Sensitivity to Error During Visuomotor Adaptation is Similarly Modulated by Abrupt, Gradual and Random Perturbation Schedules

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Running title: How prior experience modulates error sensitivity

Abstract

It has been suggested that sensorimotor adaptation involves at least two processes (i.e., fast and slow) that differ in retention and error sensitivity. Previous work has shown that repeated exposure to an abrupt force field perturbation results in greater error sensitivity for both the fast and slow processes. While this implies that the faster relearning is associated with increased error sensitivity, it remains unclear what aspects of prior experience modulate error sensitivity. In the present study, we manipulated the initial training using different perturbation schedules, thought to differentially affect fast and slow learning processes based on error magnitude, and then observed what effect prior learning had on subsequent adaptation. During initial training of a visuomotor rotation task, we exposed three groups of participants to either an abrupt, a gradual, or a random perturbation schedule. During a testing session, all three groups were subsequently exposed to an abrupt perturbation schedule. Comparing the two sessions of the control group who experienced repetition of the same perturbation, we found an increased error sensitivity for both processes. We found that the error sensitivity was increased for both the fast and slow processes, with no reliable changes in the retention, for both the gradual and structural learning groups when compared to the first session of the control group. We discuss the findings in the context of how fast and slow learning processes respond to a history of errors.

57   **Keywords**

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59   human; motor learning; two-state model; error sensitivity; savings

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61   **New & Noteworthy**

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63   We investigated what aspects of prior experience modulate error sensitivity, within the

64   framework of a two-state model of short-term sensorimotor adaptation. We manipulated initial

65   training on a visuomotor adaptation reaching task using specific perturbation schedules that are

66   thought to differentially affect fast and slow learning processes, and we tested what effect these

67   had on subsequent adaptation. We found that sensitivity to adaptation error was similarly

68   modulated by abrupt, gradual, and random perturbation schedules.

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Introduction

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77   Adaptation is often defined as an error-driven process, in which the error experienced during a

78   movement leads to a corrective adjustment in the motor output on the following movement (1-5).

79   Behavioural measures of adaptation are well characterized by state-space models (1, 4), which

80   represent trial-to-trial changes in movement as a function of how an error on a given trial affects

81   motor output on the subsequent trial. The update from one trial to the next, or the change in

82   motor output, is based on two parameters: a retention parameter which determines what

83   proportion of motor output is retained from trial to trial, and an error sensitivity parameter which

84   governs the proportion of error experienced on the current trial that is corrected for on the

85   subsequent trial.

86   Variations of the state-space model are built on the assumption that adaptation is the

87   product of multiple underlying processes with distinct timescales (3, 6-8). Researchers have

88   begun to provide neural evidence to strengthen the theory that sensorimotor learning is supported

89   by multiple processes (9, 10). An influential two-state model of short-term motor adaptation was

90   proposed by Smith et al. (3) that proposed a fast process that learns quickly but has poor

91   retention and a slow process that learns more slowly, but has strong retention.

92   The prevailing success of the two-state model continues to be that it accounts for the

93   learning phenomenon known as savings, characterized as prior learning speeding up subsequent

94   relearning (3, 11). While Smith et al. (3) initially argued that the reason for the fast relearning

95   during a second introduction of the same perturbation was due to the resistance of the slow

96   process to change, recent studies suggest that learning rate can be modified depending on factors

97   such as the uncertainty of movement error (12, 13), size of movement error (14), and a history of

98   movement errors (15-17).

99   The behavioural changes associated with savings suggest that some component of

100   memory from the initial training must lead to the faster relearning, but what is remembered and

101   recalled remains unclear (15-22). One perspective argues for the enhancement of an explicit

102   strategy (18, 20, 23), while the other side suggests that faster relearning is driven by the

103   experience of the motor errors (15-17, 24).

104   In support of the latter possibility, Herzfeld and colleagues (16) proposed that a history of

105   errors modulates the error sensitivity on each trial, systematically controlling how much the

106   motor system learns from the current motor error. They suggested that an error-based adaptation

107   model that provides for experience-dependent error sensitivity modification could account for

108   savings. Furthermore, Leow et al. (17) demonstrated that it is a memory of errors, not previous

109   actions, that is necessary for savings.

110   Recent work has shown that repeated exposure to the same force field perturbation results

111   in greater error sensitivity of both the fast and slow processes (15). While in Coltman et al. (15),

112   the error sensitivity terms for the fast and slow processes were held constant within a session, we

113   evaluated the theory of experience-dependent error sensitivity modulation in the context of

114   changes in error sensitivity from one learning session to the next. Although these results clearly

115   indicate that the motor system stored some component (i.e., memory) of prior training to speed

116   up subsequent learning, it remains unclear how the fast and slow learning processes contribute to

117   savings and what aspects of prior experience modulate error sensitivity. In other words, do both

118   fast and slow processes access a single stored component of prior training, or do they store

119   independent components? If the fast and slow processes depend on separate stored components

120   of prior training, then it may be possible to independently modulate characteristics of the fast and

121   slow processes (e.g., error sensitivity) by experimentally manipulating aspects of prior learning.

122   Recent findings demonstrate that participants do not adapt linearly in response to

123   different magnitudes of error (13, 14, 25). Additionally, Orban de Xivry and Lefevre (26)

124   propose that different perturbation schedules lead to distinct motor memories with different

125   attributes and neural representations (i.e., the amount of reorganization of the motor cortex). We

126   propose that perturbation schedules that are designed to produce learning using errors of

127   different magnitudes may have a differential effect on session-to-session changes to the fast

128   versus slow processes. In the present study, we manipulated initial training in a visuomotor

129   adaptation task using perturbation schedules which involved errors of different magnitudes, and

130   we tested what effect these different initial learning experiences had on subsequent adaptation,

131   and specifically on characteristics of the fast versus slow adaptation processes.

132   We asked one group of participants to counter a gradual perturbation schedule during

133   initial training. When a perturbation is gradually introduced, such that participants never

134   experience large errors, learning is believed to be more implicit in nature (26). We predicted that

135   when participants in this group were later tested on an abrupt perturbation, only the slow process

136   would be affected by the initial training, compared to a control group who were initially trained

137   using an abrupt perturbation. For a second group of participants, initial training was based on a

138   structural learning paradigm, involving a series of brief exposures to large, random perturbations

139   (27, 28). This perturbation schedule is thought to be based on explicit learning mechanisms (20,

140   29). During the original conception of the two-state model, Smith et al. (3) designed a rebound

141   paradigm to test the theorized characteristics of each process. Much like the brief reversal used in

142   the rebound paradigm, which includes large errors and limited exposure, the motor output during

143   this phase of the paradigm is believed to be dependent on the fast process (3). For this group we

144   predicted that when later tested on an abrupt perturbation, only the fast process would be affected

145   by the initial training, as compared to the control group.

146   We modelled perturbation-driven changes in movement with the state-space equations

147   proposed by Smith et al. (3), and focused on changes in the retention and error sensitivity

148   parameters. The model estimates function as a tool for understanding how the underlying

149   processes of adaptation were affected by the prior training. Substantiating the finding of Coltman

150   et al. (15), we confirm that repetition of the same visuomotor perturbation results in an increase

151   in error sensitivity for both processes, when comparing the two sessions of the control group. By

152   comparing the model estimates of participants in the gradual and structural learning groups to the

153   first session of the control, we expected to see changes in error sensitivity that depended on the

154   type of prior training participants experienced. Interestingly, however, we found that error

155   sensitivity of both the fast and slow processes was increased for both groups. The findings are

156   discussed in the context of storing and accessing a history of errors.

157

158   **Methods**

159   **Participants.** A total of 60 healthy young adults (age range 21-35; mean age ± sd 27.9 ± 4.2

160   years) participated in a visuomotor rotation experiment. Participants were recruited from the

161   online platform maintained by Prolific.co and received £11.25 for their participation. As part of

162   the Prolific platform, participants respond to a series of questions related to age, gender, health

163   and economic status. Based on this prescreen information, 24 participants identified as female

164   and 36 as male. Participants were recruited globally and reported being located in 17 different

165   countries (Estonia, Finland, France, Greece, Hungary, Israel, Italy, Mexico, Netherlands, Poland,

166   Portugal, Slovenia, South Africa, Spain, Sweden, United Kingdom and the United States). All

167   participants self-reported being right-handed and had normal or corrected-to-normal vision. The

168   protocol was approved by Western University's Research Ethics Board and all participants

169   indicated electronic consent.

170   **Apparatus.** Participants used a standard computer mouse and their own computer to access a

171   webpage hosted on a network computer located at Western Interdisciplinary Research Building.

172   The task was written in and controlled by JavaScript, running locally within the participants'

173   web browser.

174   Participants were asked to use a standard computer mouse and a standard credit or debit

175   card to complete a spatial calibration procedure. Participants were initially instructed how to turn

176   off the acceleration for the mouse, based on their operating system. Then, following an

177   instruction video, participants were asked to align the top of their mouse with the top of the

178   credit card. After a tone, they were instructed to move the mouse in a smooth and straight path,

179   aligning the top of their mouse with the bottom of the card. Participants were asked to hold still

180   while waiting for a second tone, indicating that they needed to realign the mouse with the top of

181   the card. This was repeated at two different speeds indicated in the video. When the calibration

182   procedure was successfully completed, participants watched an instructional video about the

183   experimental task.

184   The size and position of the stimuli were scaled based on a mouse calibration procedure.

185   Real-time position of the mouse was used to control the visual display and to provide on-line

186   visual feedback. The mouse speed was adjusted such that the distance from start position to

187   target was exactly 6 cm based on the calibration. While the physical target distance was always 6

188   cm, this translated to 300 pixels on screen. Therefore, the straight reach trajectory was 300

189   pixels, however a participant's view of this was potentially compressed or expanded relative to

190   the target value of 6 cm, depending on their monitor as well their viewing distance from the

191   monitor.

192   **Paradigm.** At the start of each trial, participants were instructed to click their mouse to begin. A

193   circular cursor (10 pixels radius) was virtually displayed on the participant's computer monitor

194   and was used to represent the position of the mouse on screen. The position of the mouse at the

195   start of the trial, represented the start position on screen. A small square (20 pixels by 20 pixels)

196   represented the target. The radial distance of the target from the start position was 300 pixels.

197   The target appeared at either 45°, 90°, or 135°, relative to the start position (where 6 cm directly

198   to the right of the start position represented 0°). The location of the target was randomized per

199   trial, per participant, such that each participant saw a different order of targets with an equal

200   number of presentations of each target over the course of a session.

201   Participants were instructed to make a straight movement from the start position to the

202   target, within a narrow temporal window. At the beginning of each trial the target appeared in

203   white. Participants were required to hold still at the start position for 500 ms, at which time the

204   target changed color to green, representing a "go" signal for participants to initiate a movement

205   to the target. In addition to the colour change of the target, a tone was used as a secondary "go"

206   signal. Participants needed to reach for the target and bring the centre of a red cursor

207   representing the position of their computer mouse within 10 pixels of the centre of the target

208   within 600–900 ms. If a participant's movement time was less than 600 ms, the target turned red

209   to indicate that the movement was "too fast". If the participant's movement time was within

210   600–900 ms, the target remained green to indicate that the movement was "good". If the

211   participant's movement time was greater than 900 ms, the target would turn blue to indicate "too

212   slow". Feedback related to movement time was displayed on the screen for 1000 ms before the

213   screen went blank and written instructions on screen indicated that the participant should return

214   the mouse to a comfortable starting position within their workspace. Participants were instructed

215   to try to obtain the "good" feedback as often as possible throughout the experiment.

216   To assist with making straight movements between the start position and the target using

217   a computer mouse, the first 20 trials of the first session represented a practice session for

218   participants. In these trials, a purple rectangle (50 pixels by 300 pixels), with two white lines on

219   either side was shown on screen, highlighting a straight path to the target. Participants were

220   instructed to keep the red cursor on the path, between the lines, toward the target. If the cursor

221   moved outside the path, the background colour changed from black to pink.

222   Participants were randomly assigned to one of three groups. Each group completed two

223   sessions (initial training and testing), separated by a 5-minute break (**Fig. 1**).

224   Each session included a total of 450 reaching movements, with a 1-minute mid-session break

225   halfway. The experimental paradigm for each session consisted of 4 epochs. The first epoch

226   (baseline) consisted of 70 trials in which participants were provided with veridical feedback of

227   the cursor position. The second epoch (adaptation) consisted of 300 trials in which a visuomotor

228   rotation was applied to the cursor feedback: an angular rotation was imposed on the cursor, such

229   that a hand movement aimed directly at a target produced a cursor movement that was rotated

230   radially about the start position and participants saw that their movement had generated an error.

231   Participants had to learn to counter the rotation by moving their hand in an equal and opposite

232   direction. With practice, participants adjusted their movements in such a manner that the visual

233   feedback produced straight trajectories from start position to the target. In the third epoch (error-

234   clamp; consisting of 30 trials) the task error was clamped to zero. During the clamp trials, the

235   angular position of the cursor relative to the start position was clamped to a straight line

236   connecting the start position to the target, while participants maintained control of the radial

237   distance of the cursor from the start position. Finally, in the fourth epoch (washout; consisting of

238   50 trials), participants were provided again with veridical feedback to bring performance back to

239   baseline.

240   During the adaptation epoch of the first session, participants experienced one of three

241   conditions: (1) a control learning group (n=20) experienced an abrupt 30° clockwise (CW)

242   rotation for all 300 trials during this phase (**Fig. 1; top**), (2) a gradual learning group, (n=20) in

243   which a rotation was increased linearly from 0° to 30° CW over 250 trials and then held at a

244   fixed 30° CW for another 50 trials (**Fig. 1; middle**), or (3) a structural learning group (n=20) in

245   which participants encountered random rotations, ranging from 60° counter-clockwise (CCW) to

246   60° CW in blocks of 6 trials with the same rotation (27, 28, 29; Fig. 1; bottom). In this group, we

247   deliberately set the average over all angles to zero, to prevent any accumulative learning. We

248   also excluded rotation sizes within 10° of the test rotation (30° CW) and its inverse (30° CCW).

249   We furthermore set the change in rotation angle to be equal to or greater than 15° to ensure the

250   errors were always large, which characteristically has the greatest influence on the fast process

251   (3, 29). During the second session, all three groups experienced an abrupt 30° CW rotation

252   during the adaptation epoch.

253   **Data Analysis.** The position of the cursor in both x (lateral) and y (sagittal), were sampled in

254   pixels at the refresh rate of their computer monitor (typically 60 Hz). Missed samples were

255   interpolated during analysis (less than 1 % of samples on average). In cases in which data were

256   acquired at higher sampling rates (for example because a participant's computer monitor refresh

257   rate exceeded 60 Hz), the data were down sampled to 60 Hz. Data were digitally smoothed using

258   a second-order low-pass Butterworth filter with a cut-off frequency of 15 Hz. All data were

259   stored for offline analysis using custom MATLAB R2020a (The MathWorks) scripts.

260   Movement trajectories were selected using an algorithm in which movement initiation

261   was defined as the time at which the tangential velocity of the mouse first exceeded 0.5 cm/s and

262   movement end was defined as the first time after peak velocity that tangential velocity fell below

263   0.5 cm/s, where peak velocity was defined as the fastest participants ever moved during the reach

264   movement. For each trial we computed the angle between the line connecting the start position

265   and the cursor position at peak velocity, and the line connecting the start position to the target.

266   We determined the average reach angle, per subject during the last 50 trials of the baseline epoch

267   and we subtracted this quantity from the reach angle measured on each trial.

268   **Model fitting.** Smith et al. (3) outlined a method for mathematically modelling an iterative

269   update of the states of the two proposed processes of short-term sensorimotor adaptation.

270   Essentially, the model involves fitting four parameters: an error sensitivity and a retention

271   parameter for both a fast and a slow process. The first parameter weighs the relative importance

272   of recalling previous motor commands, which is interpreted as the retention factor. The second

273   parameter is the sensitivity to error, which relates to the proportion of error that is corrected for

274   trial-to-trial (1, 3, 4, 30). The two important assumptions in this model are that the error

275   sensitivity is higher for the fast process compared with the slow process and that retention is

276   stronger for the slow process compared with the fast process (3). Adaptation can be decomposed

277   into a fast (**Eq. 1**) and a slow (**Eq. 2**) process, knowing that each state follows different learning

278   dynamics. The two processes are summed together to produce the overall output x (**Eq. 3**). Error,

279   denoted by e(n), arises on each trial n as the difference between the overall output xnet and the

280   task parameter r (i.e., the degree of the rotation; **Eq.4**).

281
$$x_f(n + 1) = A_f x(n) + B_f e(n) \tag{1}$$

282
$$x_s(n + 1) = A_s x(n) + B_s e(n) \tag{2}$$

283
$$x_{net}(n) = x_f(n) + x_s(n) \tag{3}$$

284
$$e(n) = r(n) - x_{net}(n) \tag{4}$$

285
286   Linear inequality constraints were defined in order to apply to standard two-state model

287   dynamics (31):

288
$$A_f \leq A_s + 0.001 \tag{5}$$

289
$$B_f \geq B_s + 0.001 \tag{6}$$

290   In order to approximate the four parameters (i.e., Af, As, Bf, and Bs), we fit the model to

291   the behavioral data (using the function *fmincon* in MATLAB r2020a) by minimizing the squared

292   difference between the estimated net output (xnet) of the model and the average participant reach

293   angle, measured on each trial. According to the methods described in Albert and Shadmehr (31),

294   we also included a mathematical formalization of visual error clamp trials and set breaks.

295   **Statistical Design.** Pairwise comparisons were performed with nonparametric bootstrap

296   hypothesis tests, as well as paired and unpaired t-tests. For statistical analyses that require

297   multiple comparisons, we used the Holm-Bonferroni correction (32). Statistical tests were

298   considered significant at $p < 0.05$. For all reported and depicted values, we report the mean and

299   SEM.

300   **Results**

301   **Figure 2** shows the hand paths from one representative participant in the control group

302   during both sessions one and two, as well as one representative participant per group in session

303   two of the structural and gradual learning groups. During the baseline epoch (left column), these

304   paths are relatively straight to the target. The representative participants were all adapting to an

305   abrupt 30° CW rotation. During the early adaptation epoch (middle column) these movements

306   were initially deviated in the CW direction, with a corrective movement at the end of the

307   trajectory to bring the cursor to the target. In all three groups, participants adapted to the 30° CW

308   rotation by the late adaptation epoch (right column), reducing their movement errors and

309   resuming relatively straight hand paths to the target.

310   We used a kinematic behavioural measure to assess changes in performance. The primary

311   outcome measure for the study was reach angle at peak velocity, which was measured as the

312   angle between the straight line connecting the start position and the cursor position at peak

313   velocity and the straight line connecting the start position to the target. The control group of

314   participants adapted their movements to an abrupt 30° CW visuomotor rotation in both the first

315   and second session. **Figure 3A** shows the angle at peak velocity for all trials in each session,

316   averaged across participants in the control group. In both sessions, participants exhibited learning

317   during the adaptation epoch, decay during the visual error clamp epoch, and a return towards

318   baseline performance during the washout epoch. During the adaptation epoch we examined the

319   learning at two different time points: early (first fifty trials during adaptation) and late (last fifty

320   trials during adaptation; **Fig. 3B**). The mean angle in the early learning phase of the second

321   session $(M = 23.7, SD = 3.15)$ was reliably greater than in the first session $[M = 19.9 , SD =$

322   4.6; paired t-test, $t(19) = -6.2, P = 3.0e-06]$, indicating savings. We did not detect a reliable

323   difference $(P = 0.08)$ between sessions during late learning.

324   A second group of participants was exposed to a gradual perturbation schedule during

325   initial training. **Figure 4A** shows the angle at peak velocity for all trials in each session, averaged

326   across participants in the gradual learning group. Participants exhibited learning during the

327   adaptation epoch, decay during the visual error clamp epoch, and a return towards baseline

328   performance during the washout epoch. A final group of participants was exposed to a series of

329   brief exposures to large, random perturbations. Each participant in this group experienced a

330   different set of randomly varying rotations. **Figure 4B** illustrates the angle at peak velocity for

331   all trials in session one for four representative individual participants from the structural learning

332   group. We observed two participants who demonstrated learning within each block of six trials,

333   but who also appeared to have maintained a fraction of error throughout the adaptation epoch

334   (**Fig. 4B**, **S2** and **S8**). In addition to a participant who adapted quickly to the randomly changing

335   perturbation (**Fig. 4B**, **S18**), we observed a participant who qualitatively showed greater

336   reduction of error in the latter half of the adaptation epoch, compared to the early half (**Fig. 4B**,

337   **S20**).

338   **Figure 5A** shows the angle at peak velocity averaged across participants for all trials in

339   session one of the control group and session two of the structural and gradual learning groups.

340   When comparing the model estimates of participants in the gradual and structural learning

341   groups during the second session to the first session of the control group, we expected to see

342   changes in error sensitivity that depended on the type of prior training participants experienced.

343   To compare the changes in angle between the control, structural and gradual learning groups, we

344   examined learning during the adaptation epoch at two different time points: early (first fifty trials

345   during adaptation) and late (last fifty trials during adaptation; **Fig. 5B**). A one-way ANOVA

346   revealed a significant effect of mean angle between the control, structural and gradual learning

347   groups during early learning [$F(2,57) = 14.4$, $P = 8.8$ e-06].

348   *Post hoc* comparisons using Tukey HSD tests indicated that the mean angle for the

349   structural learning group ($M = 24.9$, $SD = 2.9$, $P = 2.9$ e-05) and the gradual learning group ($M =$

350   24.5, $SD = 2.9$, $P = 1.4$ e-04) were reliably higher than the mean angle for the control group (M

351     $= 19.9$, $SD = 4.6$). However, there was no reliable difference detected between the structural and

352   gradual learning groups ($P = 0.9$). During late learning, we did not detect a reliable difference in

353   mean angle among the groups ($P = 0.2$). Therefore, the structural and gradual learning groups

354   demonstrated fast learning when countering an abrupt 30° CW rotation, as compared to session

355   one of the control group. While the control group represented naive learners, the prior experience

356   from session one for the structural and gradual learning groups is suggested to have facilitated

357   the improved learning. Likewise, this was observed in the control group, in which participants

358   experienced a repetition of an abrupt rotation and demonstrated savings during the second

359   session.

360   Recent work suggests that error sensitivity in sensorimotor adaptation is likely not

361   constant, but rather can vary depending on prior experience (13, 14, 16, 33). We modelled

362   movement angle across each session with the state-space equations proposed by Smith et al. (3),

363   and focused on changes in the retention and error sensitivity parameters. The main objective of

364   this study was to compare the model parameters across groups learning to counter the abrupt 30°

365   CW rotation. To do this, we used the bootstrap procedure previously reported by Coltman et al.

366   (15). In this manner, we always fit the model to averaged group data for each resampled

367   population (15, 31). The estimated posterior distributions of each of the four two-state model

368   parameter values are depicted in **Fig. 6** for sessions one and two of the control group and session

369   two of the gradual and structural learning groups. To determine whether the difference between

370   the mean of each distribution was statistically reliable, we calculated the distribution of the

371   differences in individual samples. The *insets* in **Fig. 6** show the distribution of differences found.

372   **Table 1** shows the mean and standard deviation for each of the two-state parameters for each

373   group.

374   We first compared parameter estimates from session one and session two for the control

375   group (**Fig. 6A**). Across all comparisons made between groups, we did not observe a reliable

376   difference in the retention parameters for either the fast or slow process. When participants

377   experienced repetition of the same abrupt rotation, we found a statistically reliable increase in the

378   error sensitivity parameter for both the fast (B_f, $P = 0.007$) and the slow (B_s, $P = 0.003$)

379   processes. Importantly, this comparison allowed us to demonstrate that our previous finding from

380   a force field adaptation task (15) was replicated in a visuomotor rotation task. Therefore, this

381   result suggests that both the fast and slow processes are responsive to a history of error and both

382   contribute to savings.

383   Next, we compared parameter estimates from session one of the control group with

384   session two of the structural learning group (**Fig. 6B**). Based on the theory of structural learning,

385   thought to be essential to capturing the initial rapid phase of learning, Braun et al. (27)

386   demonstrated that the benefit of knowing the underlying structure of a task is that it leads to

387   facilitated adaptation. For this group we predicted that when later tested on an abrupt

388   perturbation, only the fast process would be affected by the initial training, as compared to the

389   control group. When overall learning is decomposed into a fast and slow state, the initial rapid

390   phase of learning is dominated by the output of the fast process. Therefore, we assumed that such

391   practice would influence the fast process. In addition to a statistically reliable increase in the

392   error sensitivity parameter for the fast process (B_f, $P < 0.001$), we also found a statistically

393   reliable increase in the slow process error sensitivity (B_s, $P = 0.002$).

394   Learning is believed to be more implicit in nature when a perturbation is gradually

395   applied using small undetectable increases, so that participants never encounter large sensory

396   prediction errors(22, 26, 34). By exposing a group of participants to a gradual perturbation

397   schedule during initial training, we predicted that only the slow process would be influenced.

398   When we compared the parameter estimates from session one of the control group with session

399   two of the gradual learning group (**Fig. 6C**) we found the gradual learning group showed a

400   statistically reliable increase in the error sensitivity parameter for both the fast (B_f, $P = 0.009$)

401   and the slow (B_s, $P = 2$ e-04) processes.

402   Lastly, we compared parameter estimates between the structural and gradual learning

403   groups during session two (**Fig. 6D**). Our goal was to use two different adaptation schedules

404   thought to differentially affect fast and slow learning processes and test the idea that error

405   sensitivity for each process would be independently modulated. We expected that the error

406   sensitivity parameter for the fast process would be greater in the structural learning group

407   compared to the gradual learning group, while the error sensitivity parameter for the slow

408   process would be greater in the gradual learning group compared to the structural learning group.

409   The only statistically reliable difference was in the error sensitivity parameter for the fast process

410   that was larger for the structural learning group (B_f, $P = 0.02$).

411   From the bootstrap distributions we calculated the mean value for each parameter for

412   session one and session two of the control group, and session two of the structural and gradual

413   learning groups separately. Using these mean estimated parameter values, we used the two-state

414   model to simulate our experimental paradigm and generate simulated learning curves to visualize

415   the time course of the estimated fast and slow processes, as well as the simulated overall output.

416   **Figure 7** demonstrates that the simulated learning curves are qualitatively in good agreement

417   with the measured behavioural data. The models explains 98 - 99 % of the variance in angle over

418   the course of learning (*control session 1*: $R^2 = 0.98$, $P = 2.2$ e-04; *control session 2*: $R^2 = 0.99$, P

419      $= 1.2$ e-04; *structural session 2*: $R^2 = 0.98$, $P = 2.3$ e-04; *gradual session 2*: $R^2 = 0.99$, $P = 1.6$ e-

420   04). The model effectively captures the initial improvement in learning during the adaptation

421   epoch, the decay during the visual error clamp epoch, as well as the subsequent return towards

422   baseline performance during the washout epoch.

423   **Discussion**

424   The integration of different perturbation schedules and two-state modelling of measured

425   behavioral data allowed us to test the role of prior experience on error sensitivity modulation

426   during subsequent adaptation. The modelling of the data in turn describes adaptation as an

427   interaction between error-sensitivity and retention. It has previously been shown in the context of

428   force field learning that repetition of the same perturbation results in increased error sensitivity

429   for both the fast and slow processes of adaptation (15). We substantiated this here by

430   demonstrating that sensitivity to errors is similarly increased for both the fast and slow processes

431   during the second session of a visuomotor rotation task. We found no reliable differences in the

432   retention parameter across conditions and sessions.

433   The behavioural changes associated with savings suggest that some component of

434   memory from the initial training must lead to the faster relearning, but what is remembered and

435   recalled remains unclear. In the context of the present study, how the fast and slow processes

436   individually contribute to savings, is not well known. To address this point, we used different

437   perturbation schedules that relied on errors of different magnitudes to determine whether the

438   underlying processes of adaptation could be independently manipulated, and whether an

439   independent memory would subsequently be formed. We expected to see differences in error

440   sensitivity depending on the type of prior training participants had received and therefore

441   compared the model parameter estimates of participants in the gradual and structural learning

442   groups to the first session of the control group, but we found that error sensitivity of both the fast

443   and slow processes was increased for both groups. Such a result might suggest that sensitivity to

444   error during visuomotor adaptation is modulated by abrupt, gradual and random perturbation

445   schedules.

446   As an alternative account, savings has previously been explained by the retrieval of

447   previous successful actions, reflecting the use of an explicit strategy (18-20, 23). Within the

448   framework of a two-state model, this theory suggests that savings is driven purely by the fast

449   process, without consideration of the contributions from the slow process (35). Several

450   researchers have argued that explicit cognitive strategies can account for a significant amount of

451   learning, particularly during the early phase of learning and relearning (36-38). The dissociation

452   of learning into implicit and explicit learning processes often relies on the use of verbal aiming

453   reports prior to reaching (18, 20, 23, 38). Recent findings, however, indicate that verbal aiming

454   reports could lead to an overestimated explicit contribution to adaptation (21, 39). In fact, Leow

455   et al. (21) demonstrated that the use of shortened preparation time, designed to prevent strategic

456   re-aiming, resulted in the estimated implicit learning being larger than that which was obtained

457   from verbal reports. Furthermore, Yin and Wei (22) provide supporting evidence that savings of

458   motor adaptation is possible without forming or recalling a cognitive strategy with the use of a

459   gradually introduced visuomotor rotation during initial learning. If savings is possible, with and

460   without an explicit strategy being formed during initial learning and predominant measures of

461   implicit and explicit processes may be confounding their mode of measurement, how reliable are

462   the findings suggesting savings is driven exclusively by an explicit process?

463   The debate about the contributions of explicit/implicit and fast/slow processes to savings

464   stems from a recent proposal that fast and slow processes reflect explicit and implicit learning

465   mechanisms, respectively (35). Motor memory development is thought to be based on two

466   components: recall, which involves retrieving past motor movements, and faster relearning,

467   which involves increased sensitivity to errors (3, 40). By using the framework of a two-state

468   model we focused on the dominant component of adaptation, which is sensory prediction error,

469   and found that motor memory was associated with an increase in error sensitivity. In addition to

470   sensory prediction error, there are other possible teaching cues that might drive adaptation. When

471   researchers are focused on the more cognitive aspects of learning, exploring the use of an explicit

472   strategy, the dominant component of adaptation may likely be the reinforcement of successful

473   actions. Future research may shed light on this debate by probing both proposed methods of dual

474   processing simultaneously during learning, and by assessing more directly their shared features.

475   Another long-standing question is how quickly implicit changes in learning emerge.

476   Huberdeau and colleagues (20) demonstrated that learning of an abrupt perturbation with only a

477   few trials is sufficient to cause savings via the explicit process, based on the belief that the fast

478   learning is too short for implicit learning to take its full effect. Ruttle et al. (41) however recently

479   confronted the long standing notion that implicit learning is slowly developing, typically

480   unfolding over tens of trials. By observing changes in both internal models and state estimates of

481   limb position as a characterization of implicit learning, they found that after only one to three

482   perturbed training trials participants had changes in both reach aftereffects and a shift in hand

483   localization. Taking this into account, it seems possible that the 6-trial repetition used in the

484   structural learning task, aiming to influence the fast process, may have simultaneously influenced

485   the slow process. For that reason, it is possible that a common component of all three

486   perturbation schedules used during initial training was that the slow process accounted for a

487   significant portion of the error reduction.

488   Albert et al. (33) recently investigated the persistence of residual errors during motor

489   adaptation in the context of implicit and explicit learning systems. Of importance to the present

490   study, they propose that it is the implicit learning system which maintains a history for prior

491   errors. Our results are consistent with this hypothesis that it is the implicit process that stored

492   some component of prior training. Given the suggestion that the history of errors is stored by

493   only one of the two proposed underlying processes, this finding would be lost if learning

494   behavior was represented using a single-state model. Nevertheless, one may ask whether a two-

495   state model was necessary to represent learning in the behavioral tasks tested in the present

496   study. To address this, we calculated AIC values for both single- and two-state models fits to the

497   behavioral data. We used the data associated with the four sessions of abrupt rotations (i.e., the

498   first and second sessions of the control group, and the second session of the gradual and

499   structural learning groups) and for each we estimated the overall output based on a single-state

500   model and separately using a two-state model. Based on the model with the lowest AIC value, in

501   all four cases the best-fit model describing the measured behavioural data was the two-state

502   model. As a follow-up to our initial question, we would further suggest that the stored memory is

503   accessible to both processes during subsequent learning. As it pertains to our findings, we would

504   argue that while the fast process may not maintain a history or errors, it does have access to this

505   information in subsequent learning as evident by the increased error-sensitivity for the fast

506   process during testing in all groups.

507   Alternatively, while the experimental design and two-state model, used in the present

508   study, account well for the results of savings, recent work looking at evoked recovery (42) posits

509   that memory formation is related to the storing of information about the dynamical and sensory

510   features of the environment is related to the context with which it is associated. Understanding

511   how contextual inference can be related to and accessed by each process of the two-state model

512   can shed light on future discussions about multiple processes underlying motor learning.

513

514

Table 1. *Two-state model parameters calculated from probability distribution*

	Fast Process		Slow Process	
	A (mean ± SD)	*B* (mean ± SD)	*A* (mean ± SD)	*B* (mean ± SD)
Control Session 1	0.86 (0.02)	0.17 (0.02)	0.996 (7e-04)	0.05 (0.006)
Control Session 2	0.87 (0.03)	0.28 (0.04)	0.994 (0.001)	0.07 (0.01)
Structural Session 2	0.80 (0.05)	0.40 (0.03)	0.993 (0.002)	0.10 (0.02)
Gradual Session 2	0.87 (0.02)	0.27 (0.04)	0.994 (0.001)	0.10 (0.02)

515
516

517 **Figure Captions**

518

519 **Figure 1.** Experimental design and perturbation schedule. The experiment was divided into two
520 sessions, separated by a 5-min session break. Each session consisted of four blocks: 1) a baseline
521 period of no rotation trials, 2) an adaptation period, 3) an error clamp period, and 4) a washout
522 period. Participants were randomly assigned to one of three groups which differed in session one
523 during the adaptation period: abrupt control group, gradual learning group, or structural learning
524 group.

525

526 **Figure 2.** Hand trajectories from a representative participant in the control group during both
527 session one (light blue) and two (dark blue), and one representative participant per group in
528 session two of the structural (purple) and gradual (pink) learning groups. Baseline reaches were
529 from the last three trials (from trial 68 to trial 70) during the baseline epoch. Early and late
530 adaptation reaches were from the first (from trial 71 to 73) and last (from trial 368 to trial 370)
531 three trials of the adaptation epoch, respectively. Participants saw a random ordering of the three
532 possible targets (represented by the squares).

533

534 **Figure 3.** Control group. *A*: the average angle at peak velocity for all trials in *session 1* (light
535 blue) and *session 2* (dark blue). The shaded region denotes ± SE. *B*: comparisons between
536 *session 1* and *session 2* (dark blue) for the mean angle for the first 50 (early) and last 50 (late)
537 trials of the adaptation epoch. Circles represent individual data.

538

539 **Figure 4.** Gradual and structural learning groups. *A*: the average angle at peak velocity for all
540 trials in *session 1* of the gradual learning group. The shaded region denotes ± SE. *B*: the data
541 from four representative individual participants (S2, *top left*, S8 *top right*, S18 *bottom left*, S20
542 *bottom right*).

543

544 **Figure 5.** *A*: the average angle at peak velocity for all trials in *session 1* for the control group
545 (light blue) and *session 2* for the structural (purple) and gradual (pink) learning groups. The
546 shaded region denotes ± SE. *B*: comparisons between groups for the mean angle for the first fifty
547 (early) and last 50 (late) trials of the adaptation epoch. Circles represent individual data.

548

549 **Figure 6**. Probability distribution of the model parameters given the data. Light blue and dark
550 blue represent *session 1* and *session 2* of the control group, respectively. Purple represents
551 *session 2* of the structural learning group and Pink represents *session 2* of the gradual learning
552 group. *Inset* represents the distribution of pairwise differences. The four model parameters of the
553 two-state model are fast retention (A_f), slow retention (A_s), fast learning rate (B_f), and slow
554 learning rate (B_s).

555

556 **Figure 7**. Model simulations. Parameter estimates for each session were based on the mean
557 values from the bootstrap distributions shown in Fig. 6. The four parameters of the model are fast
558 retention (Af), fast learning rate (Bf), slow retention (As), and slow learning rate (Bs).
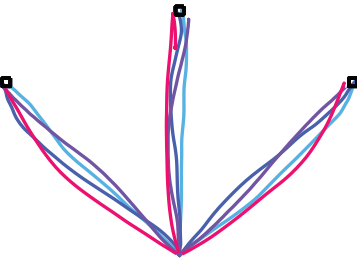
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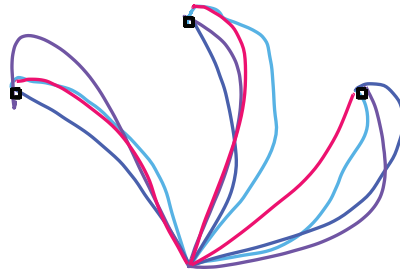651   computational biology* 7: e1001096, 2011.

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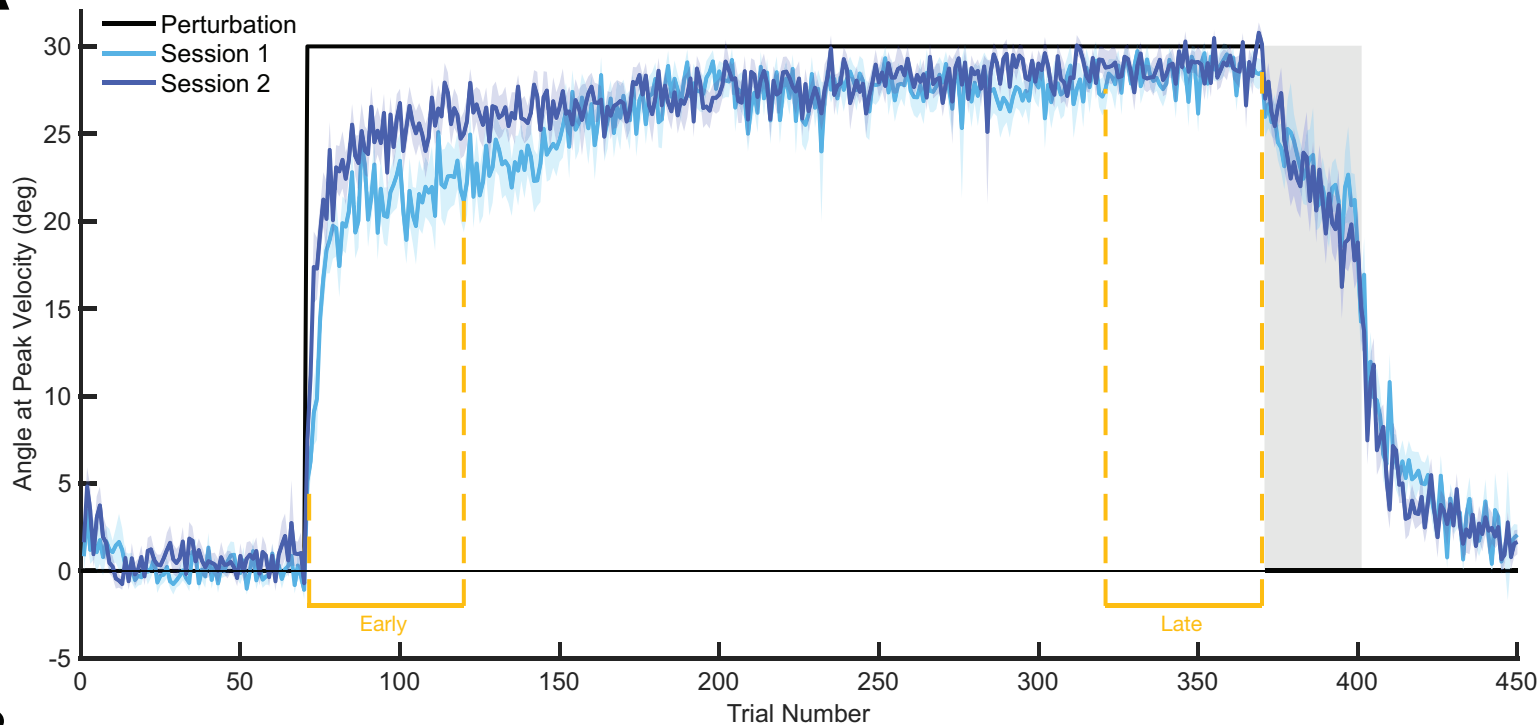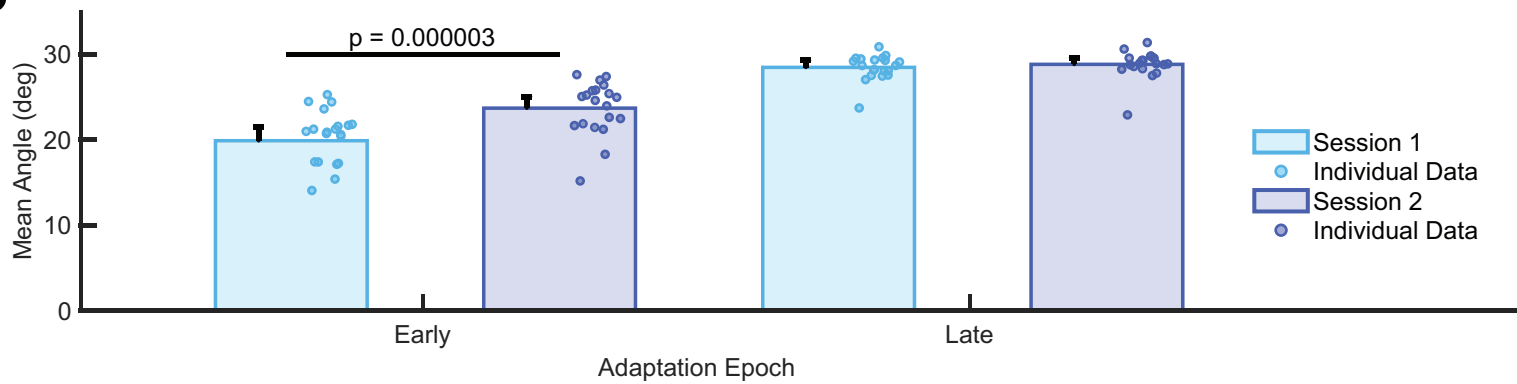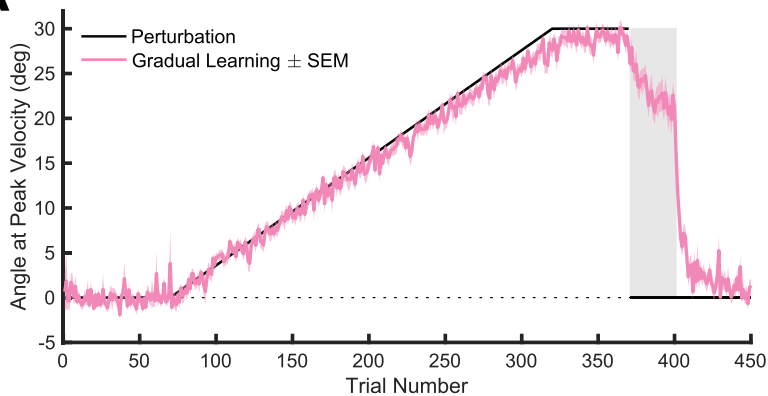663   sensorimotor repertoires. *bioRxiv* 2020.
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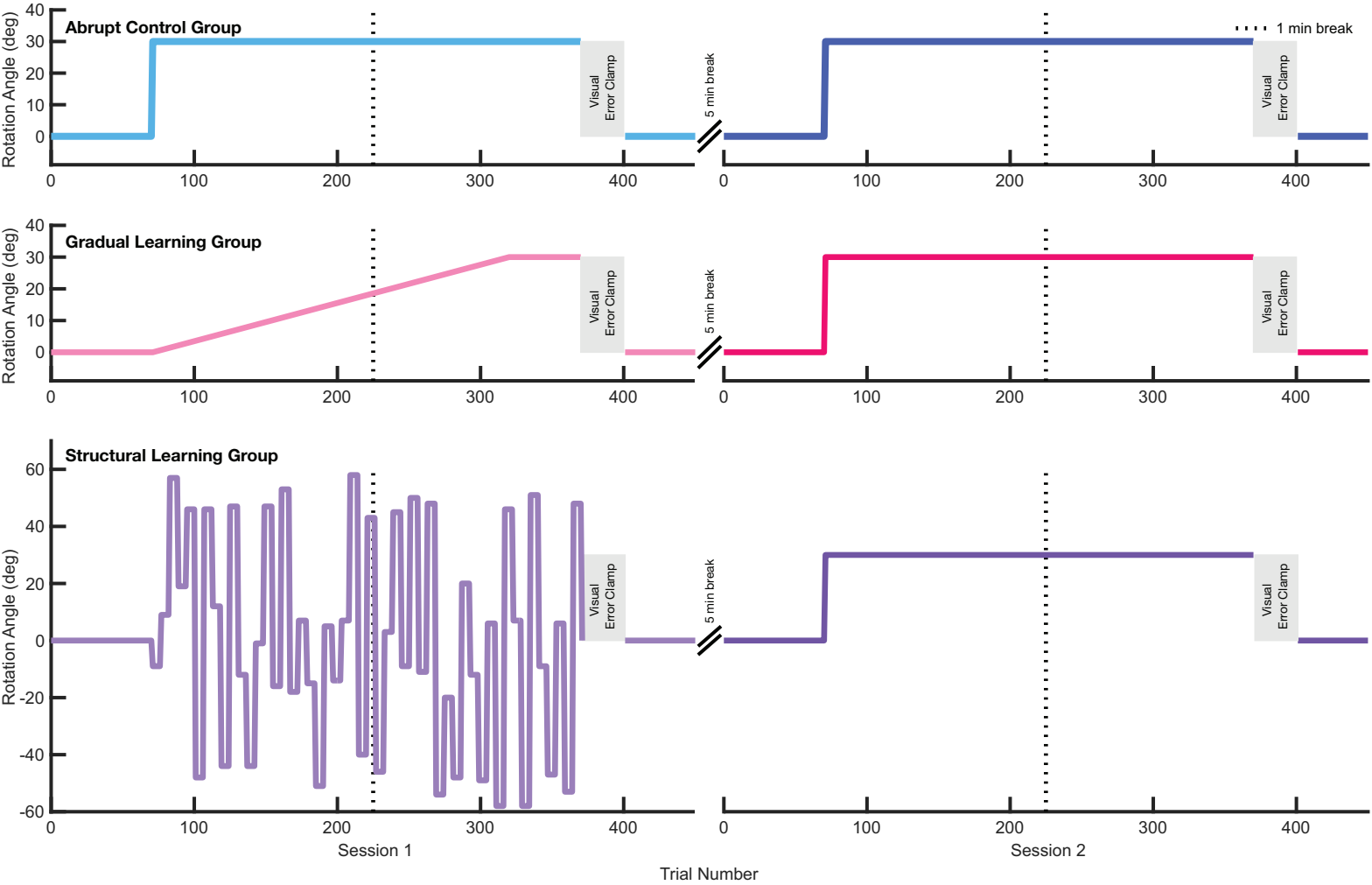
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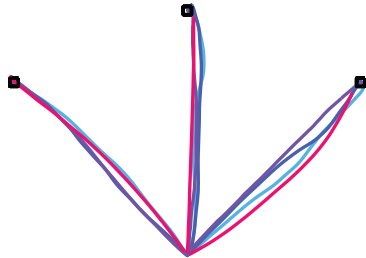
Control S1
Control S2
Structual S2
Gradual S2

A

B

A

Angle at Peak Velocity (deg) vs Trial Number

Legend:
- Perturbation
- Control S1
- Structural S2
- Gradual S2

Early, Late

B

Mean Angle (deg) vs Adaptation Epoch

Legend:
- Control S1
- Individual Data
- Structural S2
- Individual Data
- Gradual S2
- Individual Data

Early, Late

*** ***

A Control Group Session 1

As = 0.99564, Af = 0.86268
Bs = 0.048074, Bf = 0.17439

- Perturbation
- Mean data ± SEM
- Simulated output
- Estimated fast process
- Estimated slow process

B Control Group Sesssion 2

As = 0.99417, Af = 0.86517
Bs = 0.074897, Bf = 0.27736

- Perturbation
- Mean data ± SEM
- Simulated output
- Estimated fast process
- Estimated slow process

C Structural Group Session 2

As = 0.99325, Af = 0.80307
Bs = 0.10295, Bf = 0.40225

- Perturbation
- Mean data ± SEM
- Simulated output
- Estimated fast process
- Estimated slow process

D Gradual Group Session 2

As = 0.99421, Af = 0.86543
Bs = 0.099445, Bf = 0.2744

- Perturbation
- Mean data ± SEM
- Simulated output
- Estimated fast process
- Estimated slow process

Rotation Angle (degrees)

Trial Number