Introduction

Practice, in the form of movement repetition, is widely recognized as an indispensable component of motor skill acquisition (Schmidt and Lee, 2005). Even after acquiring a skill, repetition continues to play an important role. For example, repetition reduces the time required to prepare a movement (Mawase et al., 2018; Wong et al., 2017), increases movement speed (Hammerbeck et al., 2014), and biases future movements in the direction of the repeated movements, phenomena that are collectively referred to as "use-dependent learning" (Classen et al., 1998; Diedrichsen et al., 2010). The use-dependent biasing of movements may help explain why, for instance, a basketball player continues to practice her free throws years after she initially learned how to shoot, and even mimics those motions without the ball moments before shooting a free throw during a game. However, since no two movements can ever be identical, how consistent must the basketball players' motions be during practice to benefit from use-dependent learning?

Most studies of use-dependent learning have examined the phenomenon during upper-extremity movements (Classen et al., 1998; Diedrichsen et al., 2010; Orban de Xivry et al., 2011; Verstynen and Sabes, 2011). The relatively sparse literature on use-dependent learning in locomotion is surprising, given the highly repetitive nature of walking. Locomotion is, by definition, the repetition of a cyclical movement pattern until arriving at the destination. Thus, the cyclical, repetitive nature of walking creates an excellent opportunity to study use-dependent learning in an ecologically valid context.

A recent study demonstrated that use-dependent learning explains step asymmetry aftereffects in visually guided treadmill walking (Wood et al., 2020), despite previous interpretations that aftereffects observed during this paradigm were primarily due to learning from sensory

27 prediction errors, i.e., sensorimotor adaptation (Cherry-Allen et al., 2018; French et al., 2018;

28 Hussain et al., 2013; Kim and Krebs, 2012; Kim and Mugisha, 2014; Statton et al., 2016). In the

29 study by Wood et al. (2020), visual targets were used to guide participants into walking with an

30 asymmetry (i.e., a limp). Critically, for one of the experimental groups, all visual feedback was

31 veridical and participants were fully aware that they were being guided by the targets to practice

32 walking asymmetrically. Therefore, the small but persistent aftereffects observed during

33 washout, when all visual feedback was removed and participants were instructed to "walk

34 normally", were highly consistent with use-dependent learning. As repetition of novel gait

35 patterns is inherent to nearly all locomotor learning studies, these findings suggest that use-

36 dependent learning may play an important yet underappreciated role in this body of literature.

37 Thus, critical questions regarding use-dependent learning during locomotion remain: Given that

38 movement is intrinsically variable, how consistent must the walking pattern be to engage use-

39 dependent learning? Additionally, what are the computational principles underlying use-

40 dependent learning in locomotion?

41

42 Here, through computational modeling, simulations, and a series of behavioral experiments, we

43 directly tackle the question of how the consistency of movement patterns impacts use-

44 dependent learning. Our competing hypotheses are formalized by two distinct computational

45 models of how use-dependent learning may arise. In Model 1, the Strategy plus Use-Dependent

46 model, two learning processes act in parallel: A voluntary, strategic learning process that is

47 active when the goal is to match step lengths to visual targets, and in parallel, an automatic,

48 slowly updating use-dependent learning process that biases movements in the direction of

49 immediately preceding movements (Diedrichsen et al., 2010). Due to the slow learning and slow

50 forgetting nature of use-dependent learning in this model, it is robust to changes in movement

51 consistency. In Model 2, the Adaptive Bayesian model, adopted from a study of reaching

52 (Verstynen and Sabes, 2011), use-dependent learning is framed as a process of combining

53   quickly adapting prior probabilities of target (step) locations with current sensory estimates of

54   where to step. Thus, in direct contrast to the Strategy plus Use-Dependent model, the

55   magnitude of use-dependent biases is directly related to the consistency of the environment, or

56   target locations. Critically, while these two computational accounts provide putative explanations

57   for use-dependent biases, they differ markedly in their theoretical underpinnings and, to our

58   knowledge, have not been directly compared with each other. Therefore, we have designed a

59   set of walking experiments that systematically vary environmental consistency during learning

60   and assess the state of use-dependent biases during no-feedback washout trials in order to

61   discriminate between these two competing theories on the underlying constraints of use-

62   dependent learning.

63

64   **Materials and Methods**

65

66   **Behavioral Methods:**

67   *Participants:*

68   Young, healthy male and female individuals between the ages of 18-40 years will be recruited to

69   participate in this study. Potential participants will be included if they are naive to locomotor

70   learning tasks. Potential participants will be excluded if they have a history of any neurologic,

71   psychiatric or cognitive conditions, or have any cardiovascular or musculoskeletal problems that

72   limit their walking. This study has been approved by the (university name redacted until

73   approved for publication) institutional review board.

74

75   *Paradigm:*

76   Participants will perform three sessions of walking spaced 5-10 days apart. During each session

77   they will walk on a dual belt treadmill (with the belts tied throughout the experiment) at a speed

78   between 1.0 and 1.2 meters per second, selected by the participants to ensure a comfortable

79   walking speed based on their anthropometrics. Participants will wear a ceiling mounted harness,

80   which does not provide any body weight support, and hold onto a handrail for safety during all

81   walking phases. A computer monitor placed 60 cm in front of the treadmill will provide real-time

82   visual feedback of the participant's step length (Figure 1A; The Motion Monitor Toolbox,

83   Innovative Sports Training Inc., Chicago, IL, USA).

84

85   The visual feedback will be in the form of a bar graph with a blue bar representing the left leg's

86   step length and a green bar representing the right leg's step length (Figure 1B). The bars will be

87   time synchronized with each respective limb's swing phase, increasing in height until the limb

88   reaches heel strike at which point the bar will hold on the screen until the next swing phase

89   begins. There will also be a pink horizontal target line for each leg which will be derived from

90   each participant's baseline step length for each session and serve as the target during that

91   session's Learning phase.

92

93   Each of the three sessions of walking will involve a similar block schedule. Participants will first

94   be told to "look forward and walk normally" on the treadmill during the Baseline phase for 250

95   strides (i.e., 250 consecutive left heel strikes). No visual feedback will be presented on the

96   monitor during the Baseline phase. In order for participants to understand how changing each

97   step length changes the height of the bars on the screen, they will undergo a short (25 strides)

98   Orientation phase following Baseline during the first session only. During Orientation, the

99   participant will perform guided practice in changing their step lengths (green and blue bars)

100 relative to their baseline (pink horizontal target lines, one for each leg). During the Learning

101 phase, participants will be asked to hit the pink horizontal target lines exactly with each step for

102 500 strides. Both target lines will be changed relative to their baseline step length, leading the

103 participants to take a longer step with the left leg and a shorter step with the right leg. The target

104 lines will have a width of ± 2% step length change from baseline. The researcher will provide

4

105   participants with a prompt to continue hitting the target lines every 100 strides during the

106   Learning phase. During the Washout phase, the feedback will be removed from the screen and

107   participants will be asked to "look forward and walk normally" for 750 strides. The treadmill will

108   be stopped briefly between each phase so that instructions can be provided for the next phase.

109

110   *Conditions:*

111   We will systematically manipulate the independent variable, the consistency of target positions,

112   during the Learning phase. To accomplish this, participants will complete three different

113   conditions: 1) In the Constant condition, the target locations will be set to a constant 22% step

114   asymmetry throughout the Learning phase; 2) In the Low Variability condition, target locations

115   will vary, being drawn from a normal distribution with a mean of 22% and standard deviation of

116   5%; and 3) In the High Variability condition, the targets will vary more widely, being drawn from

117   a uniform distribution with a range of 5%-39% step asymmetry (Figure 1C & D). Based on our

118   pilot testing, changing the target on a stride-by-stride basis made the task too difficult for

119   participants; thus, for both the Low Variability and High Variability conditions, targets will

120   change, with equal probability, every 1-5 strides. To prevent contamination from potential order

121   effects, we will counterbalance the order of conditions across all participants.

122

123   *Data collection:*

124   Kinetic data will be collected at a frequency of 1000 Hz from the dual belt treadmill instrumented

125   with two force plates, one under each belt (Bertec, Columbus, OH, USA). Kinematic data will be

126   collected at a frequency of 100 Hz using a Vicon MX40 motion capture system with 8 cameras

127   and Nexus software (Vicon Motion Systems, Inc., London, UK). We will use a custom marker

128   set with 7 retroreflective markers, one for each heel, each lateral malleolus, and each 5th

129   metatarsal head. The seventh marker will be placed on the left 1st metatarsal head to ensure the

130   tracking system can differentiate between the right and left feet. Kinematic data will be time-

131   synchronized with kinetic data in Nexus.

132

133   *Proposed analysis pipeline:*

134   First, any gaps in the kinematic data will be filled using a Woltring filter for small gaps (1-4

135   frames) and Pattern Fill for larger gaps (>4 frames) in Nexus. The remainder of the data

136   analysis will be performed with custom-written MATLAB scripts (Mathworks, Natick, MA, USA).

137   The code/software described in the paper is freely available online at [URL redacted for double-

138   blind review]. The code is available as Extended Data. Kinematic and kinetic data will be low

139   pass filtered at 10 Hz using a 4th order Butterworth filter. Kinetic data will be used to detect heel

140   strike events when the force plate reads greater that 20 N and toe off events when the force

141   plate reads less than 20 N. Erroneous force plate events will be removed and replaced with

142   kinematic events. For heel strikes this is the most anterior position of the heel marker in the

143   sagittal plane, and for toe offs this is the most posterior position of the 5th metatarsal head in the

144   sagittal plane. Step lengths will be calculated as the sagittal difference between the leading and

145   trailing heel markers at the moment of leading heel strike. The step length during the last 50

146   strides of the Baseline phase will be averaged and used to derive each legs' respective target

147   lines during that session's learning phase. Step lengths will be used to calculate our primary

148   outcome, step asymmetry index (SAI):

149

150   $$SAI = \frac{(Step\ Length_{LEFT} - Step\ Length_{RIGHT})}{(Step\ Length_{LEFT} + Step\ Length_{RIGHT})} * 100\% \tag{1}$$

151

152   Thus, SAI represents the difference between the two step lengths normalized by their sum. We

153   express this measure as a percentage where 0% is perfect symmetry and SAIs further away

154   from 0% indicate greater asymmetry. SAI will be calculated on a stride-by-stride basis

155   throughout all walking phases. We will correct for SAI baseline biases for each participant and

156   each respective training session by subtracting the mean of the last 50 strides of the Baseline

157   phase from all strides for that respective session. The baseline corrected measure will be used

158   for the remainder of our analyses.

159

160   Our analyses of behavior during Learning will focus on checking our assumptions, based on the

161   task design and our pilot data (see Figure 4), that the mean SAI will not differ across conditions

162   (Learning SAI mean), but the SAI standard deviation (Learning SAI σ) will. The purpose of the

163   Learning phase is to provide the necessary task practice to develop potential use-dependent

164   biases. The magnitude of use-dependent biases cannot be directly measured during Learning,

165   since other processes are active during this period—cognitive strategies in the case of the

166   Strategy plus Use-Dependent model and Bayesian estimation of visual target location in the

167   case of the Adaptive Bayesian model. Thus, as expected, our models do not make qualitatively

168   different predictions regarding behavior during the Learning phase.

169

170   Our hypotheses focus on use-dependent biases, probed during the no-feedback Washout

171   phase. Use-dependent biases will be analyzed at two different time points. First, to characterize

172   the total magnitude of use-dependent learning, we will calculate the mean SAI during the first 5

173   strides of the Washout phase (Initial Bias). Second, to characterize early changes in use-

174   dependent biases during the Washout phase, we will calculate the mean SAI of strides 6-30 of

175   the Washout phase (Early Washout; Day et al., 2018; Leech et al., 2018). We will also analyze

176   the rate of washout by regressing subsequent strides onto current strides for the first 50 strides

177   of the Washout phase. We will report 1-β (slope) as it quantifies the amount of unlearning per

178   stride during the Washout phase (Kitago et al., 2013; Wood et al., 2020).

179

180   **Model-Based Methods:**

181 We have adapted two computational models of use-dependent learning that can explain

182 behavior following training with consistent targets (see simulation section); however, the two

183 models make dissociable predictions regarding the effect that changes in movement

184 consistency during Learning have on use-dependent biases. We refer to the first model as the

185 Strategy plus Use-Dependent model (Model 1). This model was inspired by a previously

186 developed dual-process model of error-based and use-dependent learning (Diedrichsen et al.,

187 2010). The second model is referred to as the Adaptive Bayesian model (Model 2) and was

188 adopted from a reaching study of use-dependent learning (Verstynen and Sabes, 2011).

189

190 *Strategy Plus Use-Dependent model:*

191 The Strategy plus Use-Dependent model conceptualizes overall motor output as the sum of two

192 parallel processes: cognitive strategy and use-dependent learning. This model attempts to

193 capture the previously reported phenomenon that participants are able to explicitly control SAI in

194 response to visual feedback, yet still demonstrate aftereffects (French et al., 2018; Long et al.,

195 2016; Wood et al., 2020). Strategic learning accounts for the voluntarily controlled component of

196 SAI, while use-dependent learning is insensitive to explicit task goals, and is instead an

197 obligatory stride-by-stride biasing of motor output based purely on recent actions (Diedrichsen

198 et al., 2010). In the context of the current study, the motor output is SAI (x): the sum of the

199 strategic process (s) and the use-dependent process (w) on each stride, n:

200

201 $x_{n+1} = s_{n+1} + w_{n+1}$ (2)

202

203 The strategic process corrects errors (e) between the motor output (x) and the target (t):

204

205 $e_n = t_n - x_n$ (3)

206     $s_{n+1} = \begin{cases} A * s_n + C * e_n, & with\ VF \\ 0, & without\ VF \end{cases}$ (4)

207     $0 < A < 1,$

208     $0 < C < 1$

209

210   In this model, A is a retention factor representing how much of the strategy (s) is retained from

211   one trial to the next, and C is the proportion of the error that is corrected for on each stride. As

212   this is a strategic, or voluntary, process, we assume that s is equal to zero when the visual

213   feedback (VF) is turned off and the participants are instructed to walk normally.

214

215   Use-dependent learning (w) occurs in parallel with strategy and becomes biased towards the

216   current motor output (x). E represents the retention factor for use-dependent learning and F is

217   the use-dependent learning rate. Note that the update is a function of the motor output, as

218   opposed to an error signal:

219

220     $w_{n+1} = E * w_n + F * x_n$ (5)

221     $0 < E < 1,$

222     $0 < F < C$

223

224   We assume the use-dependent process learns much slower than a strategic process

225   (Diedrichsen et al., 2010) and thus constrain F to be at least 5 times less than C. During

226   washout, when the visual feedback is off and there is no strategy, motor output reflects the sole

227   activity of use-dependent learning.

228

229   *Adaptive Bayesian Model:*

230   In the Adaptive Bayesian model, predicted step length is the weighted combination of expected

231   target locations based on prior experience and current sensory estimates of target location.

232

233   Formally, this model follows from Bayes' Theorem and combines the prior expectation of the

234   SAI target ($\bar{\theta}$) with the current sensory estimate of target position (θ) to compute the posterior

235   probability distribution. The model assumes that the motor output is a direct readout of the

236   maximum a posteriori (MAP) estimate (θ_{MAP}) of target location, as in Verstynen and Sabes

237   (2011):

238

239    $$\theta_{MAP} = \frac{\sigma^2_{posterior}}{\sigma^2_{prior}} * \bar{\theta} + \frac{\sigma^2_{posterior}}{\sigma^2_{likelihood}} * \theta \qquad (6)$$

240

241   We assume the prior and likelihood are normally distributed, therefore $\sigma^2_{posterior,n}$ is the variance

242   for the posterior probability and is equal to $(\sigma^{-2}_{prior,n} + \sigma^{-2}_{likelihood})^{-1}$. The mean of the likelihood

243   is centered on the true target location, θ, on each stride, n. The likelihood's variance ($\sigma^2_{likelihood}$)

244   is a free parameter representing the amount of sensory uncertainty regarding target location.

245   The adaptive nature of the model is captured by the stride-by-stride updating of the prior

246   probability's parameters $N(\bar{\theta}_n, \sigma^2_{prior,n})$:

247

248    $$\bar{\theta}_{n+1} = (1 - \beta) * \bar{\theta}_n + \beta * \theta_n \qquad (7)$$

249    $$\sigma^2_{prior,n+1} = (1 - \beta) * \sigma^2_{prior,n} + \beta * (\bar{\theta}_n - \theta_n)^2 \qquad (8)$$

250    $0 < \beta < 1,$

251    $0 < \sigma^2_{likelihood} < 100$

252

253   β is a free parameter representing the learning rate. The Adaptive Bayesian model has two free

254   parameters, in comparison to the four free parameters of the Strategy plus Use-Dependent

255   model.

256

257   Our two models provide distinct interpretations of how use-dependent biases evolve and the

258   specific constraints acting on them. The Strategy plus Use-Dependent model assumes

259   separate, yet parallel, explicit (strategy) and implicit (use-dependent) learning mechanisms. In

260   this model, use-dependent learning is persistently active, but evolves slowly in response to the

261   direction of the walking asymmetry. In direct contrast, the Adaptive Bayesian model does not

262   invoke separate explicit and implicit learning processes, but frames the problem of changing an

263   agent's behavior in response to visual targets (or the absence of them, as during Washout) as

264   one of Bayesian estimation (Ernst and Banks, 2002; Körding, 2007; Verstynen and Sabes,

265   2011; Wei and Körding, 2009). The MAP estimate may certainly result from contributions of

266   implicit and explicit mechanisms, but the model does not distinguish between the two.

267

268   **Statistical Analysis:**

269   Model fitting and model selection, in conjunction with behavioral analyses, will form the basis for

270   our inferences regarding which of the two models (hypotheses) is more strongly supported.

271

272   *Computational Models:*

273   Our competing hypotheses are encapsulated by our two computational models, the Strategy

274   plus Use-Dependent model (Model 1) and the Adaptive Bayesian model (Model 2), and their

275   corresponding predictions regarding use-dependent biases. Relative support for one model over

276   the other will be formally assessed using model selection criteria, specifically Akaike Information

277   Criterion (AIC) scores. After the data are collected, we will fit both models to individual

278   participant data from all three conditions combined, using the fmincon function in MATLAB. This

279   will allow us to obtain one set of parameter values for each model for each individual participant.

280   We will use AIC to objectively compare the model fits and compare these AIC values between

281   the two models using a paired t-test. Quality of model fits will be reported using R-squared

282   values. The number of subjects best fit by each model will be reported and presented in visual

283   format in a figure. As fits to individual data can be noisy (Wilson and Collins, 2019), we will also

284   calculate AIC scores on fits to the average learning functions across conditions. To provide

285   confidence intervals on parameter estimates, we will fit the average learning function for each of

286   10,000 bootstrapped samples and report the empirical 2.5th and 97.5th percentile values.

287

288   _Behavior:_

289   As stated above, we do not have competing hypotheses regarding the Learning phase, and we

290   expect participants to accurately follow the visual targets. This should result in Learning SAI

291   mean values that do not differ across conditions, but larger Learning SAI σ values when going

292   from Constant to Low Variability and High Variability conditions (see Pilot Data section and

293   Figure 4). These assumptions will be assessed using repeated measures ANOVA and post-hoc

294   Bonferroni-corrected pairwise comparisons if necessary.

295

296   As the Adaptive Bayesian model predicts differences in use-dependent bias across conditions,

297   we will perform statistical analyses of Initial Bias, Early Washout and washout rate using

298   separate repeated measures ANOVAs. In cases of a significant ANOVA, post-hoc pairwise

299   comparisons will be performed with Bonferroni-corrected t-tests. Because the Strategy plus

300   Use-Dependent model predicts similar use-dependent biases across conditions, we will also

301   perform equivalence tests on Initial Bias, Early Washout and washout rate using the two one-

302   sided tests (TOST) procedure (Lakens, 2017). Briefly, the TOST procedure involves two

303   composite null hypotheses that an observed effect is either below or above chosen equivalence

304   bounds (Cohen's *d* of ± 0.3; see Lakens, 2013), and thus provides a rigorous means of inferring

305   the lack of a meaningful effect.

306

307   We will report t- and F- statistics, exact p-values, means, 95% confidence intervals and

308   standardized effect sizes (Cohen's *d* for t-tests and η_p^2 for ANOVAs). For equivalence testing,

309   we will also report the empirical equivalence bounds for which we would be able to reject the

310   null hypothesis that there is an effect of condition. Assumptions of normality and equality of

311   variances will be tested with the Shapiro-Wilks test and Levene's test, respectively. In cases

312   where these assumptions are not met, we will perform non-parametric permutation tests. For

313   pairwise comparisons, we will use the difference between group means as our test statistic, to

314   be compared to a null distribution created by random shuffling of group assignment in 10,000

315   Monte Carlo simulations (resampling with replacement), to obtain an exact p-value. For

316   comparisons involving more than two conditions, we will implement a similar approach but use

317   the F-value obtained from a repeated-measure ANOVA as our test statistic.

318

319   In addition to our parametric analyses of pre-selected epochs, we will also employ a cluster

320   permutation analysis in order to assess potential SAI differences across the entire Washout

321   phases for each condition (Holmes et al., 1996; Maris and Oostenveld, 2007). In this analysis,

322   we will compare SAI differences between two conditions at a time with paired t-tests between

323   bins of 3 strides. Binning, in this case, is used to mitigate the effects of stride-to-stride SAI

324   variability on the analysis and thereby reduce the probability of a Type II error. The largest

325   cluster of consecutive significant paired t-tests (p < 0.05) will be determined and the t-statistics

326   for this cluster will be summed. The summed t-statistics will be compared to a null distribution of

327   summed t-statistics. The null distribution is built from resampling each group without

328   replacement 10,000 times and computing the largest cluster's t-statistic for each sample. This

329   null distribution serves as the null hypothesis which states that each group is sampled from the

330   same distribution. The cluster size from the empirical data is then compared to the null

331   distribution of 10,000 samples. This comparison provides a probability that the empirical cluster

332   is different from the null distribution while controlling for type I error (Maris and Oostenveld,

333   2007; Nichols and Holmes, 2002). This analysis will be performed three times to compare

334   differences between each condition.

335

336   *Power analysis:*

337   We performed a power analysis to determine the sample size required to detect differences in

338   use-dependent biases across conditions, with alpha of 0.05 and power of 0.90. Based on an

339   estimated standardized effect size (Cohen's *d*) of 0.91 from a prior study comparing locomotor

340   use-dependent biases across different magnitudes of induced stepping asymmetries during

341   learning phases (Wood et al., 2020), we will require 15 subjects. We therefore expect to recruit

342   15-21 individuals for this study in order to account for possible attrition and to exceed the

343   minimum acceptable power. This sample size will also ensure appropriate counterbalancing of

344   practice schedules across participants while also being well-above the threshold of statistical

345   power documented in comparable motor learning studies (Diedrichsen et al., 2010; French et

346   al., 2018; Long et al., 2016; Verstynen and Sabes, 2011; Wood et al., 2020).

347

348   *Data replacement:*

349   Data will only be replaced under the following conditions:

350   1) If a participant does not complete the entire learning task for all 3 conditions due to a

351   technical error or equipment failure in the middle of data collection or if the participant chooses

352   to drop out of the experiment.

353   2) If the experimenter deems the participant unsafe to continue the study, which may occur if

354   there is an injury or illness after the participant has been enrolled.

355 3) If a participant does not meet a threshold of performance on the task, which will be defined as

356 falling outside of 3 standard deviations from the mean performance in terms of target accuracy.

357 Target accuracy will be defined as the mean absolute difference between the target SAI and the

358 actual SAI measured across the entire Learning phase.

359

360 **Completed work:**

361 *Confusion Matrices:*

362 To determine whether the models are distinguishable and the best method of objective

363 comparison, we performed model recovery analysis (Hardwick et al., 2019; Wilson and Collins,

364 2019). By sequentially simulating data from each model and then comparing model fits of the

365 simulated data, we show in the confusion matrices (Figure 2) that the models are

366 distinguishable under these ideal circumstances. A confusion matrix provides the probability that

367 a randomly generated, simulated model is fit better by itself or other models using objective

368 model comparisons. Ideally, the model that generated simulated data will be better fit by itself

369 than by the other model, resulting in values closer to 1 when comparing the simulations and fits

370 from the same models (lighter colors on main diagonals in Figure 2) and values closer to 0

371 when comparing simulations and fits from opposing models (duller colors on off-diagonals in

372 Figure 2). We fit the simulated data from each model using the same fitting procedure as above

373 and found that comparison using Akaike Information Criterion (AIC) distinguishes between the

374 models better than Bayesian Information Criterion (BIC).

375

376 *Simulations:*

377 We simulated both models to demonstrate how each accounts for the consistency of practiced

378 target step lengths. The Strategy plus Use-Dependent model is robust to environmental

379 consistency in cases, as here, where there is a large asymmetry in one direction. The model

380 assumes use-dependent learning is slower to learn and washout than cognitive strategies;

15

381   therefore, as long as the practiced asymmetry is much larger than the current state of use-

382   dependent learning, the consistency of target step lengths has minimal impact on its output. The

383   Adaptive Bayesian model stands in direct contrast to this framework. In this model, the MAP

384   estimate, and thus the observed use-dependent bias during Washout, is sensitive to

385   environmental consistency: The more consistent (i.e. less variable) the schedule of target step

386   lengths, the more biased towards the prior (i.e., away from the likelihood) the MAP becomes;

387   conversely, the more variable the schedule, the less weight is given to the prior and the more

388   the MAP is pulled towards the likelihood (i.e., the actual target location).

389

390   We obtained parameters for model simulation by fitting the models to each individual from a

391   previously collected dataset (R-squared values: Adaptive Bayesian model = 0.895 ± 0.019;

392   Strategy plus Use-Dependent = 0.870 ± 0.021 [mean ± SEM]). We then simulated our proposed

393   experiment 1000 times with the mean learning function from each bootstrapped sample of the

394   individual parameter fits. Figure 3 details the simulated data from these parameters for each

395   condition. The panels in Figure 3A show each model simulation for the entire experiment.

396   Across all 3 conditions, the models diverge in their predictions regarding use-dependent biases

397   during the Washout phase.

398

399   We plotted use-dependent biases during both Initial Bias and Early Washout (Figure 3B and C).

400   Overall, the Strategy plus Use-Dependent model predicts more consistent use-dependent

401   biases across conditions for both Initial Bias and Early Washout. However, the Adaptive

402   Bayesian model demonstrates consistently decreasing aftereffects when the conditions become

403   less stable during the Learning phase. For our third point of direct comparison between model

404   predictions, we also analyzed the washout rates for each model (Figure 3D). The Strategy plus

405   Use-Dependent model predicts a consistent washout rate across conditions, whereas the

406   Adaptative Bayesian model predicts slower washout as the conditions during Learning increase

407   in variability. Based on these simulations, if the Strategy plus Use-Dependent model is a more

408   accurate model, we will observe similar use-dependent biases between conditions; however, if

409   the Adaptive Bayes model is more accurate, we should observe differences between conditions

410   in our behavioral analyses.

411

412   *Pilot Data:*

413   To assess the feasibility of our behavioral methods, and specifically, to determine if individuals

414   are able to follow frequently changing step length targets, we collected pilot data from 3

415   individuals for the High Variability condition, with 2/3 of these individual also completing the

416   Constant condition (see Figure 4). The pilot results show that participants were able to follow

417   the feedback during the High Variability condition with a mean absolute distance of 4.2 cm from

418   the targets. Furthermore, we correlated step length targets with actual step lengths for each

419   subject during the Learning phase: mean R-value = 0.59 and 0.78 for the right and left step

420   lengths, respectively ($p < 0.0001$ for all). The pilot results are also consistent with our

421   assumption that, during the Learning phase, SAI means will be similar across conditions

422   (Learning SAI mean), but SAI standard deviation (Learning SAI σ) will be different (Figure 4).

423   These pilot data will not be included in the final analysis.

424

425   **Timeline for completion:**

426   We have received IRB approval from our university for this project. However, all labs have been

427   shut-down due to the COVID-19 pandemic. Data collections are ready to be initiated as soon as

428   human research resumes at the university. Given uncertainty around when labs will be

429   reopened, we offer a proposed resubmission window between January 15th, 2021 and June

430   15th, 2021.

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Figure 1: Experimental setup. (A) Participants will walk on a treadmill while watching feedback of their step length. Their step lengths will be represented as a blue (left) and green (right) bar which increases in height during the swing phase and holds on the screen at the moment of heel strike. **(B)** During the Learning phase, the participant will aim for a pink horizontal target line which is derived from their baseline step length. On the first stride of learning the target will be offset from their baseline (**B** – top panel), and the subject will have to adjust their step length on subsequent strides to hit the target (**B** – bottom panel). **(C)** Target distribution for each condition: During the Constant condition targets will always be at 22% SAI during the Learning phase. During the Low Variability condition targets will be drawn from a normal distribution centered around 22% SAI and a standard deviation of 5% SAI. During the High Variability condition targets will be drawn from a uniform distribution between 5% and 39% SAI. Note the different scales for the y-axes. **(D)** Learning schedule for each condition: Each condition will include a Baseline (Bsl), Learning and Washout phase. Shaded regions indicate no visual feedback will be shown on the screen and participants are told to "walk normally", so the target is effectively 0% SAI. During the Learning phase targets will vary based on the condition.

Figure 2: Confusion matrices. Four different confusion matrices for each condition and all conditions combined. Lighter colors indicate higher percentages of better fits for each simulated model. Model fits were compared using AIC. AB is the Adaptive Bayesian model, S+U is the Strategy plus Use-Dependent model.

Figure 3: Simulated results. (A) The experiment was simulated 1000 times using bootstrapped samples of parameter values from a previously collected dataset. Results of the simulation are plotted as means with shaded errors indicating standard deviation of bootstrapped sample means. The first 50 strides of the Washout phase are plotted in the insets.

524   **(B)** Initial Bias is the mean of the first 5 strides of the Washout phase and **(C)** Early Washout is

525   strides 6-30 of the Washout phase. **(D)** Mean and standard deviations of washout rates for each

526   model across conditions. For panels B-D, filled circles represent the mean and error bars

527   represent one standard deviation of bootstrapped sample means. Some error bars are not

528   visible as their values are small and thus obscured by dots representing mean values.

529

530   **Figure 4: Pilot data.** Mean values are represented as horizontal bars and individual participants

531   as dots. SAI was averaged across the entire Leaning phase for each participant for the

532   Constant and High Variability conditions (Learning SAI mean). SAI standard deviation was

533   calculated across the entire Learning phase for each participant for the Constant and High

534   Variability conditions (Learning SAI σ).

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