et al., 2012; Welch, 1969). An alternative

751   possibility is that adaptation to task errors and adaptation to sensory prediction

752   occurs independently. More work is required to dissociate these possibilities.

753   We also do not yet understand the role of correcting task errors in adaptation

754   to different sensorimotor perturbations which are less likely to provoke easily

755   verbalizable strategies (e.g. force-field adaptation, split-belt treadmill adaptation) and

756   in paradigms that are less likely to be influenced by time-consuming deliberate

757   strategies, such as saccadic adaptation (Kojima et al., 2004). It is clear that volitional

758   strategies can influence adaptation in all of these paradigms (e.g., de'Sperati, 1999;

759   Hwang et al., 2006), but it is currently unclear to what extent strategies contribute to

760   improved re-adaptation in these paradigms. In split-belt treadmill adaptation for

761   example, people can strategically improve adaptation by visual feedback of their

762   perturbation-induced gait asymmetry, and yet fail to express this improvement upon

763   removal of visual feedback; thus failing to augment savings by explicit strategy use

764   (Leech et al., 2018). If and how stimulus-response associations might play a role in

765   these paradigms is even less clear. Another open question is if and how stimulus-

766   response associations are contextually dependent, as savings is clearly modulated

767   by context (Song et al., 2015; Yin et al., 2014). Furthermore, although we

768   demonstrate a role of stimulus-response associations in savings despite time-

769   pressure, we do not discount the possibility that extended training might improve

770   mental rotation skill to allow savings under time-pressure regardless of set size,

771   perturbation direction, or perturbation magnitude during adaptation to a visuomotor

772   rotation (Provost et al., 2013; Wright et al., 2008).

773 How does the brain form latent sensorimotor memories in response to task

774 errors? We speculate that task errors prompt the formation of a new motor plan,

775 which specifies the required parameters of the action required to achieve the desired

776 outcome under new conditions. Achieving a desired outcome (e.g., a cancellation of

777 task error) forms an association between the stimulus (e.g., a task error for a given

778 target) and the response (the modified movement plan needed to restore task

779 success). This association is readily retriggered by task errors. Learning to alter

780 movement plans, even without actually executing the motor plan, might play a crucial

781 role in sensorimotor adaptation (Sheahan et al., 2018; Vyas et al., 2018). For

782 example, monkeys who learn to move a cursor with a brain-machine interface (i.e.,

783 without moving their hands) show accelerated adaptation when first using their hand

784 to move a cursor (Vyas et al., 2018). Similarly, although people fail to concurrently

785 adapt to opposing perturbations, concurrent adaptation is possible when different

786 motor plans are tagged to opposing perturbations (Sheahan et al., 2018).

787 **Summary**

788 Our results show that failures to attain movement goals, or task errors, are a

789 fundamental driver of latent sensorimotor memories that improve adaptation to

790 sensorimotor perturbations. Flexible, strategic processes and inflexible cached

791 stimulus-response associations that arise in response to task errors both contribute

792 to savings in visuomotor adaptation. The data demonstrate the richness of

793 behavioural responses to sensorimotor perturbations, and suggest that some

794 principles regarding the adaptative responses to sensorimotor perturbations may be

795 more broadly applicable to alternative motor learning contexts than previously

796 recognised.

797 **References**

798 Anguera, J. A., Bernard, J. A., Jaeggi, S. M., Buschkuehl, M., Benson, B. L., Jennett, S., Humfleet, J.,
799   Reuter-Lorenz, P. A., Jonides, J., & Seidler, R. D. (2012). The effects of working memory
800   resource depletion and training on sensorimotor adaptation. *Behav Brain Res, 228*(1), 107-
801   115. doi:10.1016/j.bbr.2011.11.040
802 Avraham, G., Keizman, M., & Shmuelof, L. (2019). Environmental Consistency Modulation of Error
803   Sensitivity During Motor Adaptation is Explicitly Controlled. *BioRxiv*, 528752.
804   doi:10.1101/528752
805 Bedard, P., & Sanes, J. N. (2011). Basal ganglia-dependent processes in recalling learned visual-
806   motor adaptations. *Exp Brain Res, 209*(3), 385-393. doi:10.1007/s00221-011-2561-y
807 Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but
808   interferes with sensorimotor adaptation. *J Neurophysiol, 105*(6), 2843-2851.
809   doi:10.1152/jn.00002.2011
810 Bhat, R. B., & Sanes, J. N. (1998). Cognitive channels computing action distance and direction. *J

811   *Neurosci, 18*(18), 7566-7580.

812   Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature,*
813   *382*(6588), 252-255. doi:10.1038/382252a0

814   Braun, D. A., Aertsen, A., Wolpert, D. M., & Mehring, C. (2009). Motor task variation induces
815   structural learning. *Curr Biol, 19*(4), 352-357. doi:10.1016/j.cub.2009.01.036

816   Cassady, K., Ruitenberg, M., Koppelmans, V., Reuter-Lorenz, P., De Dios, Y., Gadd, N., Wood, S.,
817   Riascos Castenada, R., Kofman, I., Bloomberg, J., Mulavara, A., & Seidler, R. (2018). Neural
818   predictors of sensorimotor adaptation rate and savings. *Hum Brain Mapp, 39*(4), 1516-1531.
819   doi:10.1002/hbm.23924

820   Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for
821   visual-motor maps. *J Exp Psychol Hum Percept Perform, 15*(3), 493-506.

822   Day, K. A., Leech, K. A., Roemmich, R. T., & Bastian, A. J. (2018). Accelerating locomotor savings
823   in learning: compressing four training days to one. *J Neurophysiol, 119*(6), 2100-2113.
824   doi:10.1152/jn.00903.2017

825   de'Sperati, C. (1999). Saccades to mentally rotated targets. *Experimental Brain Research, 126*(4),
826   563-577. doi:DOI 10.1007/s002210050765

827   de Brouwer, A. J., Albaghdadi, M., Flanagan, R., & Gallivan, J. P. (2017). Gaze Behaviour During
828   Sensorimotor Adaptation Parcellates the Explicit and Implicit Contributions to Learning.
829   *BioRxiv*, 237651.

830   Delacre, M., Lakens, D., & Leys, C. (2017). Why Psychologists Should by Default Use Welch's t-test
831   Instead of Student's t-test. *International Review of Social Psychology, 30*(1).

832   Diedrichsen, J., Hashambhoy, Y., Rane, T., & Shadmehr, R. (2005). Neural correlates of reach errors.
833   *J Neurosci, 25*(43), 9919-9931. doi:10.1523/JNEUROSCI.1874-05.2005

834   Dietz, V., Zijlstra, W., & Duysens, J. (1994). Human neuronal interlimb coordination during split-belt
835   locomotion. *Exp Brain Res, 101*(3), 513-520.

836   Favilla, M., & De Cecco, E. (1996). Parallel direction and extent specification of planar reaching arm
837   movements in humans. *Neuropsychologia, 34*(6), 609-613.

838   Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction
839   time and reach errors during visuomotor adaptation. *Behav Brain Res, 219*(1), 8-14.
840   doi:10.1016/j.bbr.2010.11.060

841   Flook, J. P., & McGonigle, B. O. (1977). Serial adaptation to conflicting prismatic rearrangement
842   effects in monkey and man. *Perception, 6*(1), 15-29. doi:10.1068/p060015

843   Foerde, K., & Shohamy, D. (2011). The role of the basal ganglia in learning and memory: Insight
844   from Parkinson's disease. *Neurobiology of learning and memory, 96*(4), 624-636.
845   doi:10.1016/j.nlm.2011.08.006

846   Galea, J. M., Sami, S. A., Albert, N. B., & Miall, R. C. (2010). Secondary tasks impair adaptation to
847   step- and gradual-visual displacements. *Exp Brain Res, 202*(2), 473-484. doi:10.1007/s00221-
848   010-2158-x

849   Gallistel, C. R., Fairhurst, S., & Balsam, P. (2004). The learning curve: implications of a quantitative
850   analysis. *Proc Natl Acad Sci U S A, 101*(36), 13124-13131. doi:10.1073/pnas.0404965101

851   Georgopoulos, A. P., & Massey, J. T. (1987). Cognitive Spatial-Motor Processes .1. The Making of
852   Movements at Various Angles from a Stimulus Direction. *Experimental Brain Research,*
853   *65*(2), 361-370.

854   Gonzalez Castro, L. N., Hadjiosif, A. M., Hemphill, M. A., & Smith, M. A. (2014). Environmental
855   consistency determines the rate of motor adaptation. *Curr Biol, 24*(10), 1050-1061.
856   doi:10.1016/j.cub.2014.03.049

857   Hadjiosif, A., & Smith, M. (2013). *Savings is restricted to the temporally labile component of motor*
858   *adaptation.* Paper presented at the Translational and Computational Motor Control,
859   Washington DC.

860   Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The influence of movement preparation
861   time on the expression of visuomotor learning and savings. *J Neurosci, 35*(13), 5109-5117.
862   doi:10.1523/JNEUROSCI.3869-14.2015

863   Herzfeld, D. J., Vaswani, P. A., Marko, M. K., & Shadmehr, R. (2014). A memory of errors in
864   sensorimotor learning. *Science, 345*(6202), 1349-1353. doi:10.1126/science.1253138

865   Howard, I. S., Ingram, J. N., & Wolpert, D. M. (2009). A modular planar robotic manipulandum with

866   end-point torque control. *J Neurosci Methods, 181*(2), 199-211.
867   doi:10.1016/j.jneumeth.2009.05.005

868   Huang, V. S., Haith, A., Mazzoni, P., & Krakauer, J. W. (2011). Rethinking motor learning and
869   savings in adaptation paradigms: model-free memory for successful actions combines with
870   internal models. *Neuron, 70*(4), 787-801. doi:10.1016/j.neuron.2011.04.012

871   Huberdeau, D. M., Haith, A. M., & Krakauer, J. W. (2015a). Formation of a long-term memory for
872   visuomotor adaptation following only a few trials of practice. *J Neurophysiol, 114*(2), 969-
873   977. doi:10.1152/jn.00369.2015

874   Huberdeau, D. M., Krakauer, J. W., & Haith, A. M. (2015b). Dual-process decomposition in human
875   sensorimotor adaptation. *Curr Opin Neurobiol, 33*, 71-77. doi:10.1016/j.conb.2015.03.003

876   Huberdeau, D. M., Krakauer, J. W., & Haith, A. M. (2017). Practice induces a qualitative change in
877   the memory representation for visuomotor learning. *BioRxiv*, 226415.

878   Hwang, E. J., Smith, M. A., & Shadmehr, R. (2006). Dissociable effects of the implicit and explicit
879   memory systems on learning control of reaching. *Exp Brain Res, 173*(3), 425-437.
880   doi:10.1007/s00221-006-0391-0

881   Izawa, J., & Shadmehr, R. (2011). Learning from sensory and reward prediction errors during motor
882   adaptation. *PLoS Comput Biol, 7*(3), e1002012. doi:10.1371/journal.pcbi.1002012

883   Kim, H., Parvin, D., & Ivry, R. (2019). The influence of task outcome on implicit motor learning.
884   *BioRxiv*, 363606. doi:10.1101/363606

885   Kojima, Y., Iwamoto, Y., & Yoshida, K. (2004). Memory of learning facilitates saccadic adaptation in
886   the monkey. *J Neurosci, 24*(34), 7531-7539. doi:10.1523/JNEUROSCI.1741-04.2004

887   Krakauer, J. W., & Carmichael, S. T. (2017). *Broken Movement: The Neurobiology of Motor
888   Recovery After Stroke*: MIT Press.

889   Landi, S. M., Baguear, F., & Della-Maggiore, V. (2011). One Week of Motor Adaptation Induces
890   Structural Changes in Primary Motor Cortex That Predict Long-Term Memory One Year
891   Later. *Journal of Neuroscience, 31*(33), 11808-11813. doi:10.1523/Jneurosci.2253-11.2011

892   Leech, K. A., & Roemmich, R. T. (2018). Independent voluntary correction and savings in locomotor
893   learning. *J Exp Biol, 221*(Pt 15). doi:10.1242/jeb.181826

894   Leow, L.-A., De Rugy, A., Loftus, A. M., & Hammond, G. (2013). Different mechanisms
895   contributing to savings and anterograde interference are impaired in Parkinson's. *Frontiers in
896   Neuroscience*, 108.

897   Leow, L.-A., De Rugy, A., Marinovic, W., Riek, S., & Carroll, T. J. (2016). Savings for visuomotor
898   adaptation require prior history of error, not prior repetition of successful actions. *Journal of
899   Neurophysiology, 116*(4), 1603-1614.

900   Leow, L. A., Gunn, R., Marinovic, W., & Carroll, T. J. (2017). Estimating the implicit component of
901   visuomotor rotation learning by constraining movement preparation time. *J Neurophysiol,
902   118*(2), 666-676. doi:10.1152/jn.00834.2016

903   Leow, L. A., Loftus, A. M., & Hammond, G. R. (2012). Impaired savings despite intact initial
904   learning of motor adaptation in Parkinson's disease. *Exp Brain Res, 218*(2), 295-304.
905   doi:10.1007/s00221-012-3060-5

906   Leow, L. A., Marinovic, W., de Rugy, A., & Carroll, T. J. (2018). Task errors contribute to implicit
907   aftereffects in sensorimotor adaptation. *Eur J Neurosci, 48*(11), 3397-3409.
908   doi:10.1111/ejn.14213

909   Maeda, R. S., McGee, S. E., & Marigold, D. S. (2018). Long-term retention and reconsolidation of a
910   visuomotor memory. *Neurobiol Learn Mem, 155*, 313-321. doi:10.1016/j.nlm.2018.08.020

911   Malone, L. A., & Bastian, A. J. (2010). Thinking About Walking: Effects of Conscious Correction
912   Versus Distraction on Locomotor Adaptation. *Journal of Neurophysiology, 103*(4), 1954-
913   1962. doi:10.1152/jn.00832.2009

914   Marinelli, L., Crupi, D., Di Rocco, A., Bove, M., Eidelberg, D., Abbruzzese, G., & Ghilardi, M. F.
915   (2009). Learning and consolidation of visuo-motor adaptation in Parkinson's disease.
916   *Parkinsonism Relat Disord, 15*(1), 6-11. doi:10.1016/j.parkreldis.2008.02.012

917   Mawase, F., Shmuelof, L., Bar-Haim, S., & Karniel, A. (2014). Savings in locomotor adaptation
918   explained by changes in learning parameters following initial adaptation. *J Neurophysiol,
919   111*(7), 1444-1454. doi:10.1152/jn.00734.2013

920   Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during

921   visuomotor adaptation. *J Neurosci, 26*(14), 3642-3645. doi:10.1523/JNEUROSCI.5317-
922   05.2006
923   McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking Aim at the Cognitive Side of Learning in
924   Sensorimotor Adaptation Tasks. *Trends in cognitive sciences, 20*(7), 535-544.
925   doi:10.1016/j.tics.2016.05.002
926   McDougle, S. D., & Taylor, J. A. (2019). Dissociable cognitive strategies for sensorimotor learning.
927   *Nat Commun, 10*(1), 40. doi:10.1038/s41467-018-07941-0
928   Morehead, J. R., Qasim, S. E., Crossley, M. J., & Ivry, R. (2015). Savings upon Re-Aiming in
929   Visuomotor Adaptation. *J Neurosci, 35*(42), 14386-14396. doi:10.1523/JNEUROSCI.1046-
930   15.2015
931   Nikooyan, A. A., & Ahmed, A. A. (2015). Reward feedback accelerates motor learning. *J
932   Neurophysiol, 113*(2), 633-646. doi:10.1152/jn.00032.2014
933   Orban de Xivry, J. J., & Lefevre, P. (2015). Formation of model-free motor memories during motor
934   adaptation depends on perturbation schedule. *J Neurophysiol, 113*(7), 2733-2741.
935   doi:10.1152/jn.00673.2014
936   Palidis, D. J., Cashaback, J., & Gribble, P. J. b. (2018). Neural Signatures of Reward and Sensory
937   Prediction Error in Motor Learning. 262576.
938   Pellizzer, G., & Georgopoulos, A. P. (1993). Common processing constraints for visuomotor and
939   visual mental rotations. *Exp Brain Res, 93*(1), 165-172.
940   Provost, A., Johnson, B., Karayanidis, F., Brown, S. D., & Heathcote, A. (2013). Two routes to
941   expertise in mental rotation. *Cogn Sci, 37*(7), 1321-1342. doi:10.1111/cogs.12042
942   Reichenthal, M., Avraham, G., Karniel, A., & Shmuelof, L. (2016). Target size matters: target errors
943   contribute to the generalization of implicit visuomotor learning. *J Neurophysiol, 116*(2), 411-
944   424. doi:10.1152/jn.00830.2015
945   Reuter, E. M., Pearcey, G. E. P., & Carroll, T. J. (2018). Greater neural responses to trajectory errors
946   are associated with superior force field adaptation in older adults. *Exp Gerontol, 110*, 105-
947   117. doi:10.1016/j.exger.2018.05.020
948   Roemmich, R. T., & Bastian, A. J. (2015). Two ways to save a newly learned motor pattern. *J
949   Neurophysiol, 113*(10), 3519-3530. doi:10.1152/jn.00965.2014
950   Sack, A. T., Lindner, M., & Linden, D. E. J. (2007). Object- and direction-specific interference
951   between manual and mental rotation. *Perception & Psychophysics, 69*(8), 1435-1449. doi:Doi
952   10.3758/Bf03192958
953   Savoie, F. A., Thenault, F., Whittingstall, K., & Bernier, P. M. (2018). Visuomotor Prediction Errors
954   Modulate EEG Activity Over Parietal Cortex. *Sci Rep, 8*(1), 12513. doi:10.1038/s41598-018-
955   30609-0
956   Schaefer, S. Y., Shelly, I. L., & Thoroughman, K. A. (2012). Beside the point: motor adaptation
957   without feedback-based error correction in task-irrelevant conditions. *J Neurophysiol, 107*(4),
958   1247-1256. doi:10.1152/jn.00273.2011
959   Schouten, J. F., & Bekker, J. A. (1967). Reaction time and accuracy. *Acta Psychol (Amst), 27*, 143-
960   153. doi:http://dx.doi.org/10.1016/0001-6918(67)90054-6
961   Schween, R., Taube, W., Gollhofer, A., & Leukel, C. (2014). Online and post-trial feedback
962   differentially affect implicit adaptation to a visuomotor rotation. *Exp Brain Res, 232*(9), 3007-
963   3013. doi:10.1007/s00221-014-3992-z
964   Seidler, R. D., Gluskin, B. S., & Greeley, B. (2017). Right prefrontal cortex transcranial direct current
965   stimulation enhances multi-day savings in sensorimotor adaptation. *J Neurophysiol, 117*(1),
966   429-435. doi:10.1152/jn.00563.2016
967   Shadmehr, R., & Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during learning of
968   a motor task. *J Neurosci, 14*(5 Pt 2), 3208-3224.
969   Sheahan, H. R., Ingram, J. N., Zalalyte, G. M., & Wolpert, D. M. (2018). Imagery of movements
970   immediately following performance allows learning of motor skills that interfere. *Scientific
971   Reports, 8*, 299594. doi:ARTN 14330
972   10.1038/s41598-018-32606-9
973   Shohamy, D., Myers, C. E., Geghman, K. D., Sage, J., & Gluck, M. A. (2006). L-dopa impairs
974   learning, but spares generalization, in Parkinson's disease. *Neuropsychologia, 44*(5), 774-784.
975   doi:10.1016/j.neuropsychologia.2005.07.013

976   Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different
977   timescales underlie short-term motor learning. *PLoS Biol, 4*(6), e179.
978   doi:10.1371/journal.pbio.0040179
979   Song, J. H., & Bedard, P. (2015). Paradoxical benefits of dual-task contexts for visuomotor memory.
980   *Psychol Sci, 26*(2), 148-158. doi:10.1177/0956797614557868
981   Taylor, J. A., & Ivry, R. B. (2011). Flexible cognitive strategies during motor learning. *PLoS Comput
982   Biol, 7*(3), e1001096. doi:10.1371/journal.pcbi.1001096
983   Taylor, J. A., & Thoroughman, K. A. (2007). Divided attention impairs human motor adaptation but
984   not feedback control. *J Neurophysiol, 98*(1), 317-326. doi:10.1152/jn.01070.2006
985   Taylor, J. A., & Thoroughman, K. A. (2008). Motor adaptation scaled by the difficulty of a secondary
986   cognitive task. *PLOS One, 3*(6), e2485. doi:10.1371/journal.pone.0002485
987   Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2016). Effective reinforcement learning following
988   cerebellar damage requires a balance between exploration and motor noise. *Brain, 139*(Pt 1),
989   101-114. doi:10.1093/brain/awv329
990   Torrecillos, F., Albouy, P., Brochier, T., & Malfait, N. J. J. o. N. (2014). Does the processing of
991   sensory and reward-prediction errors involve common neural resources? Evidence from a
992   frontocentral negative potential modulated by movement execution errors. *34*(14), 4845-4856.
993   Uhlarik, J. J. (1973). Role of cognitive factors on adaptation to prismatic displacement. *J Exp Psychol,
994   98*(2), 223-232. doi:10.1037/h0034364
995   Vo, A., Hiebert, N. M., Seergobin, K. N., Solcz, S., Partridge, A., & MacDonald, P. A. J. F. i. h. n.
996   (2014). Dopaminergic medication impairs feedback-based stimulus-response learning but not
997   response selection in Parkinson's disease. *8*, 784.
998   von Helmholtz, H., & Southall, J. P. (1924). Helmholtz's treatise on physiological optics, Vol. 1,
999   Trans.
1000   Vyas, S., Even-Chen, N., Stavisky, S. D., Ryu, S. I., Nuyujukian, P., & Shenoy, K. V. (2018). Neural
1001   Population Dynamics Underlying Motor Learning Transfer. *Neuron, 97*(5), 1177-1186 e1173.
1002   doi:10.1016/j.neuron.2018.01.040
1003   Welch, R. B. (1969). Adaptation to prism-displaced vision: The importance of target-pointing.
1004   *Perception & Psychophysics, 5*(5), 305-309. doi:10.3758/bf03209569
1005   Wright, R., Thompson, W. L., Ganis, G., Newcombe, N. S., & Kosslyn, S. M. (2008). Training
1006   generalized spatial skills. *Psychon Bull Rev, 15*(4), 763-771.
1007   Yin, C., & Wei, K. (2014). Interference from mere thinking: mental rehearsal temporarily disrupts
1008   recall of motor memory. *J Neurophysiol, 112*(3), 594-602. doi:10.1152/jn.00070.2014
1009   Zarahn, E., Weston, G. D., Liang, J., Mazzoni, P., & Krakauer, J. W. (2008). Explaining savings for
1010   visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J
1011   Neurophysiol, 100*(5), 2537-2548. doi:10.1152/jn.90529.2008
1012