1   **Reaction times can reflect habits rather than computations**

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22   **ABSTRACT**

23

24   Reaction times (RTs) are assumed to reflect the underlying computations required for making

25   decisions and preparing actions. However, recent work has shown that movements can be

26   initiated earlier than typically expressed without affecting performance; hence, the RT may be

27   modulated by factors other than computation time. Consistent with that view, we demonstrated

28   that RTs are influenced by prior experience: when a previously performed task required a

29   specific RT to support task success, this biased the RTs in future tasks. This effect is similar to

30   the use-dependent biases observed for other movement parameters such as speed or direction.

31   Moreover, kinematic analyses revealed that these RT biases could occur without changing the

32   underlying computations required to perform the action. Thus the RT is not solely determined by

33   computational requirements but is an independent parameter that can be habitually set by prior

34   experience.

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36   **Impact Statement**

37   Although reaction times are often assumed to reflect the time required to select and prepare a

38   movement, they can be strongly influenced by prior experience.

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INTRODUCTION

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45   The reaction time (RT) is arguably the most widely used measure in neuroscience and

46   psychology for noninvasively assessing processing in the brain: it is assumed to reflect the time

47   needed to complete the perceptual and motor-planning computations required to prepare a

48   response (Donders, 1969, Sternberg, 1969, Friston et al., 1996, Spivey, 2007, Sanders, 1998).

49   This assumption appears justified by evidence that RTs are modulated by factors such as

50   stimulus complexity (Kaswan and Young, 1965, Hick, 1952, Ratcliff, 2002), stimulus-response

51   compatibility (Fitts and Seeger, 1953, Simon and Rudell, 1967, Simon and Wolf, 1963), number

52   of potential responses (Henry and Rogers, 1960, Fischman, 1984, Christina et al., 1982), or

53   required response accuracy (Fitts, 1954, Fitts, 1966, Reddi and Carpenter, 2000). As a

54   consequence of this assumption, any reduction in the RT should negatively affect the quality of

55   the resulting response. Indeed, instructing participants to respond as rapidly as possible leads to a

56   decrease in accuracy (Fitts, 1966), consistent with changes in accuracy that occur through more

57   direct manipulation of allowed preparation time (Schouten and Bekker, 1967, Ghez et al., 1997,

58   Stanford et al., 2010, Haith et al., 2016).

59   However, recent evidence shows that it is possible to reduce the RT to a large extent

60   before any decline in movement accuracy is observed. For example, when individuals are placed

61   under strict time constraints, movement accuracy and task success decline only after the RT is

62   shortened by ~80 ms (Haith et al., 2016). Similarly, startle by a loud acoustic stimulus can evoke

63   initiation of a fully prepared action ~70 ms earlier than typically observed (Valls-Sole et al.,

64   1999, Carlsen et al., 2004). These findings suggest that the RT includes some additional time that

65   is not required for computing the upcoming response, raising the possibility that other factors

66   might also influence the RT.

67   An additional clue that the RT does not strictly represent computation time comes from

68   evidence that the RT is influenced by context. This was illustrated, for example, in a recent study

69   examining the planning of intentionally curved reaches (Wong et al., 2016). In this study, the

70   RTs of simple point-to-point reaches were observed to be shorter than those of more complex

71   curved movements, consistent with the idea that RT reflects computation time. However, when

72   point-to-point movements were interleaved among curved reaches, the RTs of those point-to-

73   point reaches were surprisingly prolonged by ~90 ms, matching the RTs of the curved reaches. A

74   similar contextual effect has been observed during mental rotation: during a letter discrimination

75   task, identifying letters that are presented upright occurs at much shorter RTs when all the letters

76   are upright compared to when other letters in the same block of trials are rotated (Ilan and Miller,

77   1994). These data suggest that RTs might be subject to experience-dependent biases – akin to

78   other movement parameters such as speed or direction (Diedrichsen et al., 2010, Verstynen and

79   Sabes, 2011, Hammerbeck et al., 2014, Huang et al., 2011) – rather than arising strictly from the

80   outcome of computational requirements. That is, RTs may be subject to habit in the sense that an

81   RT of a given magnitude may become more likely to be generated in the future simply because it

82   has been generated in the past, regardless of current task requirements.

83   Here we present results from two experiments which demonstrate that the RT is subject

84   to experience-dependent effects. In the first experiment – a target-interception task – we showed

85   that experience with initiating reaches at a short or long RT exerts a corresponding bias on the

86   RTs of subsequently performed point-to-point reaches.

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87   In a second experiment, we demonstrated that these RT biases can also occur for more

88   complex curved reaches around barriers. This task can be performed with or without the

89   presence of a direct cue illustrating the appropriate trajectory, corresponding to greater or lower

90   computational requirements respectively (Wong et al., 2016). We found that participants' RTs in

91   the cued condition depended strongly on whether or not they had previously experienced the

92   uncued condition. Analysis of the kinematics of these curved reaches allowed us to determine

93   that the observed experience-dependent changes in RT were not due to habitually ignoring the

94   cue and planning the movements in a different manner, but instead to habitually adopting a

95   longer RT despite using a more rapid computation (i.e., taking advantage of the cue) to solve the

96   task. Together, these two experiments reveal that the RT does not strictly reflect the time needed

97   to complete the computations required for preparing responses, but may instead be selected

98   habitually according to prior experience.

99

100   **RESULTS**

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102   **Experiment 1: RTs were biased to be longer or shorter according to performance in a**

103   **previous task**

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105   In Experiment 1, we tested whether performance of a task that encouraged movements to

106   be generated with particular RTs could affect the RTs of subsequent movements performed in a

107   different context. We asked participants to perform an interception task to hit a target that moved

108   in a straight line toward or away from the participant (Fig. 1A). For one group of 10 participants,

109   the target always moved outward, encouraging participants to initiate reaches at shorter RTs to

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110   intercept the target before it moved beyond an invisible boundary and disappeared (see

111   Methods). For a second group of 10 participants, the target always moved inward. This

112   encouraged participants to increase their RTs, since they could reduce the effort required to

113   complete this task by waiting for the target to move closer before reaching out to hit it. In both

114   cases, participants were given no specific RT instruction. Additionally, because participants were

115   not required to stop inside the target on interception trials, participants typically generated

116   shooting movements through the target. Immediately before and after participants performed this

117   interception task, we measured their RTs for simple point-to-point reaches (wherein the hand had

118   to stop inside the target and move at a constrained speed) to assess any experience-related

119   changes in RT.

120   At baseline, participants in both groups generated point-to-point reaches with comparable

121   RTs (Table 1; no significant difference between groups: $t = -0.22$, $p = 0.82$), and were able to

122   satisfy the requested speed requirements (see Table 1 and Methods).

123   Movement of the target, either toward or away from the participant's starting position,

124   exerted a reliable influence on behavior during performance of the interception task. When the

125   target moved outward (Fig. 1B; Figure 1 source data – Outward; Table 1), participants increased

126   their movement speed (paired t-test comparing pre-training to the last training block, $t(9) = 6.30$,

127   $p < 0.001$) and decreased their RT (paired t-test comparing pre-training to the last training block,

128   $t(9) = 2.99$, $p = 0.02$) relative to their behavior on baseline point-to-point reaches. These

129   reductions in RT persisted in the final phase of the experiment when the target was again

130   stationary: RTs during the post-training point-to-point reaching block were shorter than in the

131   analogous pre-training block by 21.68 ± 6.32 ms (Fig. 1C; paired t-test comparing post to pre,

132   $t(9) = -3.43$, $p = 0.02$). This change in RT from pre-training to post-training was on average

133 76.6% of the total reduction in RT associated with the outward-interception task (i.e., pre-

134 training compared to the last outward-interception training block). Importantly, these changes in

135 RT for point-to-point movements occurred with no significant change in either peak velocity

136 (paired t-test comparing post to pre, $t(9) = 0.98$, $p = 0.70$) or endpoint error (paired t-test

137 comparing post to pre, $t(9) = 0.95$, $p = 0.70$). Thus, repeatedly generating movements at low RTs

138 led to a reduction of the RT on subsequent point-to-point reaches with no detectable decrement

139 in performance.

140   Interception of an inward-moving target exerted the opposite effect on behavior (Fig

141 1D,E; Figure 1 source data – Inward; Table 1). Relative to baseline point-to-point movements,

142 training on the inward-interception task led to a decrease of movement speed (paired t-test

143 comparing pre-training to the last training block, $t(9) = -6.82$, $p < 0.001$) and an increase in RT

144 (paired t-test comparing pre-training to the last training block, $t(9) = 2.45$, $p = 0.04$). RTs during

145 a subsequent block of point-to-point reaches increased on average by 12.87 ± 4.94 ms relative to

146 baseline, although this change was not significant (paired t-test comparing post to pre, $t(9) =$

147 2.60, $p = 0.09$) and corresponded to only 9.69% of the increase in RT observed during the

148 interception task. There was also a trend for the velocity of these reaches to increase although

149 this also was not significant (paired t-test comparing post to pre, $t(9) = 2.07$, $p = 0.14$) and there

150 was no clear change in endpoint error (paired t-test comparing post to pre, $t(9) = -0.56$, $p = 0.59$).

151   A mixed-effects model comparing the change in point-to-point RTs across the two groups

152 revealed a significant interaction (likelihood ratio test; $\chi^2(1) = 77.55$, $p < 0.001$) between the

153 direction of target motion during training (outward or inward) and the change in RT from pre-

154 training to post-training blocks (Fig. 1F). This interaction was driven by a difference in RT only

155 during the post-training block (post-hoc test, $p = 0.03$), since RTs during the pre-training block

156   were comparable. Together, these data reveal that the RT can be biased in an experience-

157   dependent manner, suggesting that the RT does not strictly reflect obligate computation time.

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159   **Experiment 2: RT biases occurred despite task-dependent changes in movement planning**

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161   To further explore the experience-dependent bias in RT, we examined this effect in a

162   more complex task that required participants to plan curved reaches around barriers. This task

163   can be performed in one of two ways: either in the absence or presence of cues that illustrate a

164   specific path around the barriers (Fig. 2A). Although the movements required to complete the

165   task are identical in both cases, the presence of a path cue has been observed to provide a

166   significant RT advantage (Wong et al., 2016). This advantage is thought to reflect a difference in

167   computational requirements between the cued and uncued conditions, with the latter condition

168   requiring an additional trajectory-planning stage to represent the path shape to be executed.

169   Hence, this task provides an assay of habitual effects on RT between two sets of movements that

170   have different planning requirements but the same execution requirements.

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172   <u>Experience-dependent RT biases were observed for curved reaches around barriers</u>

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174   In Experiment 2A, two groups of 12 participants were asked to generate reaches around

175   barriers in the presence or absence of path cues. Comparable to previous findings (Wong et al.,

176   2016), we observed that participants provided with a path cue exhibited a large RT advantage of

177   52.94 ms compared to individuals performing the task without the path cue (initial cueing

178   condition experienced by each group; uncued: 349.76 ± 8.81 ms; cued: 296.82 ± 7.68 ms; main

179   effect of condition, $\chi^2(1) = 500.61$, $p < 0.001$; Fig. 2C; Figure 2 source data). Although the RT

180   difference is smaller than observed previously (Wong et al., 2016), this is likely attributable to

181   the fact that there were fewer possible barrier configurations presented in the current task

182   compared to the previous version, i.e. consistent with Hick's law (Hick, 1952).

183   Each group was then exposed to a block of trials with the opposite cue condition (Fig.

184   2B); that is, participants who first performed cued trials were next asked to perform the task

185   without path cues, and vice versa. This switch revealed a similar experience-dependent effect as

186   in Experiment 1. Specifically, whereas there was an RT advantage associated with the

187   availability of a cue during the initial training block, when the conditions were switched the two

188   groups exhibited similar RTs regardless of the presence or absence of the cue (cueing condition

189   during the second block: uncued: 334.75 ± 8.17 ms, cued: 336.74 ± 8.01; $\chi^2(1) = 0.035$, $p = 0.85$;

190   Fig. 2C). This experience-dependent effect of path cues on the RT was confirmed by a

191   significant main effect of the order in which the cued and uncued conditions were experienced

192   ($\chi^2(1) = 11.55$, $p < 0.001$), as well as a significant interaction between condition and order ($\chi^2(1)$

193    $= 105.42$, $p < 0.001$). This effect could not be attributed to changes in the RTs of uncued trials

194   performed first compared to second ($p = 0.25$); instead, this interaction arose because RTs were

195   significantly longer on cued trials when participants had previously performed a block of uncued

196   trials ($p < 0.001$). Hence participants actually exhibited longer RTs on less computationally

197   demanding cued trials if they experienced this condition second, even though they had far more

198   experience performing a more challenging version of the task.

199   Interestingly, in Experiment 2A the RTs in the cued blocks (but not the uncued blocks)

200   exhibited a slow asymptotic decline across trials (Fig. 2D). The rate of decline was not different

201   between the two groups (non-significant interaction between group and trial, $t = -1.46$, $p = 0.14$).

202   Power-law fits to the time series of latencies yielded similar exponents for both groups (cued

203   trials experienced first: -0.025; cued trials experienced second: -0.029). This decline suggests

204   that both groups were responding to the appearance of the path cues in a similar manner, perhaps

205   by learning to take advantage of the cues when planning their movements (see the section

206   below). Nevertheless, a constant RT offset remained across the entire block, reflecting a strong,

207   persistent RT bias for the group that had prior experience with the uncued condition ($t = 8.56$, p

208   < 0.001). Hence, even in this more complex task of generating reaches around barriers, RTs

209   could be biased by prior experience.

210   In contrast to RT, task success in hitting the target while avoiding the barriers did not

211   significantly vary with cueing condition or condition order (no effect of condition, $\chi^2(1) = 2.26$, p

212    $= 0.13$; no effect of order, $\chi^2(1) = 2.50$, $p = 0.11$; non-significant interaction, $\chi^2(1) = 1.63$, $p =$

213   0.20). That is, participants who were exposed to the uncued condition first did not become much

214   more successful when they switched to the simpler, cued version of the task (uncued block:

215   81.97% ± 2.56% successful; cued block: 85.81% ± 1.62% successful; posthoc test, $p = 0.14$); nor

216   did participants who were first exposed to the cued condition become less successful when

217   switched to the more difficult uncued task (cued block: 88.41% ± 1.66% successful; cued block:

218   88.02% ± 2.73% successful; posthoc test, $p = 1.00$). Note that in all cases participants could have

219   further improved their task success. Thus while participants who initially performed the uncued

220   condition exhibited prolonged RTs in the subsequent cued condition, this RT increase did not

221   confer any performance advantage (as measured by task success) as might be expected by a

222   speed-accuracy trade-off (Fitts, 1966).

223   We observed that only the RTs of cued trials were biased by having previously performed

224   uncued trials, but no such bias was observed when performing these conditions in the opposite

225 order. Hence we wondered to what extent prior history influences this bias. Specifically, we

226 asked whether participants who had prior experience performing cued trials at low RT would still

227 exhibit an increase in cued RTs after completing an intervening block of uncued trials, or would

228 they instead always express low RTs on cued trials once they had learned to perform them at low

229 RTs. A separate group of 12 participants (Experiment 2B; Fig. 3; Figure 3 source data) were

230 therefore asked to complete three blocks of trials: cued, uncued, and a second block of cued.

231 Note, the cued blocks in this experiment have an analogous role to the pre-training and post-

232 training assessment blocks of point-to-point reaches in Experiment 1.

233   Participants in Experiment 2B initially generated cued reaches at low RTs (pre-exposure

234 cued block: 349.81 ± 36.03 ms); however, experience with performing a block of uncued trials

235 (uncued-block RT: 390.26 ± 66.37 ms) led to prolonged RTs in the second cued block (post-

236 exposure cued block: 375.09 ± 41.38 ms; effect of block, $\chi^2(2) = 532.46$, $p < 0.001$; significant

237 differences between all pairs of blocks, $p < 0.001$; Fig. 3). This increase in RT from the pre-

238 exposure to the post-exposure cued blocks reflected an average RT bias of 80.98% of the change

239 in the RT from the initial cued to the uncued block (average change could not be calculated for

240 one participant because that individual exhibited no change between the initial cued block and

241 the uncued block). Thus, RT is strongly biased by prior exposure to the uncued condition in this

242 task, even if participants had previously completed the cued task at low RT.

243

244 <u>Path cues consistently influenced how movements were planned, independent of prior experience</u>

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246   Returning to Experiment 2A, we next asked what was the source of the RT bias. One

247 possibility is that participants might simply have adopted a habitually long RT regardless of the

248   underlying computational demands of the current trial. Alternatively, participants that had

249   initially been exposed to uncued trials might have ignored the cues when they became available

250   and instead continued to plan the movement trajectories *de novo* – a more computationally

251   demanding means of planning that requires prolonged RTs (Wong et al., 2016). To distinguish

252   between these possibilities, we examined the kinematics of movements made with and without

253   path cues, to find evidence of qualitatively different modes of movement planning. Specifically,

254   we reasoned that the trajectories of movements planned using the cue should more closely

255   resemble the path cues than movements planned de novo, regardless of the RTs at which these

256   movements were initiated.

257   We found that the presence of path cues significantly influenced movement kinematics in

258   a consistent manner across participants: the shapes of the average trajectories for the cued and

259   uncued conditions (pairs of blue and green lines in Fig. 4A) were observed to be significantly

260   different for at least one point along the length of the trajectory in 70% of all the target-barrier

261   configurations performed (Fig. 4A, significant differences between trajectory pairs along the

262   movement are denoted by yellow dots). For those trajectories where differences were observed,

263   on average 21% of the movement was found to be significantly different depending on the

264   condition. These differences often occurred near the start of the movement, wherein the hand

265   passed closer to the starting barrier on cued trials. However, there was no significant effect of the

266   order in which the conditions were performed; moreover, no kinematic differences were noted

267   when comparing reaches performed in the same cueing condition (i.e., between cued trials

268   experienced first or second, or between uncued trials experienced first or second). Thus cued

269   reaches were always executed in a similar fashion regardless of whether participants had prior

270   experience with the uncued condition.

271   In fact, a Procrustes shape-comparison analysis (Goodall, 1991; Fig. 4B; Figure 4 source

272   data – Procrustes Distance) revealed that reaches significantly resembled the path cue more

273   closely when it was available (effect of condition: -0.13, 95% confidence interval: [-0.19, -0.08],

274   Bayes factor = 0). In contrast, there was no significant effect of order on trajectory shape (effect

275   of order: -0.04 [-0.1, 0.02], Bayes factor = 14.24), even when comparing only cued trials (effect

276   of order: 0.04 [-0.02, 0.09], Bayes factor = 13.63). Together, these data suggest that participants

277   used the path cue to simplify planning their movements whenever it was available (Wong et al.,

278   2016); that is, participants were changing how they planned their movements in response to the

279   cue, which resulted in quantitative changes in the kinematics of their actions such that

280   movements more closely resembled the cued paths. Similar effects were observed in Experiment

281   2B (Source data for Experiment 2B kinematics analysis); in fact, the kinematics in the second

282   cued block resembled the path cues more closely than even those of the initial cued block (effect

283   of block: -0.04, 95% confidence intervals [-0.07, -0.02], Bayes factor = 0.39) – a finding that

284   would be expected to reduce RTs as participants took advantage of the cue, not prolong them

285   (e.g., consistent with Experiment 2A). Hence despite evidence suggesting that reaches were

286   planned in an experience-independent manner according to whether a cue was present only on

287   the current trial (in particular by relying on the cue to plan the action), RTs did not consistently

288   reflect the computational benefit afforded by the path cue. Instead, RTs exhibited an experience-

289   dependent bias that was unrelated to how these reaches were being planned and executed.

290

291   **DISCUSSION**

292

293   Although the RT is typically assumed to directly reflect the computation time required to

294   plan a movement (Donders, 1969, Sternberg, 1969, Friston et al., 1996, Spivey, 2007, Sanders,

295   1998), we demonstrated here that the RT may instead be influenced by previous experience. This

296   was not simply a practice effect leading to more efficient planning of the same action; RT was

297   influenced by recently generated RTs in the past even when those RTs were produced during

298   another task with a different type of movement (e.g., in Experiment 1 the RTs of shooting

299   movements to intercept a target biased the RTs of subsequent point-to-point reaches to stationary

300   targets). This effect, while small, is comparable in magnitude to the RT changes previously

301   observed in response to the addition of a delay period between the stimulus and go cues

302   (Churchland et al., 2006), or to changes in stimulus or response complexity (Fitts, 1954, Fitts,

303   1966, Hick, 1952, Simon, 1967, Henry and Rogers, 1960, for review, see Teichner and Krebs,

304   1974). Moreover, we showed that RTs can be modulated to be either shorter or longer than

305   previously expressed depending on the nature of the interposed task, and that these effects

306   persisted across a large number of subsequent trials. Thus in general, the RT expressed on any

307   given trial may be lengthened or shortened (by 20-30 ms) strictly due to prior experience, with

308   no measurable impact on performance.

309

310   **Changes in motivation cannot explain RT biases**

311

312   Experiment 1 provides clear evidence that the RT can be modulated in an experience-

313   dependent manner as if by a habit, and that such biases persist over a long period of time.

314   However, this paradigm was unable to ascertain whether these RT biases arose because of

315   changes in the rate of computational processing, or because of manipulations on the non-

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316   computational portion of the RT. In the former case, changing the duration of computational

317   processes could increase task success, particularly when shortening the RT in the outward-

318   interception task. Thus there was a motivational incentive that could drive changes in the speed-

319   accuracy trade-off in favor of shortened RTs while maintaining consistent accuracy (e.g.,

320   motivation could have driven an increase in the rate at which evidence accumulated in a drift-

321   diffusion model of RT (Ratcliff, 1978)), much in the same way that reward can reduce RT

322   without affecting accuracy (Takikawa et al., 2002, Hubner and Schlosser, 2010, Stanford et al.,

323   2010, Manohar et al., 2015). This modified speed-accuracy trade-off may then have been

324   retained when planning subsequent point-to-point movements. Alternatively, if RT biases simply

325   reflect modulation of the non-computational portion of the RT, the manner in which movements

326   are planned should remain unchanged.

327   Two pieces of evidence from Experiment 1 speak against the hypothesis that the

328   observed changes in RT occurred through a motivational effect. First, the RT bias persisted

329   across a large number of trials (e.g., the entire next block) with no obvious decay toward the

330   initially expressed RT. This persistence stands in contrast to the short-lived effects of motivation,

331   which appear to decay after only a few subsequent trials (Takikawa et al., 2002, Xu-Wilson et

332   al., 2009, Wong et al., 2015). Second, the effect of motivation typically influences not just the

333   RT, but also movement speed and accuracy; in general, these three parameters have often been

334   observed to modulate together in response to motivation (Takikawa et al., 2002, Wong et al.,

335   2015). However, we observed no obvious changes in other movement kinematics such as

336   movement speed or accuracy that accompanied the RT biases. On the other hand, speed and

337   accuracy were constrained by task requirements during the point-to-point movement blocks.

338 Nevertheless, these data suggest that motivation alone cannot account for the long-lasting RT

339 biases observed in Experiment 1.

340

341 **Habitual initiation rather than habitual planning**

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343   The kinematically more complex trajectories required in Experiment 2 provided us with

344 greater sensitivity to examine whether RT biases arose from effects on the computational or the

345 non-computational portion of the RT. That is, we were better able to detect any execution-related

346 differences that may have arisen from subtle changes in movement planning that were associated

347 with changes in RT.

348   During Experiment 2, participants in the cued condition could have initiated their

349 movements at short RTs; however, they exhibited persistently prolonged RTs when previously

350 exposed to the more computationally demanding uncued condition. Such a bias in RT could have

351 occurred for one of two reasons. Participants may have persisted in planning trajectories in the

352 same manner as they had done without path cues, despite the availability of the path cue that

353 would eliminate the need for this planning stage (*habitual planning*). Alternatively, participants

354 may have used the path cue to reduce the computational load for planning but simply did not

355 express their prepared actions earlier; that is, perhaps the RT does not strictly reflect computation

356 time, but instead contains a manipulable, non-computational component that may be subject to

357 habit (*habitual initiation*).

358   The analysis of movement kinematics allowed us to distinguish between these two

359 alternatives. In particular, we demonstrated that movement kinematics changed in a consistent

360 manner in the presence or absence of the path cues respectively, arguing that differences in

361   movement kinematics do reflect changes in how these actions were being planned. However, we

362   observed no effect of condition order on trajectory kinematics (i.e., reach kinematics were

363   always influenced similarly by the path cues when they were available, regardless of whether

364   participants had prior experience with uncued trials), suggesting that participants did not ever

365   exhibit habitual cue-free preparation of the movement trajectory when generating reaches in the

366   presence of a cue. This is particularly evident in Experiment 2B, when movement kinematics

367   indicate a particularly strong reliance on the cue to plan the action in the second cued block even

368   though the RT did not reflect such changes in movement planning. Moreover, reaches in the

369   uncued and cued conditions were confined to different portions of the workspace, making it

370   unlikely that participants habitually applied the identical motor plans from previously-performed

371   uncued reaches. These findings stand in contrast to the RT, which did not consistently modulate

372   according to the presence or absence of the path cue, but was instead experience-dependent.

373   Hence these data suggest that unlike motor planning – which is determined by the current task at

374   hand – movement onset may be influenced in a use-dependent manner consistent with the idea of

375   habitual initiation, and therefore may not represent the actual time required to prepare a

376   movement.

377   If the RT can be habitual, this implies that the time of movement initiation is not simply

378   the end result of computational processing but may actually be represented as a separate

379   movement parameter during the pre-movement period, analogous to movement speed. Indeed,

380   previous work (Haith et al., 2016, Brown and Robbins, 1991) has suggested that movement

381   initiation may be independent of movement planning. Such a distinction between planning and

382   initiation is consistent with recent data suggesting that an initiation signature can be observed in

383   motor cortex preceding movement onset in a manner that is independent of the specific action

384   being prepared (Kaufman et al., 2016). Our finding that movement initiation can be determined

385   by prior experience, rather than the time when planning has completed, further supports this

386   view.

387   Selection of RT based on prior experience rather than computation time implies that it

388   should be possible to choose a RT that is too short to allow for all planning processes to be

389   completed prior to movement initiation. Consistent with this idea, there indeed appear to be

390   situations in which the RT is spontaneously chosen to be improperly short (Orban de Xivry et al.,

391   2017, Haith et al., 2016). In such cases, however, online corrections and refinements that occur

392   after movement initiation help ensure a successful movement outcome (Orban de Xivry et al.,

393   2017, Kohen et al., 2017, Wong and Haith, 2017). Hence, in the event that the RT is biased to be

394   shorter than the time required to complete all necessary decision-making and planning-related

395   computations, the motor system has online correction mechanisms in place to maintain overall

396   task success.

397

398   **A common feature of movement parameters is that they are subject to experience-**

399   **dependent biases**

400

401   Experience-dependent biases have been previously demonstrated for movement

402   parameters such as speed or direction. For example, repetition of movements at a particular

403   speed or toward a particular direction of the workspace strongly influences the kinematics of

404   subsequently performed reaches (Diedrichsen et al., 2010, Verstynen and Sabes, 2011,

405   Hammerbeck et al., 2014, Huang et al., 2011). Repetition has also been shown to influence the

406   direction of movement invoked by transcranial magnetic stimulation (Classen et al., 1998). In

407   these cases, however, the influence of prior experience on movement biases appears for the most

408   part to be short-lived, unlike the long-lasting effects seen here in the RT.

409   Why experience-dependent biases occur is still unclear. It has previously been proposed

410   that such biases may simply be a result of Hebbian learning (Butefisch et al., 2000, Butefisch et

411   al., 2004); repetition of the same action presumably strengthens the neural circuits that give rise

412   to that movement, making it more likely to be invoked in the future. From a theoretical

413   standpoint, experience-dependent biases have been framed in the context of a normative

414   Bayesian model in which repetition leads to the construction of a strong prior that influences the

415   preparation of future responses (Verstynen and Sabes, 2011). Regardless of whether one uses a

416   mechanistic or computational framework, however, explanations for experience-dependent

417   biases rely on the assumption that the parameter in question – e.g., speed or direction – is

418   represented as a movement parameter that can be specified prior to movement. Therefore,

419   experience-dependent biases on the RT imply that the RT is not simply the passive consequence

420   of the time required to complete computational processing, but may instead be represented as a

421   separate movement parameter that can be subject to habit.

422

423   **Conclusions**

424

425   In summary, these data support the hypothesis that the RT should be considered a distinct

426   parameter that is selected during the pre-movement period; that is, the RT (i.e., initiation) may in

427   part reflect, but is not strictly dependent upon, underlying computational processes. Thus,

428   caution must be taken when interpreting differences in RT as indicative of the existence of

429   computational stages with smaller or larger processing demands. Such RT differences may

430   simply reflect carryover from RTs recently exhibited in the past (i.e., habit), regardless of

431   computational demands.

432

MATERIALS AND METHODS

Fifty-six right-handed, adult (average age, 23.27 years old; 26 males) neurologically healthy participants were recruited for this study. Twenty individuals participated in Experiment 1 (10 individuals in each group); 24 individuals participated in Experiment 2A (12 individuals per group), and 12 individuals participated in Experiment 2B. Group sizes were chosen based on findings from previous studies (Wong et al., 2016). All participants provided written informed consent and were naive to the purposes of the study. Experimental methods were approved by the Johns Hopkins University School of Medicine institutional review board.

Participants made planar reaching movements with their right arm along the surface of a glass table. Their wrist was restrained in a wrist splint, and supported by pressurized air jets to allow frictionless movement of the elbow and shoulder. Vision of the arm was obscured by a mirror through which participants observed an LCD monitor (60 Hz), which displayed targets and a cursor representing the position of the index finger in a veridical horizontal plane. Movement of the index finger was tracked using a Flock of Birds magnetic tracking system (Ascension Technology, VT, USA) at 130 Hz.

Experimental Paradigms

Experiment 1: Interception Task

Targets appeared at any of 4 possible positions uniformly spaced every 90° along a circle from the start position. After a brief delay of 100 ms, the target immediately began moving, and

456   the participant was required to intercept the target before it vanished. In the outward-interception

457   task, the target appeared 4 cm from the start position and moved outward until it was either

458   intercepted or it reached 26 cm away from the start position, at which point it disappeared.

459   Blocks consisted of 60 reaches (15 to each of the 4 target directions presented in a pseudo-

460   randomized order); the target moved at a speed of 0.15 m/s in the first block, 0.225 m/s in the

461   second block, and 0.3 m/s for the remaining 4 blocks. In the inward-interception task, the target

462   appeared 24 cm away from the subject and began moving inward at a velocity of 0.12 m/s during

463   each of the 5 blocks of 60 trials until it was intercepted or it reached the starting position.

464   Participants had only 1 attempt to hit the target; the trial ended when the hand stopped moving

465   (velocity < 0.05 m/s) or the hand exceeded the current target radius from the starting position.

466   Prior to and following these interception blocks, participants completed 60-trial blocks in

467   which they were required to make point-to-point reaching movements to stationary targets

468   located 15 cm away from the start position, uniformly spaced every 90°. Participants were also

469   encouraged to satisfy a velocity criterion on each trial (between 0.6 and 0.9 m/s for the outward

470   interception task, or between 0.5 and 0.8 m/s for the inward interception task), although no trials

471   were excluded from analysis based on movement velocity. These differences in velocity criterion

472   were deliberately chosen to encourage reaches at speeds that were comparable to those made

473   during the interception training. Encouraged adherence to a velocity criterion simply allowed for

474   an assay of changes in RT due to training on the interception task independently of any potential

475   changes in movement speed. For both the pre- and post-training blocks, the first 10 trials were

476   discarded from analysis to ensure that block averages for each participant reflected steady-state

477   behavior.

478

479   <u>Experiment 2: Barrier Task</u>

480

481   Experimental methods were similar to a barrier-avoidance task reported previously

482   (Wong et al., 2016) in which participants were required to generate a reaching movement toward

483   a target while avoiding barriers that appeared around both the start position and the goal target.

484   Targets appeared at any of eight positions uniformly spaced every 45° along a circle of radius 12

485   cm; barriers consisted of three-sided boxes that could be oriented at any of eight angles (rotated

486   in 45° increments). Participants initiated a trial by moving their hand into a central start target;

487   after a random delay (600-1600 ms), the goal target and two barriers appeared (one around the

488   start position and one around the goal target). Participants were instructed to begin their

489   movement as soon as possible, and to reach toward the goal target while avoiding the barriers.

490   As soon as participants initiated their reach, all visual information except the start target and the

491   hand cursor disappeared. Participants stopped moving when they thought they reached the target

492   location; upon conclusion of the movement they received visual feedback about their movement

493   trajectory. In Experiment 2A, participants completed two blocks of 128 trials; in Experiment 2B,

494   participants additionally completed a third block of 128 trials.

495   During one of the two blocks (or for Experiment 2B, the first and third blocks),

496   participants were given a path cue in the form of a line drawn between the start and goal targets

497   that navigated around the barriers. Additionally, in each block targets were confined to either the

498   upper left or the lower right half of the screen such that all movements for a given block were

499   confined to specific portions of the workspace. The direction of targets was different in the first

500   and second block; thus, participants never performed the identical movements with and without a

501   path cue, although cued and uncued reaches were rotationally symmetric (affording kinematic

502 comparisons). The target direction associated with a given block was counterbalanced across

503 participants (in Experiment 2B the target direction was the same for the first and third blocks).

504   The presented path cues represented the average hand path taken to avoid the barriers

505 from a prior experiment (Wong et al., 2016). The participants in Experiment 2A were subdivided

506 evenly into two groups; in one group, participants performed uncued trials first to establish a

507 history of performing a computationally difficult task, followed by cued blocks of trials (Group

508 1: uncued trials first, cued trials second) while the remaining participants were given the opposite

509 order of blocks (Group 2: cued trials first, uncued trials second). This allowed us to examine

510 whether experience at performing reaches in the presence or absence of a path cue could bias

511 future RTs. In Experiment 2B, all participants performed a block of cued trials, a block of

512 uncued trials, and a final block of cued trials. Note that for both Experiment 2A and 2B, an equal

513 number of participants within each group experienced cued reaches to the upper left as

514 experienced cued reaches to the lower right; thus, kinematic differences across subjects could not

515 be attributed to any movement direction-specific biases.

516

517 **Data Analysis**

518

519   Data were analyzed offline using programs written in MATLAB (The MathWorks,

520 Natick, MA) and in R (R Core Team, 2016). Analysis code and data are available on GitHub at

521 https://github.com/BLAM-Lab-Projects/RT_habit (Wong, 2017). Reaches were selected

522 according to a velocity criterion (tangential velocity greater than 0.05 m/s) and verified by visual

523 inspection. For each movement, RT was computed as the time between target onset and

524 movement initiation. Inherent delays in the system were estimated to be 105 ms on average; all

525   RTs have been corrected to compensate for this delay. Velocity was calculated by taking the

526   numerical derivative of the hand position after smoothing using a second-order Savitzky-Golay

527   filter with a frame size of 19 samples. Endpoint error was calculated as the absolute radial

528   distance between the final position of the hand and the center of the target. All values are

529   reported along with S.E.M.

530   In Experiment 1, RT, peak velocity, and interception amplitude were measured during

531   interception training blocks. The amplitude of the target at the time of interception was

532   calculated as the distance of the target away from the central starting position at the first time the

533   hand entered the target; if the participant was not successful at intercepting the target, no target

534   amplitude was recorded for that trial. During pre- and post-interception blocks, RT, peak

535   velocity, and endpoint error were measured for point-to-point reaches. These three metrics were

536   compared within groups using paired t-tests, with p-values adjusted for multiple comparisons

537   using Bonferroni-Holm corrections. RT was also compared across groups using a mixed-effects

538   model in R using the *lme4* package (Bates et al., 2015), with post-hoc pairwise tests performed

539   using the generalized linear hypothesis testing function in the *multcomp* package (Hothorn et al.,

540   2008) and adjusted for multiple comparisons using the Bonferroni-Holm correction.

541   In Experiment 2, trials were excluded if participants did not complete their reach within

542   1200 ms. Additionally, since most barrier configurations had more than one possible solution

543   (e.g. above or below a barrier), we pre-selected one possible path as "canonical" and presented

544   that solution on path-cued trials; any "non-canonical" reaches were excluded to allow for a fair

545   comparison of RTs for movements of comparable kinematics. Reaches were not excluded if

546   participants simply hit one of the barriers or did not reach close enough to the target to be

547   considered successful on that trial but otherwise satisfied the inclusion criteria noted above. On

548 average across participants, about 7.5% of reaches were excluded from uncued blocks and 3.0%

549 of reaches were excluded from cued blocks.

550   RTs were compared in R with mixed-effects models using the *lme4* package (Bates et al.,

551 2015). For Experiment 2A, this model treated group (uncued reaches first or cued reaches first)

552 and condition (cued or uncued) as fixed effects and barrier configuration and participant as

553 random effects. Significant effects were determined using a likelihood ratio test to compare pairs

554 of models (with and without the factor of interest). In Experiment 2B, there was only a main

555 effect of block (1, 2, or 3), with post hoc tests performed in R using the generalized linear

556 hypothesis testing function in the *multcomp* package (Hothorn et al., 2008). All *p*-values

557 obtained from post hoc tests were adjusted for multiple comparisons using Bonferroni-Holm

558 corrections.

559   The time course of the change in RT during path-cued blocks was compared across

560 groups by fitting generalized linear models in R with factors of group and trial using the *nlme*

561 package (Pinheiro et al., 2014) to account for the autocorrelated covariance structure across time

562 within participants. These models remove any autocorrelation structure across trials for each

563 participant individually prior to examining main effects; the form of the autocorrelation structure

564 was selected by fitting Autoregressive-Moving Average (ARMA) models to the data and

565 selecting the model fit that yielded the lowest Aikake Information Criterion on average across

566 participants; this led to a choice of an ARMA(1,1) process.

567   Movement kinematics were examined using two methods. First, movements were

568 compared using tools of functional data analysis (Goldsmith and Kitago, 2015). Briefly,

569 trajectories were time-normalized and evenly resampled. For each trajectory, mean pairwise

570 differences were examined using a function-on-scalar regression model fit using a Bayesian

571   method that allows for correlations in the errors. A 95% simultaneous posterior credible interval

572   was used to identify significant differences between conditions, accounting for the multiple

573   comparisons made across time points within a single trajectory but not for multiple comparisons

574   across trajectories.

575   Second, movement trajectories were also examined by comparing the shape similarity of

576   each movement to the path cue using a Procrustes distance metric (Goodall, 1991). The

577   Procrustes distance finds the best combination of translation, rotation, and scaling to match a

578   shape to its template, then estimates the remaining dissimilarity normalized between 0 and 1,

579   where 0 implies the two shapes are perfectly matched. For each movement, the Procrustes

580   distance was estimated; then the overall distributions of Procrustes distances for the cued and

581   uncued conditions were compared using a generalized linear mixed model with a log-normal link

582   function using *brms*, an R interface to the Stan language (Buerkner, 2016, Carpenter et al., 2016,

583   Hoffman and Gelman, 2014). This generalized linear mixed model had main effects of group

584   (uncued reaches first or cued reaches first) and condition (cued or uncued); significant effects

585   were estimated by calculating Bayes factors to test the null hypothesis that the effect coefficient

586   is equal to zero (according to whether the confidence intervals of the effect included zero).

587

Figure Legends

589

590   Figure 1. Experiment 1: interception task. (A) Paradigm. Participants were first asked to perform

591   a block of point-to-point reaches. Following this, participants in the outward interception task

592   were required to hit targets that moved away from them, while participants in the inward

593   interception task were required to hit targets that moved toward them. Following this, all

594   participants completed a final block of point-to-point reaches. (B) Time course of average RT,

595   average peak velocity, and average amplitude changes during the outward-interception task.

596   Peak velocities are compared to the actual target velocity (solid gray line) and reach amplitude is

597   compared to the average target amplitude at interception (solid gray line; note for pre- and post-

598   blocks the targets remained at a fixed amplitude). For reaches made during the interception task,

599   the reported amplitude is the magnitude of the entire movement generated (i.e., until the velocity

600   of the hand returned to zero) regardless of when or whether the target was successfully

601   intercepted. Shaded regions represent S.E.M. (C) Comparison of baseline (blue) and post-

602   training (green) performance for average RT, average peak velocity, and average endpoint error;

603   each gray line is an individual participant. (D,E) As in panels A and B, but for the inward-

604   interception task. (F) Across the two tasks, there was a significant interaction between task and

605   block on average RT; this was driven by an RT shift away from baseline behavior in opposite

606   directions for the two groups following training.

607

608   Figure 2. Experiment 2A: RTs depended on prior experience in the barrier task. (A) Participants

609   reached from a start position to a target without intercepting a pair of barriers. One example

610   target and barrier configuration is shown at left. Under the path-cued condition (at right),

611 participants were also provided with a cue (solid gray line) indicating how they should get to the

612 target. Note, in both cases the barriers, target, and cue (when present) disappeared upon

613 movement onset; hence participants in the cued condition were not merely tracing the cue but

614 were required to hold the desired movement trajectory in memory, analogous to individuals

615 performing the uncued condition. (B) Participants were divided into two groups; one group

616 performed an uncued reaching block followed by a cued reaching block, while the other group

617 performed these blocks in the opposite order. (C) Upper panel, the average RT across all

618 participants for each condition (cued or uncued) for the two groups (uncued-first or cued-first).

619 Lower panel, the average difference in RT between cued and uncued reaches across all barrier

620 configurations; positive differences indicate that RTs were shorter on cued reaches compared to

621 uncued reaches. Dots represent individual participants. (D) The time course of RTs across all

622 trials, for each group (red, uncued-first group; orange; cued-first group). Black lines represent

623 power-law fits to the decay of RT during the cued blocks of trials.

624

625 Figure 3. RTs in Experiment 2B. (A) Average RTs during each block, in the order that blocks

626 were experienced in the experiment (from left to right). (B) Change in average RT between each

627 pair of blocks during the experiment; each gray line is an individual participant.

628

629 Figure 4. Movement kinematics in Experiment 2A depend on the presence of the path cue. (A)

630 Average reach trajectories across participants for each barrier configuration for uncued (blue)

631 and cued (green) conditions. Each yellow dot represents a time at which the mean trajectories

632 were found to be consistently different between conditions. Since no significant effect of order

633 was observed, data were collapsed across groups. (B) Trajectory shapes for cued and uncued

634   reaches were examined for their similarity to the path cue according to a Procrustes distance

635   analysis. A Procrustes distance of zero means the trajectory is identical in shape to the path cue.

636   Distributions of estimated Procrustes distances pooled across all trajectory shapes were averaged

637   across all participants in each group (uncued-first or cued-first) and are shown for comparison;

638   the mode of each distribution is indicated by the vertical dashed line for visualization purposes.

639   No significant effect of group was observed. (C) Average difference in Procrustes difference

640   between uncued and cued reaches for each individual participant is shown; positive differences

641   indicate that cued reaches are more similar in shape to the path cue compared to uncued reaches.

642

643

644   **Source Data Legends**

645

646   Figure 1 source data – Outward. This data set pertains to the outward-interception task, and were

647   used to calculate the summary statistics in Figure 1C and Figure 1F. This file contains measured

648   kinematic parameters (RT, peak velocity (Vpeak), and endpoint error (Err), for each trial and

649   participant during the pre-training (Block 1) and post-training (Block 2) point-to-point reaching

650   blocks. Note, the first 10 trials in each block have been excluded to evaluate steady-state

651   movement parameters.

652

653   Figure 1 source data – Inward. This data set pertains to the inward-interception task, and were

654   used to calculate the summary statistics in Figure 1E and Figure 1F. This file contains measured

655   kinematic parameters (RT, peak velocity (Vpeak), and endpoint error (Err), for each trial and

656   participant during the pre-training (Block 1) and post-training (Block 2) point-to-point reaching

657   blocks. Note, the first 10 trials in each block have been excluded to evaluate steady-state

658   movement parameters.

659

660   Figure 2 source data. This file contains RT data for Experiment 2A, used to generate Figure 2C

661   and Figure 2D. These data were also used to fit mixed-effects models for computing statistics.

662   The file contains the RT for each trial in each group (order, cued-first = 0, uncued-first = 1) and

663   condition (cued = 0, uncued = 1). Additionally, there is a factor representing the barrier

664   configuration (TB), which is assigned an arbitrary numbering from 0 to 63, which is used in the

665   mixed-effects modeling analysis.

666

667

668   Figure 3 source data. This file contains RT data from Experiment 2B, used to generate Figure 3.

669   These data were also used to fit mixed-effects models for computing statistics. The file contains

670   the RT for each trial in every condition (cued block = T, uncued = NT), for all three blocks (first

671   cued block, uncued block, second cued block). Additionally, there is a factor representing the

672   barrier configuration (TB), which is assigned an arbitrary numbering from 0 to 63, which is used

673   in the mixed-effects modeling analysis.

674

675   Source data for Experiment 2B kinematics analysis. These data contain the Procrustes Distance

676   measure (range, 0 to 1) calculated for each trajectory performed by every participant in

677   Experiment 2B. The file includes a column for condition (cued block = 0, uncued = 1) and a

678   column for block (first cued block = 1, uncued block = 2, second cued block = 3). These data

679   were used to calculate kinematic differences between blocks using a generalized linear mixed

680   model in *brms* (see Methods). There is no corresponding figure for these data, summary statistics

681   are reported in the Results.

682

683   Figure 4 source data – Procrustes Distance. These data contain Procrustes distance estimates for

684   all the trajectories performed in Experiment 2A, used to generate Figure 4B and Figure 4C. The

685   file contains the Procrustes distance for every trial in each group (order, cued-first = 0, uncued-

686   first = 1) and condition (cued = 0, uncued = 1). These data were used to examine kinematic

687   differences between conditions and groups (i.e., an effect of order) using a generalized linear

688   mixed model in *brms* (see Methods).

689

690

691   Table 1: Movement parameters for Experiment 1

692

	Reaction time (ms)	Peak velocity (m/s)	Endpoint error (cm)
	Outward Interception		
Pre-training	295.38 ± 14.98	0.66 ± 0.02	1.16 ± 0.10
Last training block	255.20 ± 7.85	1.28 ± 0.10	n/a
Post-training	273.20 ± 12.10	0.67 ± 0.01	1.32 ± 0.22
	Inward Interception		
Pre-training	290.76 ± 18.35	0.55 ± 0.02	1.09 ± 0.06
Last training block	564.82 ± 112.11	0.27 ± 0.04	n/a
Post-training	303.63 ± 17.25	0.57 ± 0.01	1.05 ± 0.04

693

694   RT, velocity, and endpoint error for the two groups in Experiment 1 for point-to-point

695   movements measured before and after training, as well as for shooting movements during the last

696   block of training. Reach velocity was required to be between 0.6 and 0.9 m/s for the outward

697   interception task and between 0.5 and 0.8 m/s for the inward interception task. Note that no

698   endpoint error is reported for the last block of training because participants reached past a

699   continuously moving target, making it difficult to define error when participants missed the

700   target during those blocks.

701

702

703 **Conflict of Interest**

704 The authors declare no competing financial interests.

705

706 **Acknowledgements**

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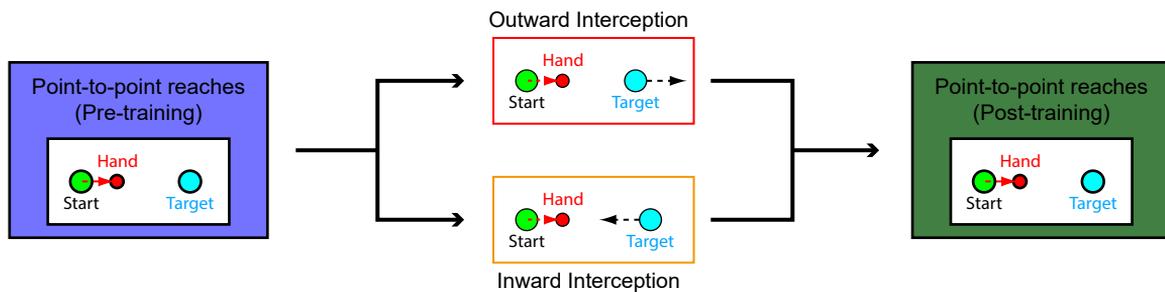803 SCHOUTEN, J. F. & BEKKER, J. A. 1967. Reaction time and accuracy. *Acta Psychol (Amst),*
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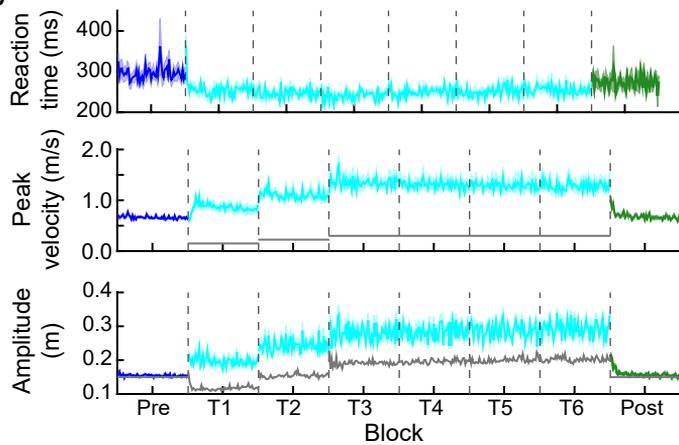806   and sex. *Ergonomics,* 10**,** 559-64.
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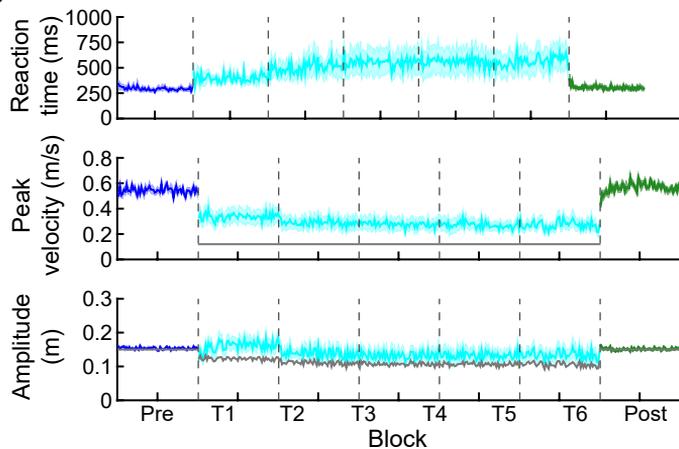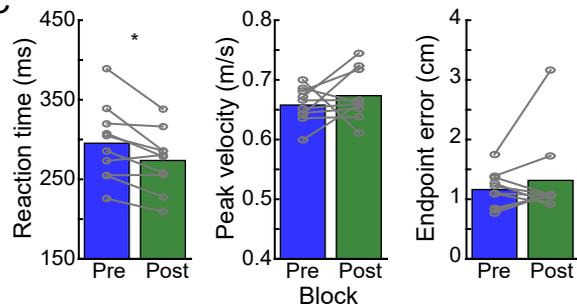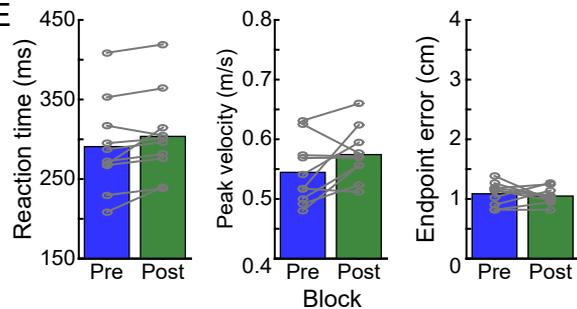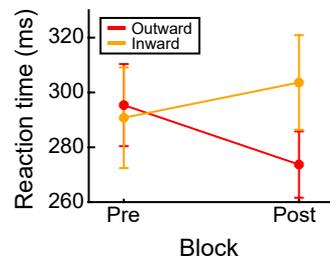838
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