1   **Sequential Effects in Reaching Reveal Efficient Coding in Motor Planning**

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3   Tianhe Wang[1,2,] *, Yifan Fang[1], David Whitney[1,2,3]

4   1 Department of Psychology, University of California, Berkeley

5   2 Department of Neuroscience, University of California, Berkeley

6   3 Vision Science Program, University of California, Berkeley

7   *Corresponding Author: tianhewang@berkeley.edu

8   **Abstract**

9   The nervous system utilizes prior information to enhance the accuracy of perception and action. Prevailing

10   models of motor control emphasize Bayesian models, which suggest that the system adjusts the current

11   motor plan by integrating information from previous observations. While Bayesian integration has been

12   extensively examined, those studies usually applied a highly stable and predictable environment. In

13   contrast, in many real-life situations, motor goals change rapidly over time in a relatively unpredictable

14   way, leaving it unclear whether Bayesian integration is useful in those natural environments. An

15   alternative model that leverages prior information to improve performance is efficient coding, which

16   suggests that the motor system maximizes the accuracy by dynamically tuning the allocation of the

17   encoding resources based on environmental statistics. To investigate whether this adaptive mechanism

18   operates in motor planning, we employed center-out reaching tasks with motor goals changing in a

19   relatively unpredictable way, where Bayesian and efficient coding models predict opposite sequential

20   effects. Consistent with the efficient coding model, we found that current movements were biased in the

21   opposite direction of previous movements. These repulsive biases were amplified by intrinsic motor

22   variability. Moreover, movement variability decreased when successive reaches were similar to each

23   other. Together, these effects support the presence of efficient coding in motor planning, a novel

24   mechanism with which the motor system maintains flexibility and high accuracy in dynamic environments.

25

26   Key words:

27   Motor control, Sequential effect, Efficient Coding, Reaching, Bayesian Model

Introduction

Our experiences shape how we perceive and interact with the world. For instance, when facing ambiguous visual stimuli, humans are more likely to identify familiar objects than novel ones[1,2]. Similarly, in reaching tasks, participants infer the state of the environment based on previous observations to apply an optimal action[3–5]. Those processes have been formalized with Bayesian observer models[2,3,6,7], which posit that the system maintains an internal prior based on past observations and integrates this prior knowledge with new sensory input to form optimal estimates[8]. This integration reduces variability in estimation, thereby increasing overall response accuracy.

The Bayesian framework has significantly influenced theories of motor control and motor learning[3,5,9,10]. For example, when localizing hand position, agents combine information from different sensory inputs in a Bayesian-optimal way[9,11,12]. Moreover, sensorimotor learning theories posit that the system uses error information to update the sensorimotor map based on a Bayes rule[13,14]. Furthermore, Bayesian principles have been applied to interpret history effects in reaching tasks. Previous research has shown that after repeatedly performing one action, future movements would be biased toward the repeated direction—a phenomenon known as use-dependent learning[15,16]. The Bayesian model explains this phenomenon by positing that the integration of previous motor goals with the current goal induces a behavioral bias toward the prior mean[17] (Fig 1a-b).

While Bayesian models have been extensively tested in motor control, these tasks often share two key characteristics that may limit the generalizability of those findings. First, the targets used in previous studies frequently possess strong statistical structures, making it easy for participants to anticipate future movements[18]. For example, many studies have sampled targets from unimodal distributions[15,17,19], allowing participants to predict the mean movement direction. Even in center-out reaching tasks, most experiments have utilized only a very small number of targets[20–23], thereby confining the possible motor plans to a very limited subspace. Second, those studies examined effects based on a stable representation of the prior, which is estimated from many observations and remains constant over time.

However, contrary to those two prerequisites, in many real-life situations, motor goals can change rapidly across time in a relatively unpredictable way[18,24]. For example, a basketball player needs to constantly change their motor plans in real-time—suddenly shifting direction, accelerating, jumping, or making quick passes—in response to the unpredictable actions of opponents and teammates. Similarly, when shopping

60   for groceries, the location of each item on the shelf varies, so reaching for one product is independent of

61   where the next one might be. In these cases, the motor system must plan each movement independently

62   rather than relying on a consistent prior. It remains unclear whether Bayesian mechanisms would be

63   beneficial in such volatile environments. Alternatively, other computational mechanisms might be applied

64   when motor goals vary on a short timescale.

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66   An alternative framework, known as efficient coding, offers a distinct perspective on how the brain is

67   constrained by environmental statistics[25,26]. Efficient coding posits that the nervous system minimizes

68   redundancy and maximizes the use of available resources (Fig 1c)[27–30]. In the perceptual domain, it refers

69   to a strategy to encode information in the most compact and effective manner[25,26]. In motor control,

70   efficient coding can be taken as a way to avoid redundancy in the control system and maximize overall

71   accuracy. For example, rather than controlling each muscle individually, the brain coordinates groups of

72   muscles into synergies or modules[31,32]. Moreover, the motor system may dynamically allocate encoding

73   resources based on environmental statistics to maximize the mutual information it carries (Fig 1c).

74   Interestingly, previous theoretical work[27,28] suggested that this process will induce an encoding bias in the

75   opposite direction of the prior mean (Fig 1d), a prediction opposite to the Bayesian model. While this

76   principle has been extensively studied in perceptual systems[25,27,33,34], it is less clear whether it applies to

77   motor planning.

78

79   To understand how motor planning is adjusted based on prior information in volatile environments, we

80   aim to examine sequential effects in a center-out reaching task where the target is randomly sampled

81   from a uniform circular distribution. As such, no mean movement direction can be predicted, and each

82   movement is completely independent. While the overall prior is not informative in this situation, the

83   system may maintain a short-term prior that is updated quickly when the goals change rapidly[35,36]. This

84   flexibility could be particularly beneficial for the motor system, which may need to repeat similar

85   movements in quick succession, though not necessarily over extended periods.

86

87   Following the Bayesian model, prior updating would generate an attractive sequential effect, where the

88   current response is biased toward previous responses that have just been performed (Fig 1a-b)[17,35,36]. This

89   effect, known as serial dependence, has been widely observed in perceptual tasks across different

90   modalities[37–40]. On the other hand, the efficient coding models predicts the current movement will be

91   biased away from the previous movement. As such, efficient coding and Bayesian integration generate

92 opposite predictions on the sequential effect, allowing us to distinguish between these two theoretical

93 frameworks in the current study. Additionally, we explored the temporal dynamics of these sequential

94 effects and how they are modulated by intrinsic motor variability, which helps further differentiate

95 between the models. The empirical and computational results together illustrate how the motor planning

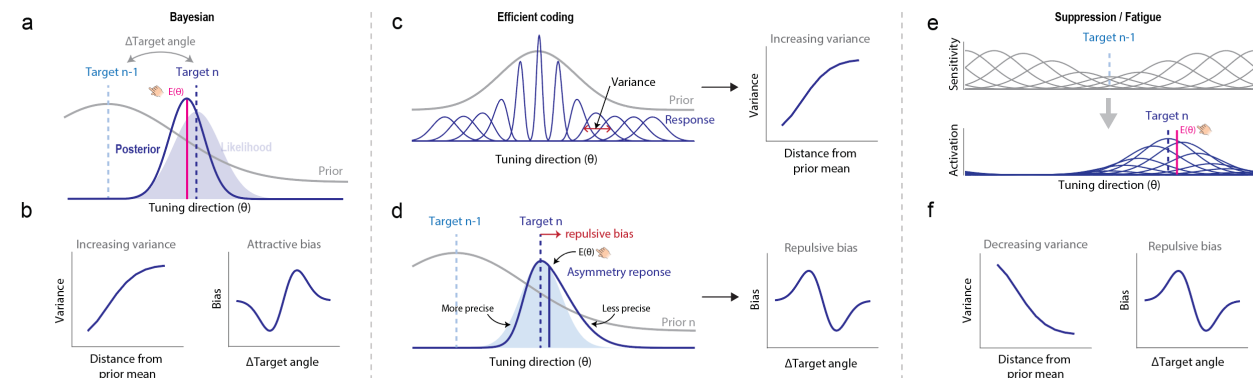96 system adapts to the statistical properties in a dynamic environment.

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Figure 1. Models for sequential effects in motor planning.

100 a) Illustration of a Bayesian model in motor planning. b) The Bayesian model predicts increasing variance and

101 attractive bias. c) Illustration of an efficient coding framework. The motor system encodes a motor command based

102 on the perceived target following an efficient coding rule. Specifically, the precision of encoding the direction of

103 movement should match the prior. The blue curves indicate the encoding function to different movement directions,

104 with its variability constrained by the prior distribution. The variability in movement (inaccuracy) increases as the

105 current movement diverges from the prior mean. d) Given the heterogeneity of encoding resources across the space,

106 the encoding function for a given movement direction is asymmetric, with a flatter tail extending away from the

107 prior (see method). Intuitively, this is because the encoding variability is smaller on the prior side and larger on the

108 opposite side. E(θ) represents the mean of this distribution, which is biased in the direction opposite to the prior

109 mean. The shaded blue distribution illustrates the response in the absence of efficient coding. In this context, we

110 assume the prior is primarily influenced by the movement direction in the previous (n-1) trial. As such, the efficient

111 coding model predicts a repulsive sequential bias. e) Illustration of the suppression model. The sensitivity of the unit

112 tuned to the previous movement decreases, which causes an asymmetric representation of the subsequent

113 movement direction. f) The suppression model predicts decreasing variance and repulsive bias.

114

Results

116 A repulsive sequential bias in reaching

117 To examine motor sequential effects in an unpredictable environment, in Exp 1, we employed an online

118 reaching experiment where participants control a cursor with a trackpad. In each trial, a target appeared

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119   at a random position along an invisible circle and participants made a center-out reaching movement from

120   a central start position towards the target (Fig 2a). The cursor was invisible during the movement to

121   prevent online corrections. Endpoint feedback was provided after the movement to indicate the hand

122   position at the target radius.
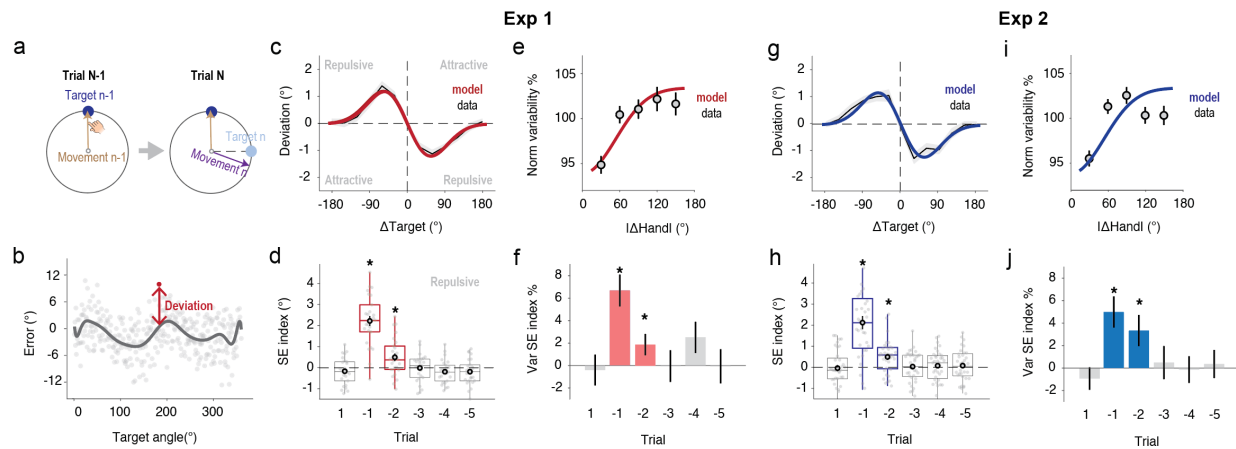
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Figure 2. Sequential effects in reaching. a) An illustration of the repulsive bias predicted by the efficient coding model. b) The motor bias of a sample participant. The gray curve shows the smoothed motor bias function. The deviation was defined as the difference between the current response and the bias. d) Sequential bias in Exp 1: The motor deviation of trial n was plotted as a function of the difference in the target angle between trial N and trial N-1 (Δtarget). This figure shows a repulsive sequential effect. e) SE index showing the influence of the target in trial N+1, and trials N-1 to N-5 on the direction of reaching in trial n. f) The normalized movement variance increased with the distance between movement N and the movement N-1 ($|\Delta$hand$|$). g) Sequential effect (SE) index derived from a general linear model between normalized movement variance and $|\Delta$hand$|$ for trial N+1, and trials N-1 to N-5. h-k). Sequential effects in Exp 2. The only difference between Exp 1 and 2 was the lack of feedback in Exp 2. Results were very similar to panel c-f. In c, e, g, i, the black curve indicates data, and the colored curve indicates the prediction of the best-fitted efficient coding model (see method). Error bars and shaded areas indicate standard error. *, $p<0.02$.

138   To obtain an accurate assessment of the sequential effect, we eliminated the impact of systematic bias

139   by fitting a motor bias function based on the target position (Fig S2) for each participant. The residual

140   error, representing the deviation from this fitted motor bias function (Fig 2b), was defined as the

141   deviation[35,36,41,42] and was used to analyze the sequential effects.

142

143   We observed a repulsive sequential bias in reaching. When movement deviation is plotted as a function

144   of the angular difference between the current and previous targets (ΔTarget). We found that the direction

145   of movement in the current trial (trial n) was biased away from the previous target (trial n-1, Fig 2c), with

146   the magnitude of this repulsive effect increasing with ΔTarget, peaking at 1.5° for a ΔTarget of

147   approximately 60°. This bias function aligns with predictions from the efficient coding model rather than

148   the Bayesian model. To quantify the size of the sequential bias, we calculated a sequential effect (SE)

149   index, defined as the difference between the average bias for Δ Target from -90° to 0° and 0° to 90°. A

150   positive SE index signified a repulsive effect. We found an SE index significantly larger than 0 in trial N-1

151   (t(25)=9.5, p<.001, d=1.9) and trial N-2 (t(25)=2.8, p=0.010, d=0.55), but not in trial N-3 (t(25)=-0.10,

152   p=0.92, d=-0.02; Fig 2d). We further showed that the attenuation of the sequential effects depended on

153   both passing time and intervening information by manipulating the inter-trial-intervals in Exp S1 (See

154   Supplementary Result 1, Fig S1).

155

156   <u>Sequential effects in reaching align with the efficient coding model</u>

157   The repulsive sequential biases observed in Exp 1 support the predictions of the efficient coding model

158   rather than the Bayesian model. However, we note that an alternative explanation for this effect could be

159   suppressive modulation or fatigue affecting the units tuned to the recently performed movement

160   direction. The suppression model predicts a repulsive sequential bias due to the asymmetric responses of

161   units on the suppressed and unsuppressed sides (Fig. 1e). However, unlike the efficient coding and

162   Bayesian models, which both facilitate the processing of repeated stimuli, the suppression model posits

163   that movements closer to the previous movement are encoded with less precision and exhibit greater

164   variability compared to those further away (Fig. 1f).

165

166   To compare the efficient coding model and the suppression model, we measured the sequential effect as

167   a function of movement variance. Consistent with the efficient coding model, the movement variance

168   increased with the distance between the directions of two consecutive movements (Fig 2g–h). As such,

169   the repulsive sequential bias is unlikely to be due to fatigue. We quantified this effect by fitting a sigmoid

170   function with motor variance as the dependent variable and the difference in hand angle as the

171   independent variable, pooling data from all participants. The SE index was defined as the amplitude of the

172   sigmoid predicted by the best-fit function (Fig 2e). Similar to the sequential bias, this SE index of

173   movement variance dropped rapidly across trials: a significant effect was found for only trial N-1 (p < 0.001)

174   and N-2 (p = 0.026, Fig 2f), as measured by bootstrap resampling. The effect disappeared for trial N-3 (p

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175 = 0.98), which occurred ~6s prior. The sequential effect in movement variance confirms that, while there

176 was a repulsive bias, the motor system utilizes previous information to increase overall accuracy in

177 reaching, consistent with the key idea of the efficient coding model.

178

179 We note that a potential issue in Exp 1 is that endpoint feedback could facilitate the recalibration of the

180 sensorimotor system. This recalibration process might be specific to areas near the recently reached

181 positions, potentially contributing to the observed sequential effect in motor variance. To eliminate the

182 potential influence of sensorimotor recalibration, we conducted a replication of Exp 1 without endpoint

183 feedback (Exp 2). The results showed remarkably similar sequential effects in both movement bias and

184 variance (Fig 2g-j), confirming that these effects were independent of visual feedback or sensorimotor

185 recalibration.

186

187 <u>Dissociating sequential effect in movement and perception.</u>

188 Sequential effects have been widely observed in perceptual tasks[37,38,43]. While we tried to minimize the

189 role of visual uncertainty and perceptual working memory in Exp 1, a more rigorous examination was

190 necessary to differentiate effects originating in the motor versus the perceptual systems[44]. To this end, in

191 Exp 3 we implemented a design where participants were instructed to either move directly towards the

192 target (Standard condition, 75% of trials) or in the opposite direction (Opposite condition, 25% of trials).

193 As a critical test of the source of these sequential effects in Exp 1, we analyzed scenarios where trial N-1

194 was an Opposite trial and trial N was a Standard trial (Fig 3a, bottom). In such cases, the inconsistency

195 between movement direction and target in trial N allowed us to disentangle the influences of target

196 location representation from the motor control itself. If the repulsive bias was primarily driven by motor

197 factors, the direction in trial N would be repelled by the movement in trial N-1. Conversely, if perception

198 of the target location was the cause, trial N's reaching direction would be repelled by the perceived

199 location of the target in trial N-1.

200

201 When two consecutive trials were both Standard trials (Fig 3a, top), we observed a repulsive bias similar

202 to that in Exp 1 (Fig 3b). Crucially, when trial N-1 was an Opposite trial and trial N was a Standard trial, the

203 direction in trial N was repelled away by the previous *reaching movement* ($t(40)=4.4$, $p<.001$, d=0.68), not

204 by the previous target location (Fig 3c). The magnitude of this repulsive effect from the previous

205 movement was comparable to that observed when both trials N and N-1 were Standard conditions,

206 indicated by the SE indexes ($t(40)=0.70$, $p=.49$, d=0.11; Fig 3d). Moreover, when examining the sequential

207 effect on motor variance, we found that variance increased with the difference in hand angle ($p<.001$,

208 Bootstrap, Fig 3e) rather than the difference in target angle ($p=0.20$, Fig 3f-g). These results suggested

209 that the sequential effects in Exp 1-2 were rooted in the motor system rather than the perceptual system.
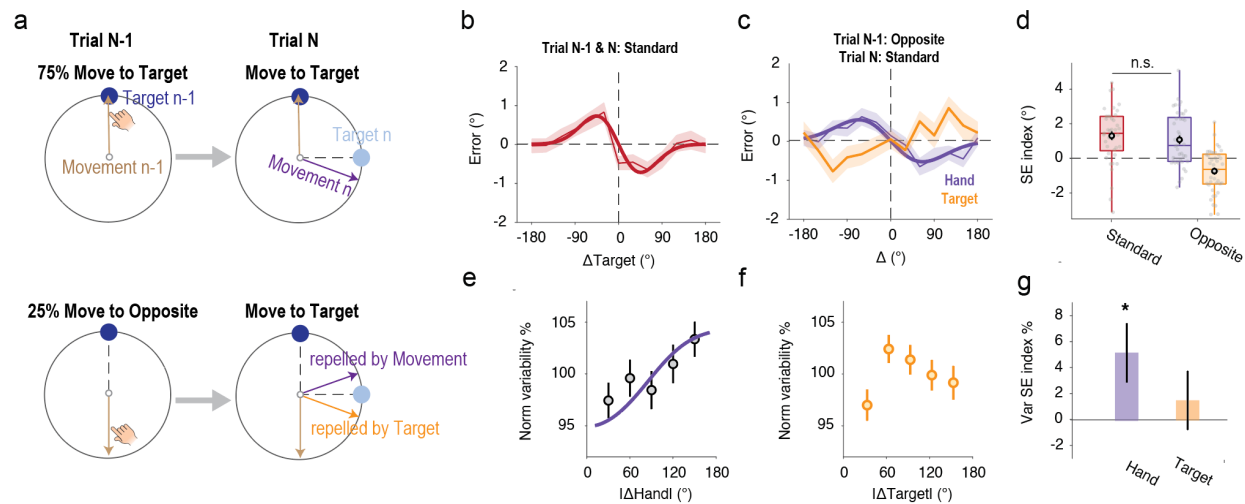
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212 **Figure 3. Sequential effects in reaching were associated with motor movement rather than perception.** a) Design

213 of Exp 3: In 75% of trials, participants were directed to move towards the target (Standard), and in 25% of trials, they

214 were directed to move in the opposite direction of the target (Opposite). A repulsive effect was expected when both

215 trials N and N-1 were Standard trials (top row). In cases where trial N was a Standard trial and trial N-1 was an

216 Opposite trial, the design allowed examination of whether the repulsive effect was triggered by target perception

217 or movement (bottom row). b-c) The sequential effect of motor bias when both trial N and trial N-1 were Standard

218 trials (b) or when trial N-1 was an Opposite trial and trial N was a Standard trial (c). The thin lines with shaded error

219 bars indicate data, and the thick curve indicates the prediction of the efficient coding model. d) The sequential bias

220 was similar across panels b and e when the SE index after the Opposite trial was measured based on Δ Hand rather

221 than Δ Target. e-f) After an Opposite trial, movement variance increased as a function of Δ Hand (e) rather than Δ

222 Target (f). The motor variance increased with Δ Hand rather than Δ Target. g) The coefficients of linear regression

223 measured from panel e-f. Error bars and shaded areas indicate standard error. *, p<.001.

224

225 We have shown that the sequential bias in Exp 1-3 was caused by movement; However, it remains possible

226 that this effect could be mediated by perception. For instance, the movement from trial N-1 might repulse

227 the perception in trial N, thereby affecting the subsequent movement (mediated hypothesis).

228 Alternatively, the current movement could be directly repelled away by the previous movement (direct

229 hypothesis). To distinguish between these hypotheses, we examined cases where trial N-1 was a Standard

230 trial and trial N an Opposite trial (Fig S3a). Under the mediated hypothesis, the current perception is

231   repelled away from the previous movement, so that we would expect the current movement to be

232   attracted towards the movement N-1 when participants are instructed to move in a direction opposite

233   that of target N. In contrast, the direct hypothesis predicts the current movement to be repelled from the

234   target/movement in N-1 (Fig S3b). Our findings aligned with the direct hypothesis (Fig S3c-d). Based on

235   the results in Exp 3, we concluded that the current movement was directly influenced by the previous

236   movement.

237

238   We also observed a priming effect in reaction time in Exp 1-3. Consistent with the notion of efficient

239   coding, reaction times were shorter when the current target was close to the previous target (Fig S4a-b).

240   However, this effect may pertain more to target detection than motor planning. The reaction time for the

241   current trial was influenced by targets presented more than 10 trials in the past (Fig S4c-d), which was

242   very different from the temporal dynamics of sequential effects in movement direction or motor variance

243   (Fig 2d, f). Moreover, in Exp 3, the reaction time priming effect was similar after both Opposite and

244   Standard trials (Fig S4e), suggesting the effect may be related to target detection rather than reaching,

245   per se.

246

247   Encoding noise enhances the repulsive sequential bias.

248   Another key prediction of the efficient coding theory is that the sequential bias should be modulated by

249   encoding noise. Specifically, increased noise within the system should lead to a broader distribution of

250   the response signal. Consequently, the average response of the system will exhibit a larger repulsive bias

251   relative to the prior mean (Fig 4a). To examine this, we compared the sequential bias in reaching

252   movements between the dominant hand and the non-dominant hand, with the premise that encoding a

253   movement with the non-dominant hand incorporates more noise (Fig 4b), which should increase the

254   repulsive bias. In Exp 4, we performed a similar center-out reaching task and participants were randomly

255   instructed to use one hand per trial. To make sure that participants adhered to the instruction, we

256   performed this experiment in a lab setup with the experimenter supervising the task (Fig 4c). Participants

257   moved their occluded hand on a tablet, with the visual stimulus displayed on a monitor directly above (Fig

258   4c). Consistent with our assumption, participants showed significantly lower motor variability with the

259   dominant hand compared to the non-dominant hand ($t(23)=4.9$, $p<0.001$, d=1.0; Fig 4d).
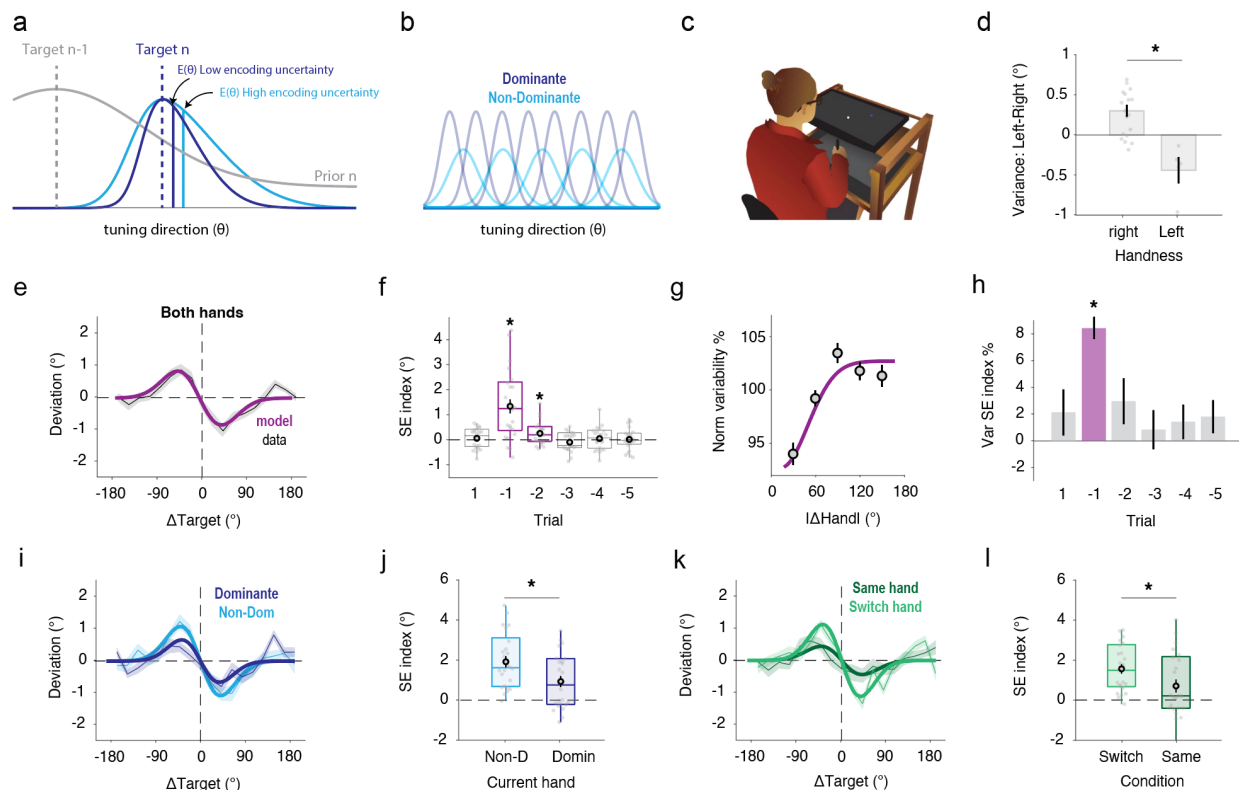
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Figure 4. The repulsive sequential bias increased with the encoding noise in the motor system. a) Illustration of how encoding noise increases the repulsive bias based on the efficient coding model. b) We assumed that the non-dominant hand has fewer movement planning units with higher encoding uncertainty, indicated by a broader tuning profile. c) Illustration of the lab-based setup. d) Difference in motor variance between the left and right hand. Right-handed participants showed nosier movements using their left hand and vice versa. e-f) The sequential effect of motor bias (e) and the SE index (f) when data from both hands were collapsed. g-h) Sequential effect of motor variance (g) and (h) the estimated coefficients from a general linear model. i-j) A stronger repulsive bias was observed when the current movement was performed using the non-dominant hand compared to the dominant hand. k-l) A stronger repulsive bias was observed when participants switched hands compared to the situation when they used the same hand for trial N-1 and trial N. Error bars and shaded areas indicate standard error. *, p<.001.

The results from Exp 4 provide compelling support for the efficient coding model. All main results were consistent with what we had observed in the online experiments. When we combined the data across the two hands, we observed a repulsive sequential bias (N-1: $t(23)=4.7$, $p<.001$, d=0.96; N-2: $t(23)=2.6$, p=.02, d=0.55; Fig 4e-f) and increased movement variance (N-1: $p<.001$, Bootstrap, Fig 4g-h). Importantly, we observed a larger sequential bias when the current movement was performed using the non-dominant hand compared to the dominant hand ($t(23)=4.7$, p<0.001, d=0.97; Fig 4i-j), supporting the prediction of

11

279   the efficient coding theory that bias escalates with encoding noise in the motor system. Interestingly, we

280   also observed a larger sequential bias when participants switched their hands (namely using different

281   hands in trial N and N-1) compared to using the same hand (t(23)=6.7, p<0.001, d=1.4; Fig 4k-l). This effect

282   is likely due to dynamic allocation of encoding resources across hands, leading to increased encoding

283   variability immediately after a hand switch and, consequently, a larger bias. Alternatively, more units

284   might be recruited when repeating a movement with one hand, reducing encoding noise as well as the

285   sequential bias.

286

287   To further examine how the variability in the motor system influences the sequential bias, we analyzed

288   the correlation between motor variance and the sequential effect (SE) index in Exp 4. Consistent with the

289   prediction of the efficient coding theory, we found a positive correlation between individual differences

290   in variance and the SE index for both hands (Fig 5a). A positive correlation was also found when we re-

291   examined the data from Exp 1 and 3 (Fig 5b-c). Those results together further supported the hypothesis

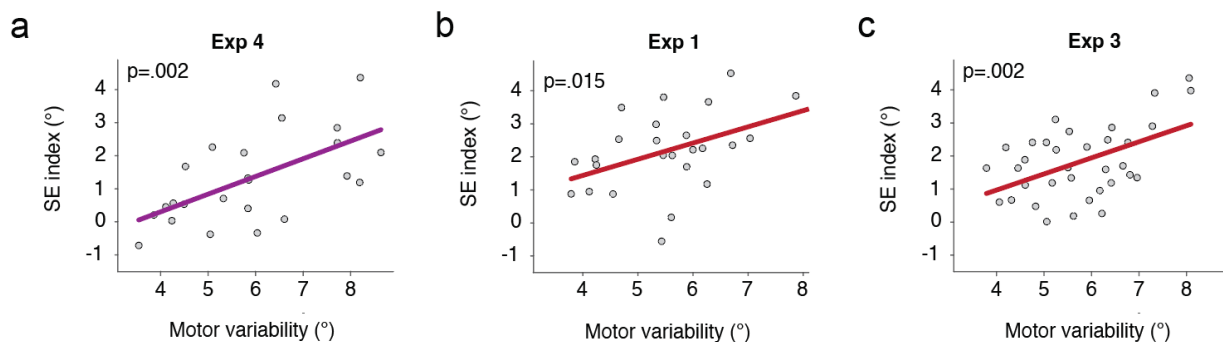292   that motor planning follows the principles of efficient coding.

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294
295   **Figure 5. The repulsive sequential bias increased with the motor variability across participants.** Correlation

296   between the SE index and the motor variance for Exp 4 (a), Exp 1 (b), and Exp 3 (c). Each dot is one participant. The

297   colored line shows the best-fitted linear model. The p-value was measured from the Pearson correlation.

298

299   **Discussion**

300   The nervous system is dynamically tuned based on past experiences to be optimally prepared for the

301   current task. These adaptive processes induce sequential effects in behavior[38]. In the present study, we

302   examined the computational principles that govern the sequential effects in motor planning using

303   reaching tasks with targets randomly sampled from a uniform circular distribution. Contrary to the

304   prevailing belief that motor control is predominantly governed by Bayesian principles[3,9,10,45], we

305   demonstrated a novel repulsive sequential bias in which the current movement is biased away from the

306   direction of the previous movement. This anti-Bayesian behavior suggests that, in less predictable

307   environments, an alternative mechanism may also exist in motor control.

308

309   Interestingly, the sequential effects we observed indicate that motor planning follows the efficient coding

310   model, a theory that posits the nervous system maximizes mutual information by dynamically allocating

311   resources to follow the prior distribution[25,27,28]. Efficient coding has been widely applied to perceptual

312   systems[27,33,34,46], and our results extend these principles to motor control. Our results confirm three key

313   predictions of the efficient coding model in motor planning. First, the sequential bias was repulsive.

314   Second, this effect was amplified when reaching variance increased, as evidenced by differences between

315   the left and right hands and the strong effect of individual differences in motor variability. Third, motor

316   variance also exhibited a sequential effect, with movements closer to the previous one showing lower

317   variability and higher accuracy. Together, these sequential effects in reaching would not result from

318   simple fatigue. Instead, they reflect an adaptive mechanism that enhances motor accuracy.

319

320   The temporal dynamics of the sequential effect highlight the flexibility of the motor system in adapting to

321   environmental statistics. Remarkably, the repulsive effect diminished after only three trials (or ~30s based

322   on Exp S1), suggesting that priors for efficient coding might be maintained by motor working memory[47].

323   This adaptability is likely to be ideal for motor planning, since one may need to repeat some quick actions,

324   such as pressing a buzzer or knocking on a door. In contrast, it is less common for identical reaching

325   movements to be necessary after a lapse of a minute. Consistent with this notion, in Exp 4, we found that

326   the sequential effect decreased when participants consistently used one hand, as opposed to alternating

327   between hands. This observation suggests that encoding resources can be preferentially allocated to the

328   active hand when repeating the movement with the same hand, thereby increasing motor accuracy.

329

330   Sequential effects are well-established in the visual system[37,48,49], but our results clearly distinguish current

331   motor effects from the visual serial dependence reported in previous studies. First, the direction of the

332   motor sequential bias observed in our study is opposite to the serial dependence typically seen in visual

333   tasks[37,41,43,49]. In our motor tasks, the current movement is repelled from the previous movement, whereas

334   in visual perception tasks, the perceived target is usually attracted toward the previous target position[41].

335   Second, when perception and movement are in opposite directions (Exp 4), sequential effects are

336   determined by the movement direction rather than the target position[43]. Third, our sequential effects are

337　significantly modulated by handedness, further suggesting that they are associated with movement rather

338　than perception.

339

340　The opposite directions of sequential biases in the motor and visual systems may reflect their distinct

341　functional purposes and underlying mechanisms. In visual perception, the physical world is continuous

342　and relatively stable[50–52], making it crucial for the visual system to maintain a consistent representation of

343　the environment[39]. Thus, employing Bayesian decoding—which induces an attractive effect—is beneficial

344　for visual perception, ensuring a coherent and reliable perception of the environment[40,53].

345

346　While the objects of perception in the world are physically stable, the actions we need to make upon these

347　objects can change from moment to moment. The motor system, therefore, operates under distinct

348　constraints. As motor goals can vary quickly over time[20], an attractive bias may not benefit motor planning

349　in such dynamic contexts, whereas a decorrelation mechanism, such as efficient coding, may help to

350　minimize repetitive errors and counteract attractive biases from other sources. Additionally, Bayesian

351　integration is typically associated with decoding processes that interpret sensory inputs based on prior

352　knowledge[27,29], whereas motor planning, at least by definition, is an encoding rather than decoding

353　process, making Bayesian decoding mechanisms less applicable.

354

355　An open question remains whether the repulsive motor bias and the attractive biases induced by visual

356　serial dependence may counterbalance each other. To isolate motor effects, we designed our study to

357　minimize potential visual influences. For instance, visual effects are usually linked to perceptual

358　uncertainty[27,54,55]. A typical visual task for serial dependence usually features vague targets, brief

359　presentations, or disappearance upon response. In contrast, our study used high-contrast targets that

360　remained visible during movement. Future studies could employ motor tasks with higher perceptual

361　uncertainty, allowing both visual serial dependence and motor sequential effects to be observed. It is

362　possible that the strengths of visual and motor effects are correlated and thus counteract each other.

363

364　Interestingly, the sequential bias identified in our study contrasts with a history-influenced effect known

365　as use-dependent learning in motor control. Use-dependent learning refers to a bias toward repeated

366　movements in the same direction[15,16,56], aligned with predictions of a Bayesian model. However, use-

367　dependent learning only occurs for relatively predictable targets, whereas targets in our experiment were

368　completely random. Moreover, the time course of use-dependent learning is very different from the

369   repulsive sequential bias we observed. Use-dependent learning typically requires multiple trials to

370   manifest[15,19,22], whereas the current repulsive effect emerges after a single trial. Finally, use dependent

371   learning usually last for tens of trials while the repulsive sequential effect reported here lasted for only

372   two trials.

373

374   Our results suggest that the differing timescales of use-dependent learning and efficient coding may

375   reflect a progressive shift of motor control strategy in developing a skilled movement. The repulsive bias

376   induced by efficient coding could be beneficial in a volatile environment for several reasons, such as

377   reducing repeated errors and enhancing sensitivity to changes in the environment, body, or target[57,58].

378   However, there are instances where repeated, stable movement is desirable, such as when hammering a

379   nail while holding it steady with one's fingers. Initially, efficient coding may increase the precision of

380   movements. Those movements might be slow and performed with caution so that the system can correct

381   for undesired exploratory errors with online control. As the activity continues, use-dependent learning

382   dominates to stabilize the movement, facilitating smooth and stable repetition without conscious control.

383   Future studies should explore the intriguing possibility that there is a transition between efficient coding

384   and use-dependent learning, which may reveal how the system balances the competing needs of flexibility

385   and stability in motor planning.

386

387   **Methods**

388   <u>Participants</u>

389   Testing was conducted online for Exp 1, 2, 3, S1 and in the lab for Exp 4. For the online studies, 154 young

390   adults (76 female, age: 26.7 ± 4.9 y) were recruited using the Prolific.io. The participants performed the

391   experiment on their personal computers through a web-based platform for motor learning experiments.

392   Based on a prescreening survey employed by Prolific, the participants were right-handed and had normal

393   or corrected-to-normal visions. These participants were paid \$8/h. For the lab-based experiments, we

394   recruited 24 undergraduate students (15 female, mean age = 21.42y, SD = 3.78y) from the University of

395   California, Berkeley community. 19 of the participants were right-handed and 5 of them were left-handed

396   based on their scores on the Edinburgh handedness test[59] and had normal or corrected-to-normal vision.

397   These participants were paid \$20/h. All experimental protocols were approved by the Institutional Review

398   Board at the University of California, Berkeley. Informed consent was obtained from all participants.

399

400   <u>Design and procedure</u>

401   *Experiment 1*

402   Exp 1-3 were performed using our web-based experimental platform[60,61]. The code was written in

403   JavaScript and presented via Google Chrome, designed to run on any laptop computer. Visual stimuli were

404   presented on the laptop monitor and movements were produced on the trackpad. Data was collected and

405   stored using Google Firebase.

406

407   26 participants (20 females) took part in Exp 1. To start each trial, the participant moved the cursor to a

408   white circle (radius: 1% of the screen height) positioned in the center of the screen. After 500 ms, a blue

409   target circle (radius: 1% of the screen height) appeared with the radial distance set to 40% of the screen

410   size. Target locations were randomly generated from 1°-360° with a minimum step of 1°. The participant

411   was instructed to produce a rapid shooting movement, attempting to move through the target. A

412   feedback cursor (radius: 0.6% of screen height) appeared for 100 ms when the amplitude of the

413   movement reached the target distance, indicating the angular position of the hand at that distance. The

414   feedback cursor and target were then extinguished. If the movement time was >300 ms, the message

415   "Too Slow" was presented on the screen for 500ms. At the end of the trial, the position of the cursor was

416   reset to a random position within a circle centered at the start position with a radius 4% of the target

417   distance. The participant moved the cursor back to the start position to initiate the next trial. Each

418   participant completed 1080 trials in total.

419

420   *Experiment S1*

421   We aimed to examine the temporal modulation of serial dependence in Exp 3. Compared to Exp 1, we

422   extended the inter-trial interval to either 6s (n = 28, 10 females) or 18s (n = 23, 12 females) for two groups

423   of participants, respectively. A message "wait" would be presented on the monitor between two trails.

424   Participants were instructed to put their right hand on the trackpad and rest until they saw the message

425   "move to center" which indicated the start of a new trial. Participant completed 880 (6s condition) or 360

426   trials (18s condition).

427

428   *Experiment 2*

429   To confirm the effect observed in Exp 1a was not due to the existence of endpoint feedback, we replicated

430   Exp 1 in 2 without presenting any feedback after the movement. Other details of Exp 2 were identical to

431   Exp 1. 36 participants (21 females) took part in Exp 2.

432

16

433 *Experiment 3*

434 Exp 3 was designed to examine whether the sequential effect was induced by perception or movement.

435 41 participants (13 females) took part in Exp 4. The procedure of Exp 3 was essentially the same as in Exp

436 1. To evaluate whether this repulsive effect was perception-based or motor-based, we included trials (25%)

437 in which the participants were instructed to move in the opposite direction of the target. Before each trial,

438 an instruction message would appear on the screen to instruct participants to either "move to target" or

439 "move to opposite." There were no consecutive "opposite" trails. Each participant completed 960 trials

440 in total.

441

442 *Experiment 4*

443 Exp 4 was designed to examine how motor variability influences the sequential reaching bias. 24

444 participants (15 females, 19 right-handed and 5 left-handed) performed the experiment in the lab setup.

445 Participants performed a center-out reaching task, holding a digitizing pen in the right or left hand to make

446 horizontal movements on a digitizing tablet (49.3cm x 32.7cm, sampling rate= 100 Hz; Wacom, Vancouver,

447 WA). The stimuli were displayed on a 120 Hz, 17-in. monitor (Planar Systems, Hillsboro, OR), which was

448 mounted horizontally above the tablet (25 cm), to preclude vision of the limb. The experiment was

449 controlled by custom software coded in MATLAB (The MathWorks, Natick, MA), using Psychtoolbox

450 extensions, and ran on a Dell OptiPlex 7040 computer (Dell, Round Rock, TX) with Windows 7 operating

451 system (Microsoft Co., Redmond, WA).

452

453 Participants made reaches from the center of the workspace to targets positioned at a radial distance of

454 8 cm. The start position and target location were indicated by a white annulus (1.2 cm diameter) and a

455 filled blue circle (1.6 cm), respectively. Vision of the hand was occluded by the monitor, and the lights

456 were extinguished in the room to minimize peripheral vision of the arm. Feedback, when provided, was

457 in the form of a 4 mm white cursor that appeared on the computer monitor, aligned with the position of

458 the digitizing pen.

459

460 To start each trial, a letter "R" or "L" would be presented within the start circle to inform participant which

461 hand to use on this trial. Participants used the instructed hand to hold the pen and put the other hand on

462 the side. The experimenter supervised the whole experiment to make sure the participant applied the

463 correct hand. After maintaining the cursor within the start circle for 500 ms, a target appeared. The

464 participant was instructed to make a rapid slicing movement through the target. Right after their

465   movement amplitude reached 8 cm, a cursor would be presented at that position for 1 s, providing

466   feedback of the accuracy of the movement (angular position with respect to the target). After this interval,

467   the target and cursor were extinguished. Another letter appeared at the start position and participants

468   changed hand accordingly. To guide the participant back to the start position without providing angular

469   information about hand position, a white ring appeared denoting the participant's radial distance from

470   the start position. Once the participant moved within 2 cm of the start position, the ring was extinguished,

471   and a veridical cursor appeared to allow the participant to move their hand to the start position. If the

472   movement time was >300 ms, the audio "Too Slow" was played right after the reaching.

473

474   The required hand was pseudorandomized so there were 4 left-hand and 4 right-hand trials within every

475   8 trials. Target locations were randomized in a way that both hands would visit targets from 1°-360° (with

476   a step of 1°) within every 720 trials. The whole experiment included 2160 trials and took about 4 h.

477   However, we allowed participants to end the experiment based on their convenience. 14 out of 24

478   participants finished all trials; other participants finished 1000~2000 trials.

479

480   <u>Data Analysis</u>

481   We calculated the error of hand angle as a difference between the hand position when it reached the

482   target distance and the target position. A positive hand angle denoted that the hand position was more

483   clockwise than the target at the target radius. Trials with a movement duration longer than 500 ms or an

484   error larger than 60° were excluded from the analyses. For the web-based experiment, 1.5% trials were

485   removed. For the lab-based experiment, 0.4% of trials were removed.

486

487   To analyze the sequential effect in movement, we regressed out the influence of systematic bias.

488   Specifically, we fitted a function between motor bias and target angle using a polynomial function with a

489   maximal power of 10 for each participant. We then subtracted this motor bias function from the motor

490   error. The residual error was defined as motor "deviation" and applied to analyze the sequential

491   effect[35,36,41,42].

492

493   To analyze the sequential bias of the movement direction, we measured the function of how motor

494   deviation changed as a function of the difference of target position between trial N-1 and trial N (defined

495   as ΔTarget). A function lies in Quadrants II and IV will suggest that the movement error was in the opposite

496   direction of the previous target. To quantify sequential bias, we introduced the SE index that takes the

18

497   difference between the average error within -90°-0° Δ Target and the average error within 0°-90° Δ Target.

498   A positive SE index means a repulsive sequential effect and vice versa.

499

500   To further examine how the variability in the motor system influences the sequential bias, we calculated

501   the Pearson correlation between motor variance and the SE index, for Exp 1, Exp 3, and Exp 4 (only for

502   trails after a standard trial). The motor variance was very large in the no-feedback condition of Exp 2

503   compared to all other experiments, likely because of the drifting sensorimotor map without visual

504   calibration[62,63]. As such, the motor variance in Exp 2 was not a good measurement of encoding variability.

505

506   To analyze the sequential effect in motor variance, we calculated the absolute difference between the

507   movement N-1 and movement N (|Δ Hand|). We flipped the sign of the deviation if Δ Hand was negative.

508   Then we calculated the variance of deviation within each bin of 30°. The variance was then normalized by

509   the average the average variance for each participant. To examine the tendency of how variance changed

510   as a function of |Δ Hand|, we applied a general linear model:

$$variance = a + \frac{b-a}{e^{-c|\Delta \text{Hand}|}} \tag{1}$$

512   where a, b, c are the three free parameters. The SE index was defined as the change in the output of the

513   function when |Δ Hand| increases from 30° to 150°. To estimate the distribution of the SE index, we

514   applied bootstrap resampling 1000 times.

515

516   To analyze the priming effect in the reaction direction, we normalized the reaction time (RT) by

517   subtracting the average reaction of each participant. We then plotted a function of how the normalized

518   RT changes as a function of |Δ Target|. The RT SE index is the difference between the average normalized

519   RT within 180°-90° |Δ Target| and the average RT within 0°-90° |Δ Target|. Simple t-tests were conducted

520   to determine whether the SE indexes were significantly different from 0. We confirmed that the data met

521   the assumptions of a Gaussian distribution and homoscedasticity for all tests. The significance level was

522   set at $p < 0.05$ (two-tailed).

523

524   **Model**

525   <u>Efficient coding model</u>

526   We assumed that the motor system encodes a movement direction (m) based on an observed target

527   direction (θ) following the rule of efficient coding. This model is based on previous models of efficient

528   coding in perception[26,27,29]. A key assumption of the model is that the encoding system allocates its

19

529   resources to maximize the mutual information $I[\theta,m]$ between input θ and output m. By imposing a

530   constraint to bound the total coding resources of the system[27], this requires the Fisher information $J(\theta)$ to

531   be matched to the stimulus prior distribution $(p(\theta))$: $p(\theta) \propto J(\theta)$. As such, coding resources are allocated

532   such that the most likely movement direction is coded with the highest accuracy.

533

534   We next calculated the likelihood functions of how the system responds to different target directions with

535   constraints of the prior distribution. Technically, the likelihood functions can be computed by assuming a

536   symmetric Gaussian noise structure in a space where the Fisher information is uniform (the motor space,

537     $\tilde{\theta}$), and then transforming those symmetric likelihood functions back to the target space (θ). To construct

538   a motor space with uniform Fisher information based on the prior distribution of θ, one defines a mapping

539   F from the target space (θ) to the motor space ($\tilde{\theta}$), following[27]:

$$\tilde{\theta} = F(\theta) = \int_0^\theta p(\chi)d\chi \qquad [2]$$

541

542   Given an input θ, the output m is computed as follows[26]. We first calculated the response value r, which

543   would be of the form $\theta + \epsilon$, where ϵ represents an error due to the intrinsic encoding noise of the system.

544   Note that ϵ follows an asymmetric distribution in the target space (Fig 1b). Let $\tilde{\epsilon}$ represent the

545   transformation of ϵ to the motor space. Since we were assuming $\tilde{\epsilon}$ has a symmetric Gaussian distribution,

546   the response value in the motor space would be $\tilde{r} = F(\theta) + \tilde{\epsilon}$, where $\tilde{\epsilon} \sim N(0, \sigma^2)$; which gives a

547   response value in the target space of:

$$r = F^{-1}(F(\theta) + \tilde{\epsilon}) \qquad [3]$$

549

550   Next, we assumed that the system knows that its response r is noisy. Therefore, it generates a

551   distribution of the form $r + \delta$, where δ follows the same distribution as ϵ. If $\tilde{\delta}$ represents the

552   transformation of δ to the motor space, this distribution will be of the form $F^{-1}(r + \delta)$, where

553     $\tilde{\delta} \sim N(0, \sigma^2)$. Finally, the system returns the expected value of this distribution as the output m:

$$m = E((F^{-1}(r + \tilde{\delta}); \tilde{\delta}) \qquad [4]$$

555

556   where $E(X; z)$ means the expected X as z varies. We defined $\phi(\tilde{\theta}) = F^{-1}(\tilde{\theta})$. In the small-noise limit, we

557   can take a second-order Taylor expansion:

$$F^{-1}(F(\theta) + \epsilon) \approx F^{-1}(F(\theta)) + \phi'(F(\theta)) \times (\epsilon + \delta) + (1/2)\phi''(F(\theta)) \times (\epsilon + \delta)^2 \qquad [5]$$

559

20

560   Considering [3]-[5] together, we have:

$$m \approx \theta + \phi'\big(F(\theta)\big)\epsilon + \frac{1}{2}\phi''(\sigma^2 + \epsilon^2) \qquad [6]$$

562   To estimate the motor bias predicted by the model, we calculated the expected value of m $(\hat{m})$ when ϵ

563   varies can be expressed as:

$$\hat{m} = E(m; \tilde{\epsilon}) \approx \theta + \phi''\sigma^2 \qquad [7]$$

565   And the variance of m across trials can be expressed as:

$$\mathrm{var}(m) \approx (\phi'\sigma)^2 \qquad [8]$$

567

568   Since the sequential effect in movement is influenced principally by the last movement, we assumed the

569   prior of the motor planning system is a mix of a uniform distribution across the whole space and a

570   Gaussian distribution centered at the last target direction (θ_{n-1}):

$$p(\theta) \propto k * U(0, 360) + (1-k)N(\theta_{n-1}, \rho^2) \qquad [9]$$

572   where k is a scale factor controlling the relative contribution of the two distributions; ρ indicates the width

573   of influence from the previous trial. To simulate the bias and the variance predicted by this efficient coding

574   model, we computed the numerical approximation of ϕ'' and ϕ' based on this prior function using an

575   incremental approach.

576

577   This model includes three free parameters: k and ρ, which determine the shape of the prior, and σ which

578   reflects the encoding noise. Since many parameter sets can produce similar bias patterns but different

579   variance functions, we fitted the model by constraining both the bias and variance functions. Specifically,

580   we predicted the deviations using the model and calculated the mean squared error (MSE) between these

581   predictions and the observed data across all trials and participants. Additionally, we computed the

582   variance function and calculated the MSE between the predicted function and the empirical group-level

583   variance. We then minimized the sum of these two MSEs to determine the best-fitting parameters.

584

585   <u>Repeated Suppression model</u>

586   We considered two alternative models to explain the sequential effects in the motor planning. The first

587   model is a repeated suppression model, which assumes that neurons tuned to a specific direction become

588   less sensitive after repeating a similar movement. Those modulations can enhance the sensitivity to the

589   changes in the environment or/and encourage exploration. Here we applied a population coding model

590   with a group of neurons with Gaussian-shaped tunning functions. For a target direction θ, the unit tunned

591   to i ($i \in [0, \pi]$) direction generates a response r_i as follow:

592 $$r_i = Norm(\theta, i, d) \tag{10}$$

593 where $Norm(\theta, i, d)$ is the probability density function of a Gaussian distribution with a mean of i and

594 standard deviation of d. The output of the system is determined by summing the activation of all neurons:

595 $$\boldsymbol{m} = \sum_i s_i r_i \boldsymbol{v}_i \tag{11}$$

596 where $\boldsymbol{v}_i$ is a vector representing the tuning direction of unit i, $\boldsymbol{m}$ is a vector pointing towards the

597 movement direction, and s_i is the sensitivity of unit i. After a movement in trial n, s_i is updated based on

598 the strength of the activation in unit i:

599 $$s_i\,(n+1) = 1 - ar_i(n) \tag{12}$$

600 where $a \in [0,1]$ is the suppression rate. As such, units that response more to the target in trial n will be

601 more suppressed in the next trial.

602

603 <u>Bayesian Decoding model</u>

604 The second alternative model we applied is a classic Bayesian Decoding model that utilizes the prior

605 distribution of θ to improve performance[3,64,65]. The system generates a response r based on a target

606 direction θ. Considering Gaussian encoding noise, the relationship between r and θ can be expressed as

607 follows:

608 $$p(r|\theta) = Norm(\theta, \sigma) \tag{13}$$

609 Importantly, the model assumes that the system utilizes both the prior and this likelihood function to form

610 a posterior estimation following Bayesian rules:

611 $$p(\theta|r) = \frac{p(\theta)p(r|\theta)}{p(r)} \tag{14}$$

612 where $p(r)$ is a constant; $p(\theta)$ is the prior; $p(r|\theta)$ is the likelihood; and $p(\theta|r)$ is the posterior. The

613 output of the system (m) is the posterior mean. For the Bayesian model, we used the same prior

614 distribution (see [9]) as the efficient coding model.

615

616

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618

619

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621

622

623 **Competing interests**

22

624   We have nothing to declare.

625

626   **Data availability**

627   All data and code are available at https://github.com/shion707/MotorEC.

628

629   **Reference**

630

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758   **Supplementary Information**

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760   <u>Supplementary Result 1: Temporal dynamics of the sequential effects in Reaching</u>

761   In Exp 1-2, we observed a repulsive effect only from the 1-back and 2-back trials. This motivated us to

762   further examine the temporal regulation of the repulsive sequential effect. We tested whether the rapid

763   drop in the sequential effect solely depended on time, or whether it also depended on the number of

764   trials. As such, in Exp S1, we extended the inter-trial interval (ITI) to either 6s or 18s for two groups of

765   participants and compared the results with Exp 1 (0s ITI) (Fig S1). While the strength of the sequential

766   effects decreased with time, both the repulsive bias (t(23)=5.2, p<0.001) and the variance modulation

767   (p=0.020) could be observed for trial N-1 if participants simply wait for 6s between two trials. This result

768   contrasted with the N-3 trial in Exp 1, which was ~6s prior to the current movement (Fig S1b, d), but no

769   sequential was observed. Moreover, the repulsive bias remained significant even in the 18s ITI condition

770   (Fig S1b). The SE index of the motor variance in the 18s ITI conditions showed a positive trend but did

771   not reach significance (p=0.16, Fig S1d). These results suggested that the attenuation of the sequential

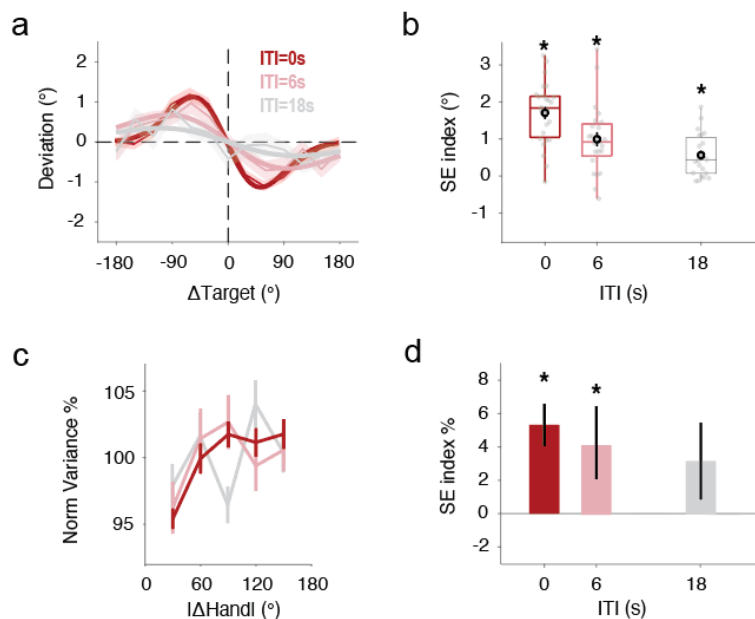772   effects depended on both passing time and intervening information.

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Figure S1. Temporal dynamics of the Sequential effects in reaching. (a) Sequential effect in movement direction for three ITI conditions. The thinner lines indicate the data, and the thicker lines indicate the prediction of the efficient coding model. (b) SE index with different ITI. Different from what has been observed in the 3-back condition in Exp 1 (which had a ~6s delay), the SE index was significant in the 6s and 18s ITI conditions, indicating the effect decreased with both time and trial number. Error bar and shad area indicate standard error. (c-d) Sequential effect in motor variance was modulated by ITI. A significant SE index was found in the 6s ITI condition. *, p<.02.
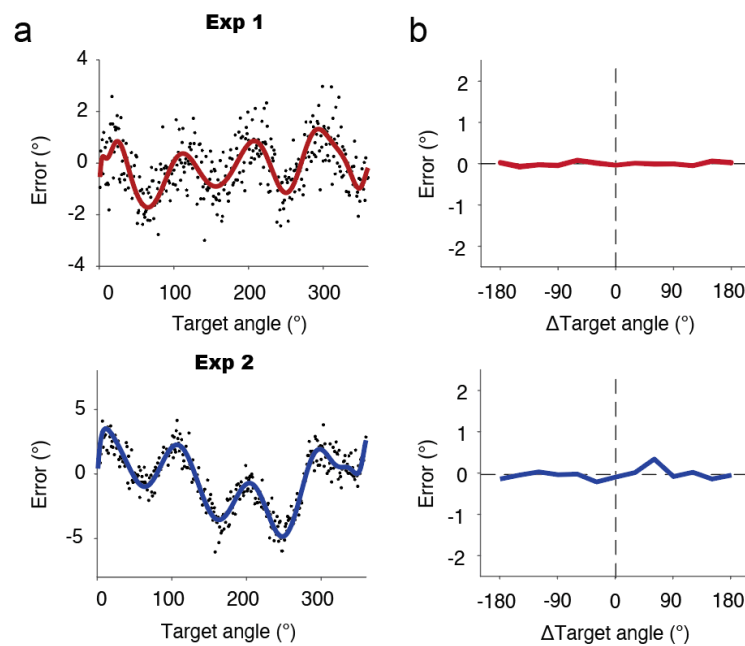
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Figure S2. Systematic motor biases did not generate sequential effects. a) Systematic motor bias relative to target position in Exp 1 (upper panel) and 2 (lower panel). Participants exhibited greater bias in Exp 2, where feedback was absent. Black dots indicate data. The thick line represents a smoothed function, obtained by fitting a polynomial function with a maximum degree of 20. b) Simulation of sequential bias based on the motor bias function and the sequence of targets presented to participants. The systematic motor bias did not generate any sequential effect.
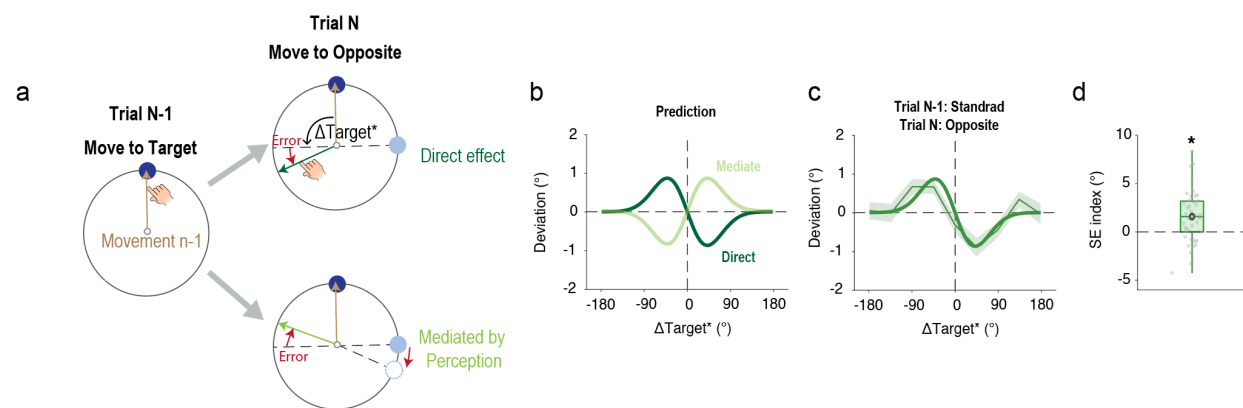
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Figure S3. The current movement was directly influenced by the previous movement, with no mediation of perception. a) When trial N was an Opposite trial and trial N-1 was a Standard trial, it allowed for examination of whether the effect was directly caused by the previous movement repelling the current movement (direct hypothesis). Alternatively, it could be that the previous movement repelled the perception of the current target's position, thus indirectly influencing the movement direction (mediated hypothesis). Here, Δ Target* was defined as the difference between the opposite position of the current target and the position of the previous target. b) Different predictions of the sequential bias following the direct hypothesis and mediated hypothesis, respectively. c) Sequential bias observed in Exp 3 was consistent with the direct hypothesis. The thin lines with shaded error bars indicate data, and the thick curve indicates the prediction of the efficient coding model. Shaded areas indicate standard error. d) SE index indicates that the current movement was significantly repelled away from the previous movement. *, p<.001.
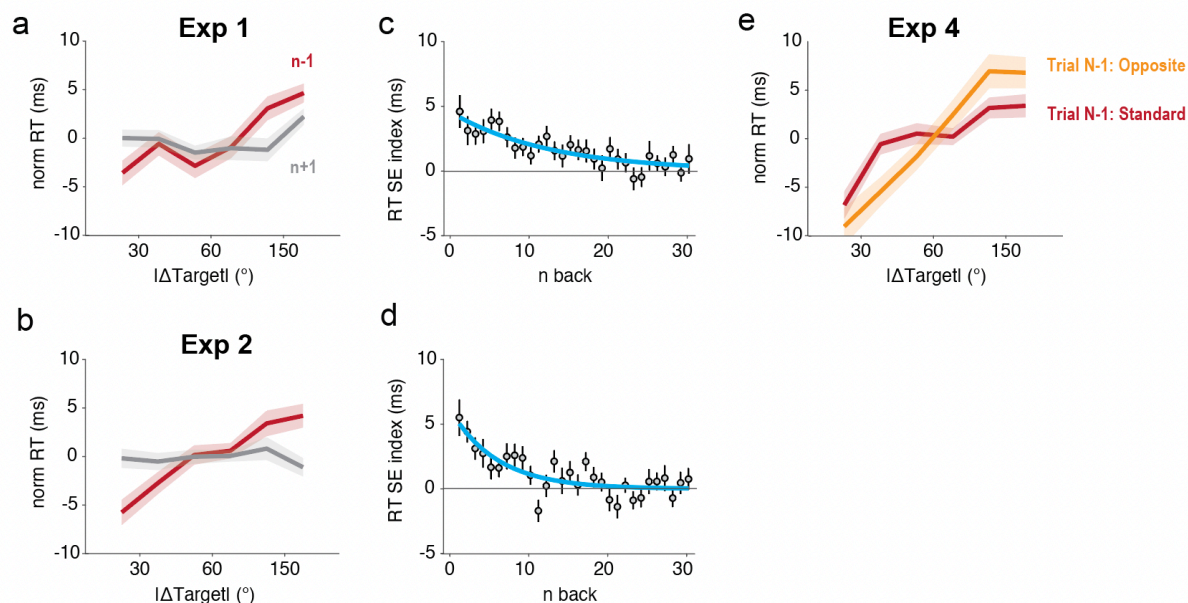
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Figure S4. Priming of Reaction Times. a-b) Reaction time increased when the target in the previous (n-1) trial was further away from the current (n) trial in Exp 1-2. Reaction time was not correlated with the future trial (n+1). c-d) The SE index for reaction time lasted for more than 10 trials, differing from the temporal dynamics of sequential effects in movement direction or motor variance. e) The priming of reaction time was similar after an Opposite trial or a Standard trial in Exp 4, suggesting that the reaction time priming is mainly associated with previous target detection or localization.