1   **Efficient Coding in Motor Planning**

2

3   Tianhe Wang[1,2,4] *, Yifan Fang[1,4], 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   4 Those authors contribute equally

8   *Corresponding Author: tianhewang@berkeley.edu

9   **Abstract**

10   A paramount challenge for the brain is to precisely model the world and control behavior within the

11   confines of limited encoding capacities. Efficient coding theory posits a unified framework for

12   understanding how neural systems enhance encoding accuracy by tuning to environmental statistics.

13   While this theory has been thoroughly explored within the perceptual realm, it is less clear how efficient

14   coding applies to the motor system. Here, we probe the core principles of efficient coding theory through

15   center-out reaching tasks. Our results reveal novel sequential effects in motor planning. Specifically,

16   current movements are biased in a direction opposite to recent movements, and movement variance

17   increases with the angular divergence between successive actions. These effects are modulated by the

18   variability within the motor system: a larger repulsive bias is observed when movements are performed

19   with the nondominant hand compared to the dominant hand, and in individuals exhibiting higher motor

20   variance compared to those with lower variance. These behavioral findings align with the predictions of

21   an efficient coding model, suggesting that the motor system rapidly adapts to the context to enhance

22   accuracy in motor planning.

Introduction

Our experiences shape the way we perceive and interact with the world. A fundamental mechanism that contributes to this adaptive behavior is efficient coding, a unified theory positing that neural systems allocate limited resources to optimally encode information from the environment[1–4]. For instance, the system may preferentially allocate more coding resources to stimuli that appear more frequently and fewer resources to those that are rarer, thereby maximizing overall accuracy[5,6].

The principle of efficient coding has been extensively examined in perceptual systems[7–9]. The key assumption of efficient coding is that encoding accuracy for a stimulus increases when it is closer to the prior expectation and decreases as it deviates from this prior. This non-uniform resource allocation can introduce systematic perceptual distortions, constrained by the prior distribution[10]. This model successfully explains how environmental statistics shape the systematic biases in various visual tasks, including orientation, location, and color perception[11,12]. Moreover, efficient coding has also been applied to understand sequential biases in visual perception that are induced by trial-by-trial updating of the encoding resource[13]. Beyond visual perception, efficient coding explains the prioritization of certain sounds over others based on environmental relevance and frequency of occurrence[4]. Additionally, efficient coding principles extend to the processing of abstract information. For instance, the biases and variability associated with encoding subjective values are modulated by the statistical context in a manner that improves accuracy and reduces redundancy[14,15].

While efficient coding is generally applicable to perceptual systems, it remains less clear whether those principles can be applied to other systems. For example, organisms must plan their movements rapidly and precisely for survival. However, motor planning involves computations in high-dimensional spaces, which can demand substantial computational resources[16–18]. As such, it is plausible to propose that the motor system adapts to environmental statistics by adhering to efficient coding principle, which, in turn, enhance movement accuracy.

To examine whether motor planning follows the principles of efficient coding, we examined experience-dependent modulations in reaching. As mentioned above, efficient coding theory assumes that neural systems adapt to the environmental statistics by allocating resources preferentially to more probable stimuli or movements (Fig 1c)[1,15]. This can be achieved by sharpening the tunning curve of the units around the prior and/or modifying the density of the tunning units over space. In either case, a movement

55   direction aligned with the prior will be more precisely encoded, and the variability in movement will

56   escalate when its direction diverges from the prior (Fig 1d).

57

58   Moreover, the differential allocation of coding resources across the space will introduce an encoding

59   bias[10,11]. In visual perception, efficient coding leads to aftereffects, where perception is biased in the

60   direction opposite to previously viewed stimuli[19]. This mechanism reduces redundancy in sensory

61   representation and enhances sensitivity to new information. Similarly, when encoding a specific

62   movement direction, the efficient coding model suggests that the encoding resources are imbalanced on

63   the two sides of the movement direction. As a result, the population distributional response to this

64   movement direction will also be asymmetric, with a higher encoding accuracy on the prior side and a flat

65   tail pointing away from the prior mean (Fig 1e). As such, the mean direction encoded by the neural

66   population will be biased in a direction opposite the prior mean (Fig 1f).

67

68   Other models offer alternative frameworks for understanding how prior expectations improve encoding

69   accuracy[10,20]. For example, Bayesian models suggest that perception arises from combining prior

70   expectations with incoming sensory information to compute a posterior estimate. As a result, they predict

71   that current movements or perceptions will be biased toward prior expectations. Importantly, this is

72   opposite to the repulsive biases predicted by the efficient coding model. The Bayesian framework has

73   been successful in explaining various perceptual and motor biases[11,21,22]. Therefore, we consider the

74   Bayesian model as an alternative to compare with our efficient coding model in predicting sequential

75   effects in motor tasks.

76

77   While the visual world is relatively stable and continuous, motor goals can vary significantly over short

78   time scales[23]. Consider, for example, the actions required when shopping: reaching for a milk box, placing

79   it in a cart, and pushing the cart away, all within a matter of seconds. Instead of relying on a static prior

80   for motor planning, the sensorimotor system may continuously update its priors based on the current

81   motor goal to facilitate efficient coding. In other words, priors for motor planning might be largely shaped

82   by recent movements. Based on this assumption, the efficient coding theory will predict specific

83   sequential effects on movement bias and variance in a center-out reaching task (Fig 1d&f). Other

84   frameworks, such as Bayesian models, make different predictions. We aim to test these competing

85   predictions in the following experiments.

86

87
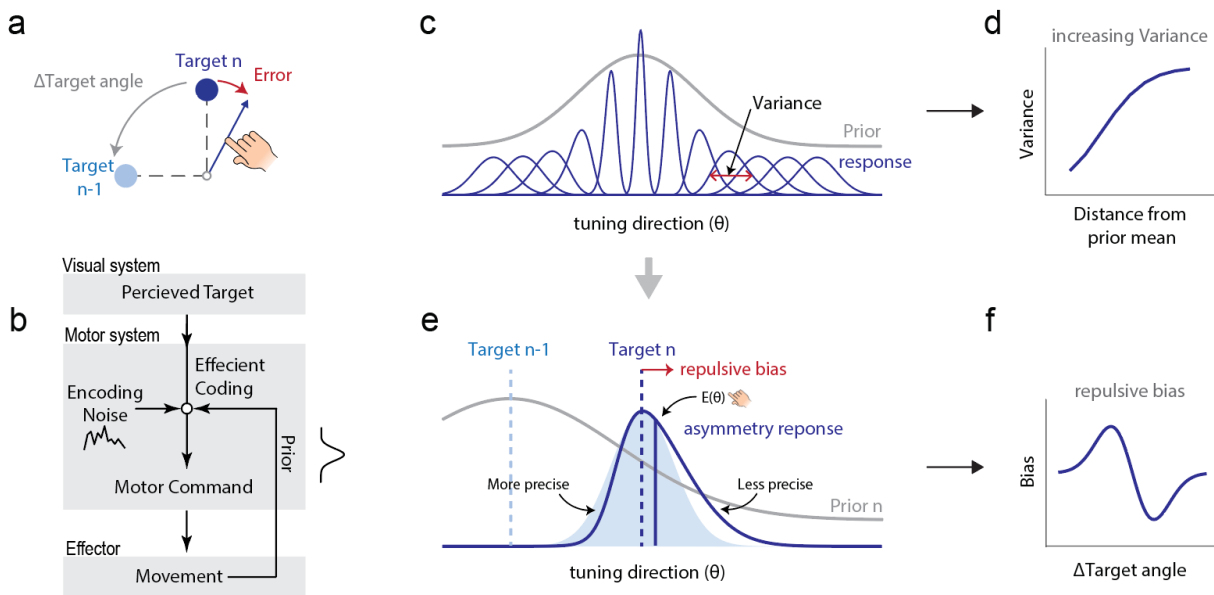
Figure 1. An efficient coding framework for motor control. a) Illustration of a reaching task. b) Schematic of an efficient coding framework. The motor system encodes a motor command based on the perceived target. The effector implements the motor command, which serves as a prior that drives the motor system to re-allocate its coding resource following the efficient coding rule. c) The precision of encoding the direction of movement is influenced by the prior. d) The model posits that as the current movement diverges from the prior mean, the variance in movement direction escalates. e) For a given movement direction, encoding is more precise on the side closer to the prior and less accurate on the opposite side. As a result, the representation of a movement direction becomes asymmetric, with a flatter tail extending away from the prior. E(θ) represents the mean of this distribution, which is biased in the direction opposite to the prior mean. The shaded blue distribution illustrates the response in the absence of efficient coding. In this context, we assume the prior is primarily influenced by the movement direction in the previous (n-1) trial. f) The efficient coding model predicts a repulsive sequential bias in reaching tasks.

Results

Sequential effects in reaching aligns with the efficient coding model

To examine sequential effects predicted by the efficient coding theory, in Exp 1, we employed an online reaching experiment where participants control a cursor with a trackpad. In each trial, a target appeared at a random position along an invisible circle and participants made a center-out reaching movement from a central start position towards the target (Fig 2a). The cursor was invisible during the movement to

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

109   position at the target radius.

110

111
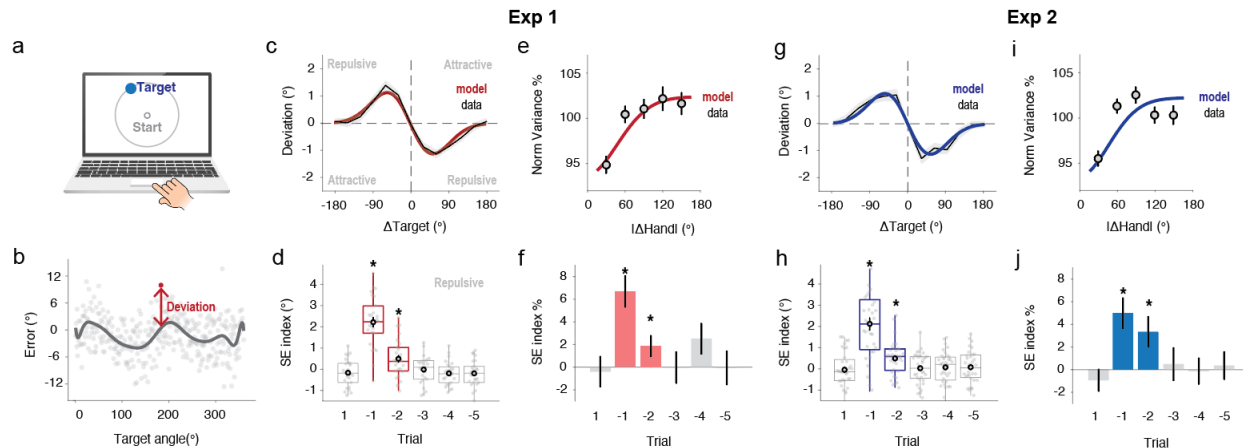
Figure 2. Sequential effects in reaching. a) An illustration of the repulsive bias predicted by the efficient coding model. b) The motor bias of a sample participant. The gray curve shows the smoothed motor bias function. The deviation was defined as the difference between the current response and the 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. The black curve indicates data, and the red curve indicates the prediction of the efficient coding model. 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 (|Δhand|). g) Sequential effect (SE) index derived from a general linear model between normalized movement variance and |Δhand| 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. Error bars and shaded areas indicate standard error. *, p<.02.

To obtain an accurate assessment of the sequential effect, we eliminated the impact of systematic bias by fitting a motor bias function based on the target position (Fig S1) for each participant. The residual error, representing the deviation from this fitted motor bias function (Fig 2b), was defined as the deviation[13,24–26] and was used to analyze the sequential effects.

To examine the sequential effect in reaching biases, we plotted movement deviation as a function of the angular difference between the current and previous targets (ΔTarget). We found that the direction of movement in the current trial (trial n) was biased away from the previous target (trial n-1, Fig 2c), with

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

134   approximately 60°. This bias function aligned well with predictions from an efficient coding model. To

135   quantify the size of the sequential bias, we calculated a sequential effect (SE) index, defined as the

136   difference between the average bias for Δ Target from -90° to 0° and 0° to 90°. A positive SE index signified

137   a repulsive effect. We found an SE index significantly larger than 0 in trial N-1 ($t(25)=9.5$, $p<.001$, d=1.9)

138   and trial N-2 ($t(25)=2.8$, $p=.010$, d=0.55), but not in trial N-3 ($t(25)=-0.10$, $p=0.92$, d=-0.02; Fig 2d). With a

139   median trial duration of 2.08s (SD: 1.05s), this result suggested rapid updating of prior expectations by

140   the motor system.

141

142   We then measured the sequential effect as a function of movement variance. Again, consistent with the

143   prediction of the efficient coding model, the movement variance increased with the distance between the

144   directions of the two consecutive movements (Fig 2g-h). We quantified this effect by fitting a sigmoid

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

146   independent variable, pooling data from all participants. The SE index was defined as the sigmoid

147   amplitude predicted by the best-fit function (Fig 2e). Similar to what we have observed for the sequential

148   bias, this SE index of the movement variance dropped rapidly across trials: a significant effect was found

149   for trial N-1 ($p<0.001$, Bootstrap) and N-2 ($p=0.026$, Fig 2f), measured by bootstrap resampling. The effect

150   disappeared for trial N-3 ($p=0.98$), which occurred only ~6 seconds prior.

151

152   In Exp 1, we showed that the sequential effects in the motor bias and movement variation are consistent

153   with the efficient coding model. However, we noted that endpoint feedback was provided after reaching,

154   facilitating the recalibration of the sensorimotor system. This recalibration process might be specific to

155   areas near the recently reached positions, potentially contributing to the observed sequential effect in

156   motor variance. To eliminate the potential influence of sensorimotor recalibration, we conducted a

157   replication of Exp 1 without endpoint feedback (Exp 2). The results showed remarkably similar sequential

158   effects in both movement bias and variance (Fig 2g-j), confirming that these effects were independent of

159   visual feedback or sensorimotor recalibration.

160

161   The results in Exp 1-2 established a sequential effect in reaching movements that aligns with the

162   predictions of the efficient coding model. In the following session, we considered two alternative models

163   proposed to explain sequential effects. The first model we evaluated was the Bayesian model [20,21,27], which

164   is widely used to explain how prior expectations influence behavior. According to Bayesian principles, the

165   system integrates prior knowledge with current observations to form a posterior estimate (Fig 3a). This

166   process allows the system to reduce encoding noise. However, importantly, the posterior skews the

167   average response toward the prior and leads to an attractive sequential bias (Fig 3b), which contradicts

168   the repulsive bias as observed in behavioral results (Fig 2c).

169

170   Another alternative model we evaluated was the repeated suppression model[28,29]. This model suggests

171   that after observing a stimulus or executing a movement, neurons tuned to that direction become less

172   sensitive due to fatigue or active suppression, a mechanism that favors novel stimuli to avoid encoding

173   redundancy. The suppression model predicts a repulsive sequential bias due to the asymmetric response

174   of units on the suppressed and unsuppressed sides (Fig 3c). However, unlike the efficient coding model,

175   which facilitates the processing of repeated stimuli, the suppression mechanism increases sensitivity to

176   stimuli that change[30,31]. As a result, the model posits that movements closer to the previous one are

177   encoded with less precision and exhibit greater variability compared to movements further away (Fig 3d).

178   This prediction stands in opposition to the sequential effects observed in our experiments (Fig 2e). As such,

179   the unique sequential effects in reaching suggest that motor planning follows efficient coding principles.

180
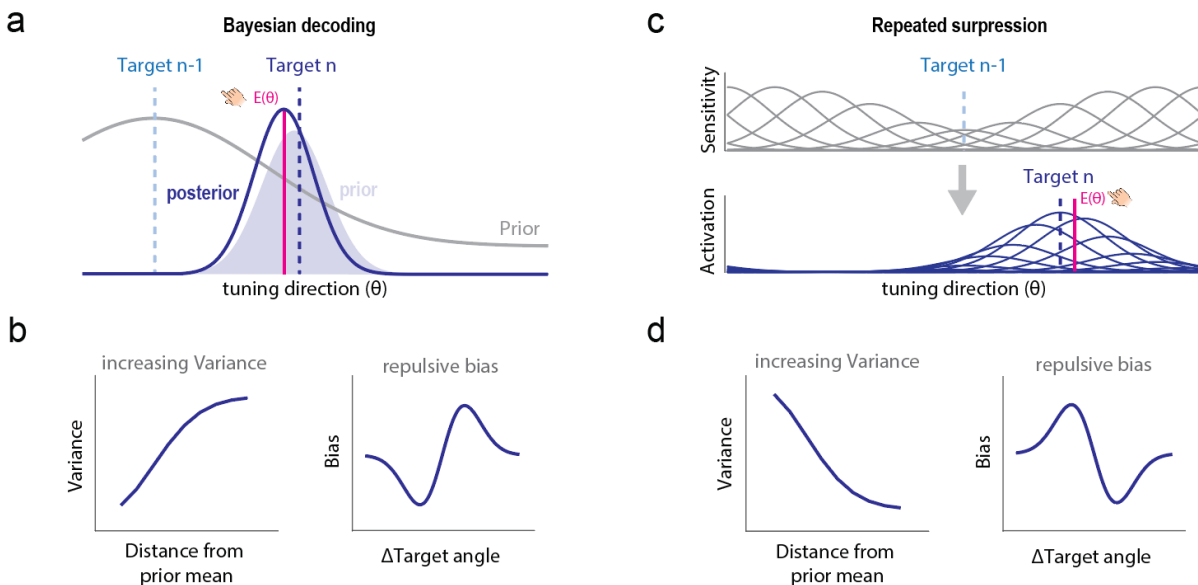
181

182   **Figure 3. The repeated suppression model and Bayesian model cannot explain the sequential effects in reaching.**

183   a) Schematic of the Bayesian decoding model. b) This model predicts increasing variance and attractive bias. c)

184   Schematic of the Repeated suppression model. The sensitivity of the unit tuned to the previous movement decreases,

185   which causes an asymmetric representation of the subsequent movement direction. d) The Repeated suppression

186   model predicts decreasing variance and repulsive bias. Neither of these models were able to explain the sequential

187   effects observed in behavioral results (Fig. 2).

188

189   <u>Temporal dynamics of the sequential effect</u>

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

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

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

193   trials. As such, in Exp 3, we extended the inter-trial interval (ITI) to either 6s or 18s for two groups of

194   participants and compared the results with Exp 1 (0s ITI) (Fig 4). While the strength of the sequential

195   effects decreased with time, both the repulsive bias ($t(26)=5.9$, $p<0.001$, d=1.2) and the variance

196   modulation ($p<0.001$, Bootstrap) could be observed for trial N-1 if participants simply wait for 6s between

197   two trials. This result contrasted with the N-3 trial in Exp 1, which was ~6s prior to the current movement

198   (Fig 4b, d), but no sequential was observed. Moreover, the repulsive bias remained significant even in the

199   18s ITI condition (Fig 4b, $t(22)=3.4$, $p=0.002$, d=0.72). The SE index of the motor variance in the 18s ITI

200   conditions showed a positive trend but did not reach significance ($p=0.16$, Fig 4d). These results suggested

201   that the attenuation of the sequential effects depended on both passing time and intervening information.

202

203
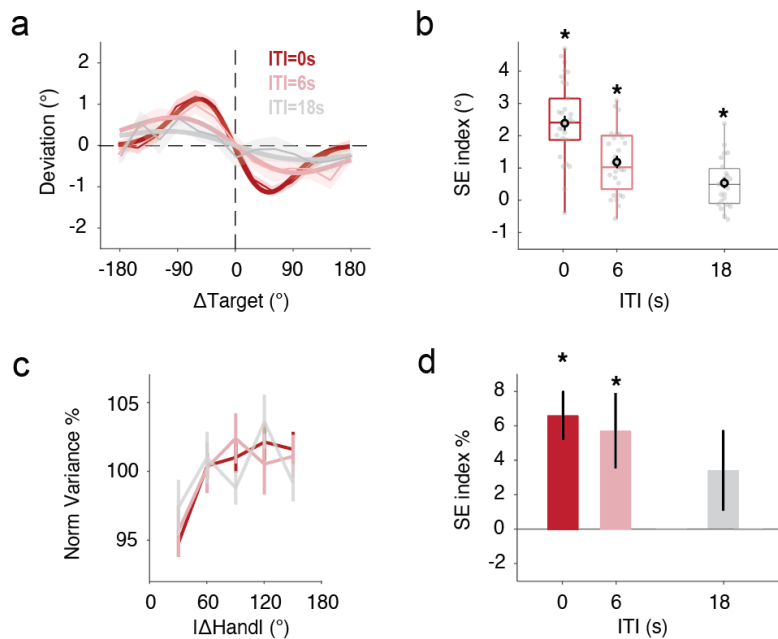
Figure 4. Temporal dynamics of the Sequential effects in reaching. (a) Sequential effect in movement direction for

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

9

207 1 (which had a ~6s delay), the SE index was significant in the 6s and 18s ITI conditions, indicating the effect decreased

208 with both time and trial number. Error bar and shad area indicate standard error. (c-d) Sequential effect in motor

209 variance was modulated by ITI. A significant SE index was found in the 6s ITI condition. *, p<.002.

210

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

212 Sequential effects have been widely observed in perceptual tasks[22,32,33]. While we tried to minimize the

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

214 necessary to differentiate effects originating in the motor versus the perceptual systems[34]. To this end, in

215 Experiment 4 we implemented a design where participants were instructed to either move directly

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

217 of trials). As a critical test of the source of these sequential effects in Exp 1, we analyzed scenarios where

218 trial N-1 was an Opposite trial and trial N was a Standard trial (Fig 5a, bottom). In such cases, the

219 inconsistency between movement direction and target in trial N allowed us to disentangle the influences

220 of target location representation from the motor control itself. If the repulsive bias was primarily driven

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

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

223 perceived location of the target in trial N-1.

224

225 When two consecutive trials were both Standard trials (Fig 5a, top), we observed a repulsive bias similar

226 to that in Exp 1 (Fig 5b). Crucially, when trial N-1 was an Opposite trial and trial N was a Standard trial, the

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

228 by the previous target location (Fig 5c). The magnitude of this repulsive effect from the previous

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

230 indicated by the SE indexes ($t(40)=0.70$, *p*=.49, d=0.11; Fig 5d). Moreover, when examining the sequential

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

232 Bootstrap, Fig 5e) rather than the difference in target angle (*p*=.20, Fig 5f-g). These results suggested that

233 the sequential effects in Exp 1-2 were rooted in the motor system rather than the perceptual system.

234

235
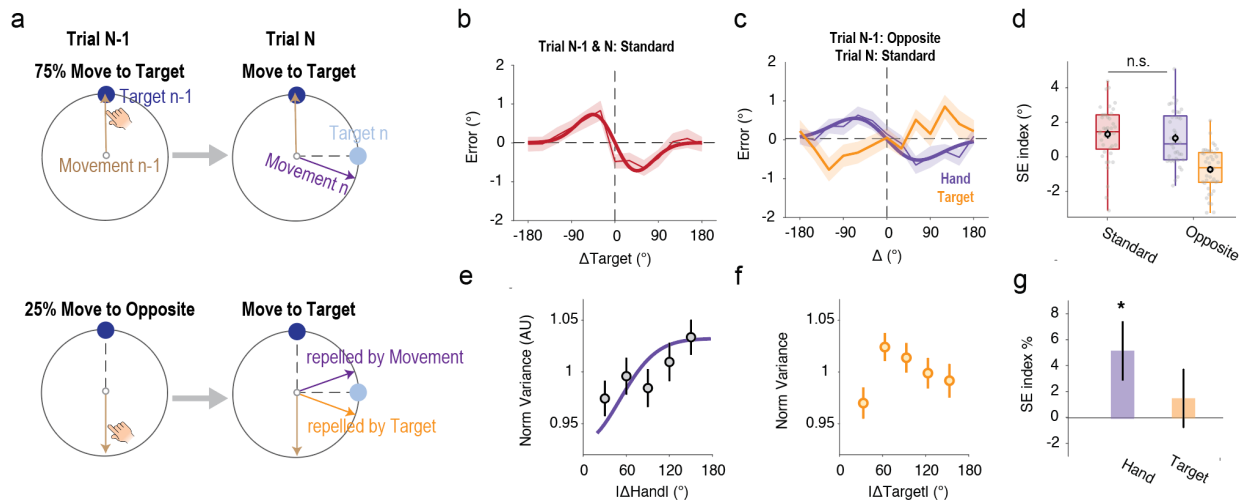
236

Figure 5. Sequential effects in reaching were associated with motor movement rather than perception. a) Design of Exp 3: In 75% of trials, participants were directed to move towards the target (Standard), and in 25% of trials, they were directed to move in the opposite direction of the target (Opposite). A repulsive effect was expected when both 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 Opposite trial, the design allowed examination of whether the repulsive effect was triggered by target perception or movement (bottom row). b-c) The sequential effect of motor bias when both trial N and trial N-1 were Standard 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 bars indicate data, and the thick curve indicates the prediction of the efficient coding model. d) The sequential bias was similar across panels b and e when the SE index after the Opposite trial was measured based on Δhand rather than Δtarget. e-f) After an Opposite trial, movement variance increased as a function of Δhand (e) rather than Δtarget (f). The motor variance increased with Δhand rather than Δtarget. g) The coefficients of linear regression measured from panel e-f. Error bars and shaded areas indicate standard error. *, p<.001.

249

We have shown that the sequential bias in Exp 1-4 was caused by movement; However, it remains possible that this effect could be mediated by perception. For instance, the movement from trial N-1 might repulse the perception in trial N, thereby affecting the subsequent movement (mediated hypothesis). Alternatively, the current movement could be directly repelled away by the previous movement (direct hypothesis). To distinguish between these hypotheses, we examined cases where trial N-1 was a Standard trial and trial N an Opposite trial (Fig S2a). Under the mediated hypothesis, the current perception is repelled away from the previous movement, so that we would expect the current movement to be attracted towards the movement N-1 when participants are instructed to move in a direction opposite that of target N. In contrast, the direct hypothesis predicts the current movement to be repelled from the

259   target/movement in N-1 (Fig S2b). Our findings aligned with the direct hypothesis (Fig S2c-d). Based on

260   the results in Exp 4, we concluded that the current movement was directly influenced by the previous

261   movement.

262

263   We also observed a priming effect in reaction time in Exp 1-4. Consistent with the notion of efficient

264   coding, reaction times were shorter when the current target was close to the previous target (Fig S3a-b).

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

266   current trial was influenced by targets presented more than 10 trials in the past (Fig S3c-d), which was

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

268   (Fig 3e). Moreover, in Exp 4, the reaction time priming effect was similar after both Opposite and Standard

269   trials (Fig S3e), suggesting the effect may be related to target detection rather than reaching, per se.

270

271   <u>Encoding noise enhances the repulsive sequential bias.</u>

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

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

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

275   relative to the prior mean (Fig 6a). To examine this, we compared the sequential bias in reaching

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

277   movement with the non-dominant hand incorporates more noise (Fig 6b), which should increase the

278   repulsive bias. In Exp 5, we performed a similar center-out reaching task and participants were randomly

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

280   performed this experiment in a lab setup with the experimenter supervising the task (Fig 6c). Participants

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

282   6c). Consistent with our assumption, participants showed significantly lower motor variability with the

283   dominant hand compared to the non-dominant hand ($t(23)=4.9$, $p<.001$, d=1.0; Fig 6d).

284

285
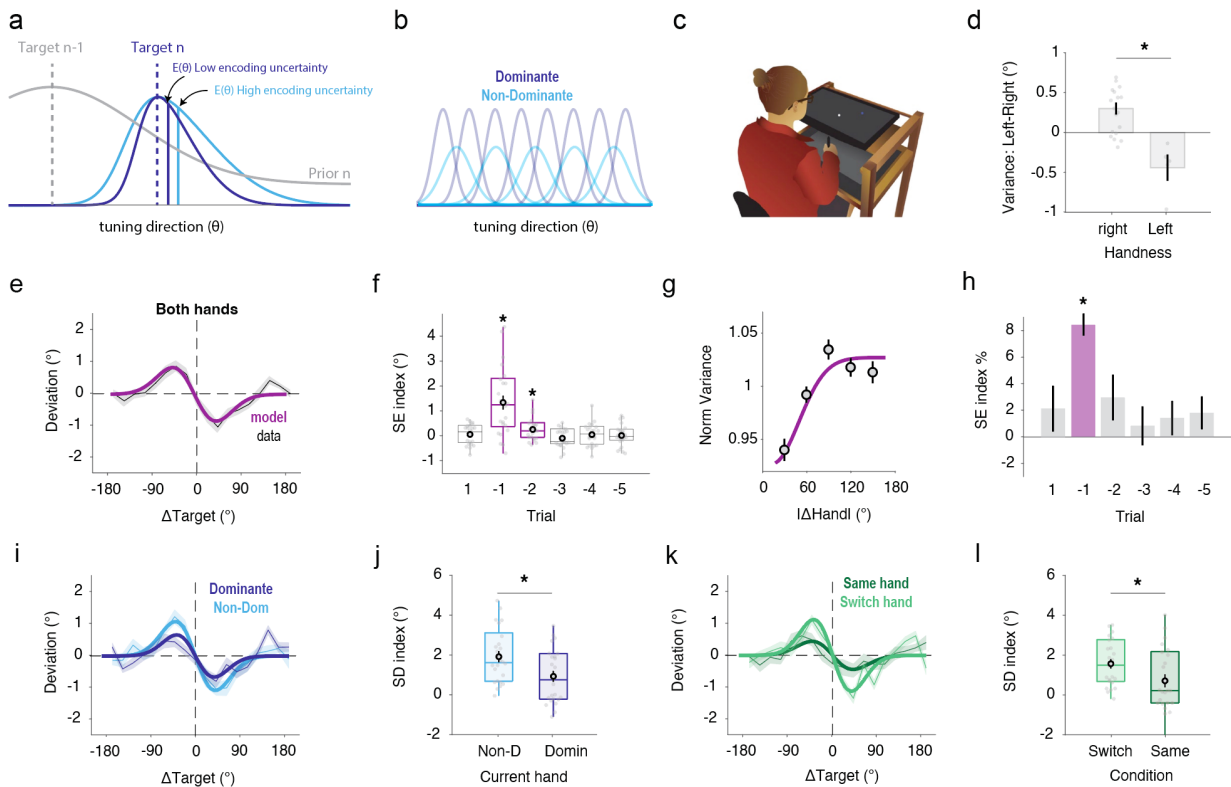
Figure 6. The repulsive sequential bias increased with the encoding noise in the motor system. a) Illustration of how encoding noise increases the repulsive bias based on the efficient coding model. b) We assumed that the non-dominant hand has fewer movement planning units with higher encoding uncertainty, 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 5 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 6e-f) and increased movement variance (N-1: $p<.001$, Bootstrap, Fig 6g-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<.001, d=0.97; Fig 6i-j), supporting the prediction of

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

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

306   hands in trial N and N-1) compared to using the same hand (t(23)=6.7, p<0.001, d=1.4; Fig 6k-l). This effect

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

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

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

310   sequential bias.

311

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

313   the correlation between motor variance and the SE index in Exp 5. Consistent with the prediction of the

314   efficient coding theory, we found a positive correlation between individual differences in variance and the

315   SE index for both hands (Fig 7a). A positive correlation was also found when we re-examined the data

316   from Exp 1 and 4 (Fig 7b-c). Those results together further supported the hypothesis that motor planning

317   follows the principles of efficient coding.

318

319
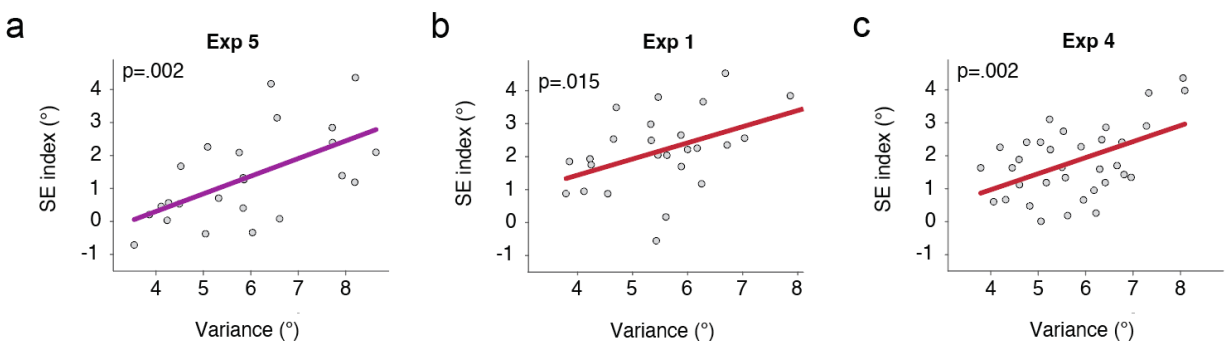
Figure 7. The repulsive sequential bias increased with the motor variability across participants. Correlation between the SE index and the motor variance for Exp 5 (a), Exp 1 (b), and Exp 4 (c). Each dot is one participant. The colored line shows the best-fitted linear model. The p-value was measured from the Pearson correlation.

Discussion

328   Motor planning requires rapid computations in high-dimensional spaces[17,35,36]. Our study investigated

329   whether the motor system employs efficient coding mechanisms to improve encoding accuracy. Efficient

330   coding, a theory initially applied to perceptual systems, posits that neural systems allocate resources in a

331   manner that optimizes the overall information encoded[1,4,14]. Specifically, the system prioritizes encoding

332   resources for more probable stimuli/movements over less frequent ones, leading to heterogeneous

333   accuracy across the task space as well as systematic biases in the percepts/movements[10–13,15]. The current

334   study confirmed these key predictions of efficient coding in a series of experiments using planar reaching

335   tasks, suggesting that motor planning is indeed subject to efficient coding principles.

336

337   When testing the efficient coding model, we identified two novel sequential effects in reaching tasks. First,

338   reaching variability increased when the current reaching direction deviated significantly from the previous

339   direction. This modulation in variability suggests that the motor system dynamically adjusts its encoding

340   resources based on recent movements, resulting in movements closer to prior expectations being

341   encoded with higher precision. Second, the current reaching direction was biased away from the previous

342   reaching direction. This repulsive bias is a by-product of the efficient coding model: due to the asymmetric

343   representation of movement directions, the noise distribution causes movements to shift in the opposite

344   direction from the prior.

345

346   Additionally, we observed that the strength of this bias increases with encoding noise. This correlation

347   was evident both within participants, where the non-dominant hand showed a stronger sequential effect

348   compared to the dominant hand, and between participants, where individuals with higher motor

349   variability exhibited a stronger repulsive bias. Together, these results confirmed that efficient coding

350   principles hold for motor planning.

351

352   The temporal dynamics of the sequential effect highlighted the flexibility in the motor system to

353   dynamically reallocate resources. The principles of efficient coding have been tested through systematic

354   biases shaped by long-term priors[14,15], often influenced by life-long experiences[10,11]. In our study, we

355   extended this principle to explain trial-by-trial biases in movement. Remarkably, the repulsive effect

356   extinguished after only 3 trials (or 6 seconds), suggesting that priors in the motor system updated rapidly.

357   This rapid adaptability might be optimal for motor planning, given the frequent and swift variations in the

358   goals and interactions of the motor system with objects over time[23]. In line with the notion of dynamic

359   priors, the sequential effect decreased when participants consistently used one hand, as opposed to

360   alternating between hands. This observation suggested that encoding resources are preferentially

361   allocated to the active hand, thereby reducing encoding noise.

362

363   While previous studies suggest that uncertainty in visual perception can also generate sequential

364   effects[22,37–39], our design specifically minimized the influence of those visual effects. Typical visual tasks

365   embed high visual uncertainty: the targets are often vague, presented for a short duration, and disappear

366   when participants make their response[33]. In contrast, our study presented a high-contrast target that

367   remained visible during the movement. This design would minimize perceptual serial dependence, as

368   previous studies found[24].

369

370   Our results also clearly dissociated the current motor sequential effects from the visual serial dependence

371   reported in other studies. First, the direction of the motor sequential bias observed in our study is

372   opposite to the serial dependence typically seen in visual tasks[22,24,33,39]. In our motor tasks, the current

373   movement is repulsed away from the previous movement, whereas in visual perception tasks, the

374   perceived target is usually attracted towards the previous target position. Second, the tuning properties

375   of the sequential effects differ between visual and motor tasks; the repulsive bias in motor tasks peaks at

376   around 60°, whereas the sequential effect in vision is usually narrower, peaking at less than 30°[33]. Third,

377   our sequential effects are significantly modulated by handedness, further suggesting an association with

378   movement rather than perception.

379

380   The opposite directions of the sequential biases in motor and visual systems might reflect their different

381   functional purposes and underlying mechanisms. In visual perception, maintaining a stable and consistent

382   representation of the world is crucial[40–42]. This stability is achieved through Bayesian decoding[13,43–45],

383   where the system interprets current evidence based on prior knowledge. This mechanism ensures a

384   coherent and reliable perception of the environment, albeit at the potential cost of an attractive bias.

385   Because objects in the world are, typically, physically stable, these attractive biases can be beneficial[46,47].

386

387   While the objects of perception in the world have identities that are physically stable, the actions we need

388   to make upon these objects can and do change from moment to moment. The motor system, therefore,

389   operates under distinct constraints. Motor planning, at least by definition, is an encoding process rather

390   than a decoding process[48,49], making the Bayesian decoding mechanism less applicable. Additionally,

391   motor goals can vary quickly over time[23], so assimilation of past movements does not present a clear

392   benefit for the motor system. Instead, a decorrelation mechanism can be beneficial for minimizing

393   repetitive mistakes or biases induced by the perceptual system and other sources[50]. As such, the repulsive

394   effect observed in our study serves these purposes, promoting the exploration of diverse motor strategies

395   in a dynamic environment while avoiding redundancy.

396

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

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

399   movements in the same direction[51–53]. However, the time course of use-dependent learning is very

400   different from the repulsive sequential bias we observed. First, use-dependent learning typically requires

401   multiple trials to manifest[51,54,55], whereas the current repulsive effect emerges after a single trial.

402   Moreover, use dependent learning usually last for tens of trials while the repulsive sequential effect lasted

403   for only two trials.

404

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

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

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

408   reducing repeated errors and enhancing sensitivity to changes in the environment or target[17,50]. However,

409   there are instances where repeated, stable movement is desirable, such as when hammering a nail while

410   holding it steady with one's fingers. Initially, efficient coding may increase the precision of movements.

411   Those movement might be slow and performed with caution so that the system can correct for undesired

412   exploratory errors with online control. As the activity continues, use-dependent learning dominates to

413   stabilize the movement, facilitating smooth and stable repetition without conscious control. Future

414   studies should explore the intriguing possibility that there is a transition between efficient coding and use-

415   dependent learning, which may reveal how the system balances the competing needs of flexibility and

416   stability in motor planning.

417

418

419   **Methods**

420

421   Participants

422   Testing was conducted online for Exp 1, 2, 3, 4 and in the lab for Exp 5. For the online studies, 154 young

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

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

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

17

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

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

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

429   based on their scores on the Edinburgh handedness test[56] and had normal or corrected-to-normal vision.

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

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

432

433   <u>Design and procedure</u>

434   *Experiment 1*

435   Exp 1-4 were performed using our web-based experimental platform[57,58]. The code was written in

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

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

438   stored using Google Firebase.

439

440   26 participants (20 females) took part in Exp 1. To start each trial, the participant moved the cursor to a

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

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

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

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

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

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

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

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

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

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

451   participant completed 1080 trials in total.

452

453   *Experiment 2*

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

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

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

457

Experiment 3

We aimed to examine the temporal modulation of serial dependence in Exp 3. Compared to Exp 1, we extended the inter-trial interval to either 6s (n = 28, 10 females) or 18s (n = 23, 12 females) for two groups of participants, respectively. A message "wait" would be presented on the monitor between two trails. Participants were instructed to put their right hand on the trackpad and rest until they saw the message "move to center" which indicated the start of a new trial. Participant completed 880 (6s condition) or 360 trials (18s condition).

Experiment 4

Exp 4 was designed to examine whether the sequential effect was induced by perception or movement. 41 participants (13 females) took part in Exp 4. The procedure of Exp 4 was essentially the same as in Exp 1. To evaluate whether this repulsive effect was perception-based or motor-based, we included trials (25%) in which the participants were instructed to move in the opposite direction of the target. Before each trial, an instruction message would appear on the screen to instruct participants to either "move to target" or "move to opposite." There were no consecutive "opposite" trails. Each participant completed 960 trials in total.

Experiment 5

Exp 5 was designed to examine how motor variability influences the sequential reaching bias. 24 participants (15 females, 19 right-handed and 5 left-handed) performed the experiment in the lab setup. Participants performed a center-out reaching task, holding a digitizing pen in the right or left hand to make horizontal movements on a digitizing tablet (49.3cm x 32.7cm, sampling rate= 100 Hz; Wacom, Vancouver, WA). The stimuli were displayed on a 120 Hz, 17-in. monitor (Planar Systems, Hillsboro, OR), which was mounted horizontally above the tablet (25 cm), to preclude vision of the limb. The experiment was controlled by custom software coded in MATLAB (The MathWorks, Natick, MA), using Psychtoolbox extensions, and ran on a Dell OptiPlex 7040 computer (Dell, Round Rock, TX) with Windows 7 operating system (Microsoft Co., Redmond, WA).

Participants made reaches from the center of the workspace to targets positioned at a radial distance of 8 cm. The start position and target location were indicated by a white annulus (1.2 cm diameter) and a filled blue circle (1.6 cm), respectively. Vision of the hand was occluded by the monitor, and the lights were extinguished in the room to minimize peripheral vision of the arm. Feedback, when provided, was

19

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

491   the digitizing pen.

492

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

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

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

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

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

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

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

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

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

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

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

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

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

506

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

508   8 trials. Target locations were randomized in a way that both hands would visit targets from 1°-360° (with

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

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

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

512

513   Data Analysis

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

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

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

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

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

519

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

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

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

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

524   effect[13,24–26].

525

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

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

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

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

530   difference between the average error within -90°-0° ΔTarget and the average error within 0°-90° ΔTarget.

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

532

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

534   the Pearson correlation between motor variance and the SE index, for Exp 1, Exp 5, and Exp 4 (only for

535   trails after a standard trial). We did not perform the correlation analysis for Exp 2-3. The motor variance

536   was very large in the no-feedback condition of Exp 2 compared to all other experiments, likely because of

537   the drifting sensorimotor map without visual calibration[59,60]. As such, the motor variance in Exp 2 was not

538   a good measurement of encoding variability. We also excluded Exp 3 given the temporal decay of the

539   sequential effect due to the long ITI.

540

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

542   movement N-1 and movement N (|ΔHand|). We flipped the sign of the deviation if ΔHand was negative.

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

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

545   as a function of |ΔHand|, we applied a general linear model:

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

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

548   function when |ΔHand| increases from 30° to 150°. To estimate the distribution of the SE index, we

549   applied bootstrap resampling 1000 times.

550

551

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

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

554   RT changes as a function of |ΔTarget|. The RT SE index is the difference between the average normalized

555   RT within 180°-90° |ΔTarget| and the average RT within 0°-90° |ΔTarget|. Simple t-tests were conducted

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

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

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

559

560   **Model**

561   <u>Efficient coding model</u>

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

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

564   coding in perception[10,12,15]. A key assumption of the model is that the encoding system allocates its

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

566   constraint to bound the total coding resources of the system[10], this requires the Fisher information $J(\theta)$ to

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

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

569

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

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

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

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

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

575   F from the target space (θ) to the motor space ($\tilde{\theta}$), following[10]:

576 $$\tilde{\theta} = F(\theta) = \int_0^\theta p(\chi)d\chi \qquad [2]$$

577

578   Given an input θ, the output m is computed as follows[15]. We first calculated the response value r, which

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

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

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

582   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

583   response value in the target space of:

584 $$r = F^{-1}(F(\theta) + \tilde{\epsilon}) \qquad [3]$$

22

585

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

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

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

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

590
$$m = E((F^{-1}(r + \tilde{\delta}); \tilde{\delta}) \qquad [4]$$

591

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

593   can take a second-order Taylor expansion:

594
$$F^{-1}(F(\theta) + \epsilon) \approx F^{-1}(F(\theta)) + \phi'(F(\theta)) \times (\epsilon + \delta) + (1/2)\phi''(F(\theta)) \times (\epsilon + \delta)^2 \qquad [5]$$

595

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

597
$$m \approx \theta + \phi'(F(\theta))\epsilon + \frac{1}{2}\phi''(\sigma^2 + \epsilon^2) \qquad [6]$$

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

599   varies can be expressed as:

600
$$\hat{m} = E(m; \tilde{\epsilon}) \approx \theta + \phi''\sigma^2 \qquad [7]$$

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

602
$$\text{var}(m) \approx (\phi'\sigma)^2 \qquad [8]$$

603

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

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

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

607
$$p(\theta) \propto k * U(0, 360) + (1 - k)N(\theta_{n-1}, \rho^2) \qquad [9]$$

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

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

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

611   incremental approach.

612

613   <u>Repeated Suppression model</u>

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

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

23

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

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

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

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

$$r_i = Norm(\theta, i, d) \qquad [10]$$

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

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

$$\boldsymbol{m} = \sum_i s_i r_i \boldsymbol{v}_i \qquad [11]$$

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

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

626 the strength of the activation in unit i:

$$s_i(n+1) = 1 - ar_i(n) \qquad [12]$$

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

629 more suppressed in the next trial.

630

631 <u>Bayesian Decoding model</u>

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

633 distribution of θ to improve performance[20,21,61]. The system generates a response r based on a target

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

635 follows:

$$p(r|\theta) = Norm(\theta, \sigma) \qquad [13]$$

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

638 a posterior estimation following Bayesian rules:

$$p(\theta|r) = \frac{p(\theta)p(r|\theta)}{p(r)} \qquad [14]$$

640 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

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

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

643

644

645 **Funding**

647

651   **Competing interests**

652   We have nothing to declare.

653

654   **Data availability**

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

656

657   **Reference**

658

659   1.   Ganguli, D. & Simoncelli, E. P. Efficient sensory encoding and Bayesian inference with

660   heterogeneous neural populations. *Neural Comput.* **26**, 2103–2134 (2014).

661   2.   Barlow, H. B. Possible principles underlying the transformations of sensory messages. in *Sensory*

662   *Communication* 216–234 (The MIT Press, 2012).

663   3.   Attneave, F. Some informational aspects of visual perception. *Psychol. Rev.* **61**, 183–193 (1954).

664   4.   Lewicki, M. S. Efficient coding of natural sounds. *Nat. Neurosci.* **5**, 356–363 (2002).

665   5.   Simoncelli, E. P. Vision and the statistics of the visual environment. *Curr. Opin. Neurobiol.* **13**, 144–

666   149 (2003).

667   6.   Ming, V. L. & Holt, L. L. Efficient coding in human auditory perception. *J. Acoust. Soc. Am.* **126**,

668   1312–1320 (2009).

669   7.   Geisler, W. S. Visual perception and the statistical properties of natural scenes. *Annu. Rev. Psychol.*

670   **59**, 167–192 (2008).

671   8.   Doi, E. *et al.* Efficient coding of spatial information in the primate retina. *J. Neurosci.* **32**, 16256–

672   16264 (2012).

673   9.   May, K. A. & Zhaoping, L. Efficient coding theory predicts a tilt aftereffect from viewing untilted

674   patterns. *Curr. Biol.* **26**, 1571–1576 (2016).

675   10. Wei, X.-X. & Stocker, A. A. A Bayesian observer model constrained by efficient coding can explain

676   "anti-Bayesian" percepts. *Nat. Neurosci.* **18**, 1509–1517 (2015).

677   11. Hahn, M. & Wei, X.-X. A unifying theory explains seemingly contradictory biases in perceptual

678   estimation. *Nat. Neurosci.* (2024)

679   12. Wei, X.-X. & Stocker, A. A. Lawful relation between perceptual bias and discriminability. *Proc. Natl.*

680   *Acad. Sci. U. S. A.* **114**, 10244–10249 (2017).

681   13. Fritsche, M., Spaak, E. & de Lange, F. P. A Bayesian and efficient observer model explains

682   concurrent attractive and repulsive history biases in visual perception. *Elife* **9**, (2020).

683   14. Louie, K. & Glimcher, P. W. Efficient coding and the neural representation of value. *Ann. N. Y. Acad.*

684   *Sci.* **1251**, 13–32 (2012).

685   15. Polanía, R., Woodford, M. & Ruff, C. C. Efficient coding of subjective value. *Nat. Neurosci.* **22**, 134–

686   142 (1/2019).

687   16. Wong, A. L., Haith, A. M. & Krakauer, J. W. Motor Planning. *Neuroscientist* **21**, 385–398 (2015).

688   17. Hayes, K. C. & Marteniuk, R. G. 9 - Dimensions of Motor Task Complexity. in *Motor Control* (ed.

689   Stelmach, G. E.) 201–228 (Academic Press, 1976).

690   18. Perrier, P. About speech motor control complexity. *Speech production: Models, phonetic processes,*

691   *and* 13–26 (2006).

692   19. Patten, M. L., Mannion, D. J. & Clifford, C. W. G. Correlates of perceptual orientation biases in

693   human primary visual cortex. *J. Neurosci.* **37**, 4744–4750 (2017).

694   20. Körding, K. P. & Wolpert, D. M. Bayesian integration in sensorimotor learning. *Nature* **427**, 244–247

695   (2004).

696   21. Jazayeri, M. & Shadlen, M. N. Temporal context calibrates interval timing. *Nat. Neurosci.* **13**, 1020–

697   1026 (2010).

698   22. Fischer, J. & Whitney, D. Serial dependence in visual perception. *Nat. Neurosci.* **17**, 738–743 (2014).

699   23. Wong, A. L. & Haith, A. M. Motor planning flexibly optimizes performance under uncertainty about

700   task goals. *Nat. Commun.* **8**, 14624 (2017).

701   24. Manassi, M., Liberman, A., Kosovicheva, A., Zhang, K. & Whitney, D. Serial dependence in position

702   occurs at the time of perception. *Psychon. Bull. Rev.* **25**, 2245–2253 (2018).

703   25. Pascucci, D. *et al.* Laws of concatenated perception: Vision goes for novelty, decisions for

704   perseverance. *PLoS Biol.* **17**, e3000144 (2019).

705   26. Wang, T. *et al.* A unitary mechanism underlies adaptation to both local and global environmental

706   statistics in time perception. *PLoS Comput. Biol.* **19**, e1011116 (2023).

707   27. Ma, W. J., Beck, J. M., Latham, P. E. & Pouget, A. Bayesian inference with probabilistic population

708   codes. *Nat. Neurosci.* **9**, 1432–1438 (2006).

709   28. Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M. & Egner, T. Neural repetition

710   suppression reflects fulfilled perceptual expectations. *Nat. Neurosci.* **11**, 1004–1006 (2008).

711   29. Auksztulewicz, R. & Friston, K. Repetition suppression and its contextual determinants in predictive

712   coding. *Cortex* **80**, 125–140 (2016).

713   30. Kohn, A. Visual adaptation: physiology, mechanisms, and functional benefits. *J. Neurophysiol.* **97**,

714   3155–3164 (2007).

715   31. Wainwright, M. J. Visual adaptation as optimal information transmission. *Vision Res.* **39**, 3960–3974

716   (1999).

717   32. Kiyonaga, A., Scimeca, J. M., Bliss, D. P. & Whitney, D. Serial Dependence across Perception,

718   Attention, and Memory. *Trends Cogn. Sci.* **21**, 493–497 (2017).

719   33. Manassi, M., Murai, Y. & Whitney, D. Serial dependence in visual perception: A meta-analysis and

720   review. *J. Vis.* **23**, 18–18 (2023).

721   34. Cicchini, G. M., Mikellidou, K. & Burr, D. Serial dependencies act directly on perception. *J. Vis.* **17**, 6–

722   6 (2017).

723   35. Newell, K., Vaillancourt, D. & Sosnoff, J. Aging, complexity, and motor performance. in *Handbook of*

724   *the Psychology of Aging* 163–182 (Elsevier, 2006).

725   36. Rosenbaum, D. A. *Human Motor Control*. (Academic Press, San Diego, CA, 2009).

726   37. Bliss, D. P., Sun, J. J. & D'Esposito, M. Serial dependence is absent at the time of perception but

727   increases in visual working memory. *Sci. Rep.* **7**, 14739 (2017).

728   38. Manassi, M. & Whitney, D. Illusion of visual stability through active perceptual serial dependence.

729   *Sci. Adv.* **8**, eabk2480 (2022).

730   39. Fornaciai, M. & Park, J. Attractive Serial Dependence in the Absence of an Explicit Task. *Psychol. Sci.*

731   **29**, 437–446 (2018).

732   40. Angelini, M. & Santucci, G. On visual stability and visual consistency for progressive visual analytics.

733   in *Proceedings of the 12th International Joint Conference on Computer Vision, Imaging and*

734   *Computer Graphics Theory and Applications* (SCITEPRESS - Science and Technology Publications,

735   2017).

736   41. Pazhoohi, F. Visual experience: Sensation, cognition and constancy. *Eur. J. Psychol.* **10**, 204–207

737   (2014).

738   42. Epstein, W. *Stability and Constancy in Visual Perception*. (John Wiley & Sons, Nashville, TN, 1977).

739   43. Ding, S., Cueva, C. J., Tsodyks, M. & Qian, N. Visual perception as retrospective Bayesian decoding

740   from high- to low-level features. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E9115–E9124 (2017).

741   44. Chikkerur, S., Serre, T., Tan, C. & Poggio, T. What and where: a Bayesian inference theory of

742   attention. *Vision Res.* **50**, 2233–2247 (2010).

743   45. Kersten, D., Mamassian, P. & Yuille, A. Object perception as Bayesian inference. *Annu. Rev. Psychol.*

744   **55**, 271–304 (2004).

745   46. Cicchini, G. M., Mikellidou, K. & Burr, D. C. The functional role of serial dependence. *Proc. R. Soc. B.*

746   **285**, 20181722 (2018).

747   47. Manassi, M. & Whitney, D. Continuity fields enhance visual perception through positive serial

748   dependence. *Nature Reviews Psychology* (2024).

749   48. Rickert, J., Riehle, A., Aertsen, A., Rotter, S. & Nawrot, M. P. Dynamic encoding of movement

750   direction in motor cortical neurons. *J. Neurosci.* **29**, 13870–13882 (2009).

751   49. Hatsopoulos, N. G., Xu, Q. & Amit, Y. Encoding of movement fragments in the motor cortex. *J.*

752   *Neurosci.* **27**, 5105–5114 (2007).

753   50. Eckmann, S., Klimmasch, L., Shi, B. E. & Triesch, J. Active efficient coding explains the development

754   of binocular vision and its failure in amblyopia. *Proceedings of the National Academy of Sciences*

755   **117**, 6156–6162 (2020).

756   51. Diedrichsen, J., White, O., Newman, D. & Lally, N. Use-dependent and error-based learning of

757   motor behaviors. *J. Neurosci.* **30**, 5159–5166 (2010).

758   52. Classen, J., Liepert, J., Wise, S. P., Hallett, M. & Cohen, L. G. Rapid plasticity of human cortical

759   movement representation induced by practice. *J. Neurophysiol.* **79**, 1117–1123 (1998).

760   53. Butefisch, C. M. *et al.* Mechanisms of use-dependent plasticity in the human motor cortex. *Proc.*

761   *Natl. Acad. Sci. U. S. A.* **97**, 3661–3665 (2000).

762   54. Tsay, J. S. *et al.* Dissociable use-dependent processes for volitional goal-directed reaching. *Proc.*

763   *Biol. Sci.* **289**, 20220415 (2022).

764   55. Marinovic, W., Poh, E., de Rugy, A. & Carroll, T. J. Action history influences subsequent movement

765   via two distinct processes. *Elife* **6**, (2017).

766   56. Oldfield, R. C. The assessment and analysis of handedness: The Edinburgh inventory.

767   *Neuropsychologia* **9**, 97–113 (1971).

768   57. Tsay, J. S., Ivry, R. B., Lee, A. & Avraham, G. Moving outside the lab: The viability of conducting

769   sensorimotor learning studies online. *Neurons, Behavior, Data analysis, and Theory* (2021)

770   doi:10.51628/001c.26985.

771 58. Wang, T., Avraham, G., Tsay, J. S., Thummala, T. & Ivry, R. B. Advanced feedback enhances

772   sensorimotor adaptation. *Curr. Biol.* (2024) doi:10.1016/j.cub.2024.01.073.

773 59. Smeets, J. B. J., van den Dobbelsteen, J. J., de Grave, D. D. J., van Beers, R. J. & Brenner, E. Sensory

774   integration does not lead to sensory calibration. *Proceedings of the National Academy of Sciences*

775   **103**, 18781–18786 (2006).

776 60. Wann, J. & Ibrahim, S. Does limb proprioception drift? *Exp. Brain Res.* **91**, (1992).

777 61. Ma, W. J. Organizing probabilistic models of perception. *Trends Cogn. Sci.* **16**, 511–518 (2012).

778

779 **Supplementary figures**

780
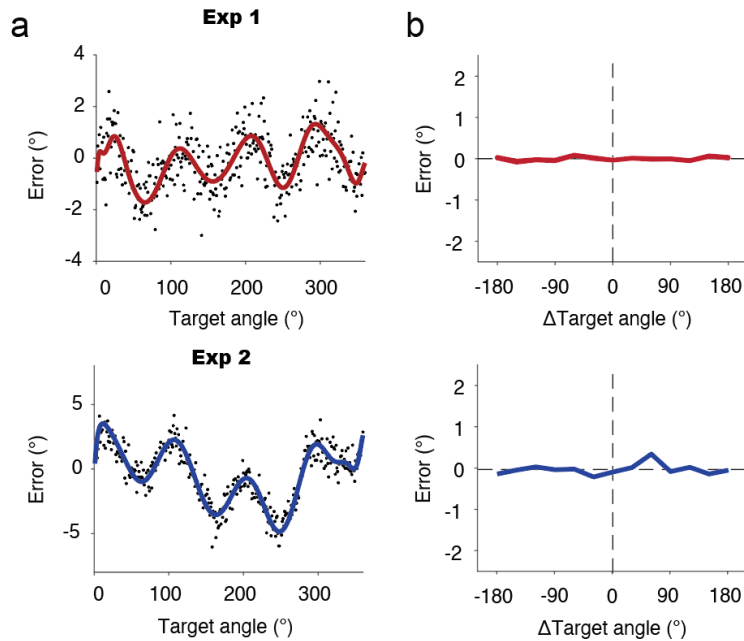
781

782 **Figure S1. Systematic motor biases did not generate sequential effects.** a) Systematic motor bias relative to target

783 position in Exp 1 (upper panel) and 2 (lower panel). Participants exhibited greater bias in Exp 2, where feedback was

784 absent. Black dots indicate data. The thick line represents a smoothed function, obtained by fitting a polynomial

785 function with a maximum degree of 20. b) Simulation of sequential bias based on the motor bias function and the

786 sequence of targets presented to participants. The systematic motor bias did not generate any sequential effect.

787

788
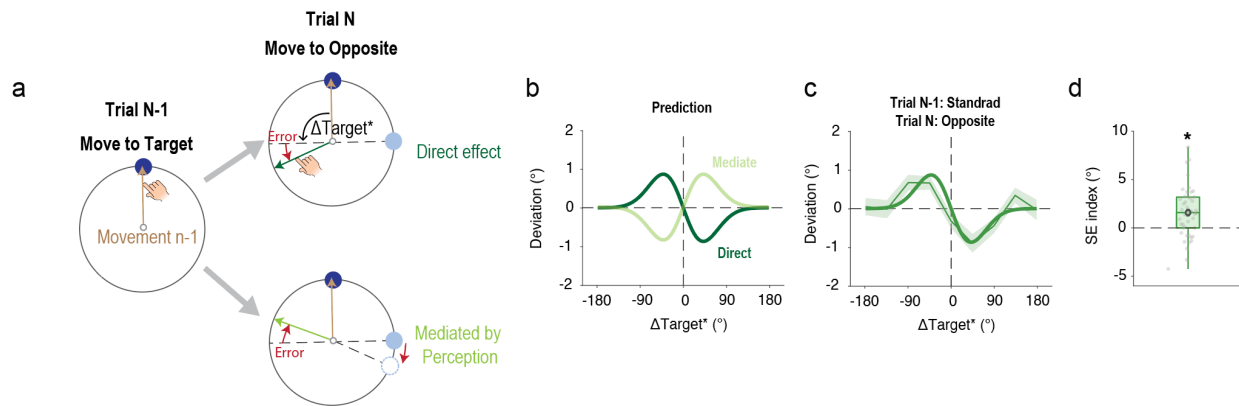
789

790 **Figure S2. The current movement was directly influenced by the previous movement, with no mediation of**

791 **perception.** a) When trial N was an Opposite trial and trial N-1 was a Standard trial, it allowed for examination of

792 whether the effect was directly caused by the previous movement repelling the current movement (direct

793 hypothesis). Alternatively, it could be that the previous movement repelled the perception of the current target's

794 position, thus indirectly influencing the movement direction (mediated hypothesis). Here, Δ Target* was defined as

795 the difference between the opposite position of the current target and the position of the previous target. b)

796 Different predictions of the sequential bias following the direct hypothesis and mediated hypothesis, respectively.

797 c) Sequential bias observed in Exp 3 was consistent with the direct hypothesis. The thin lines with shaded error bars
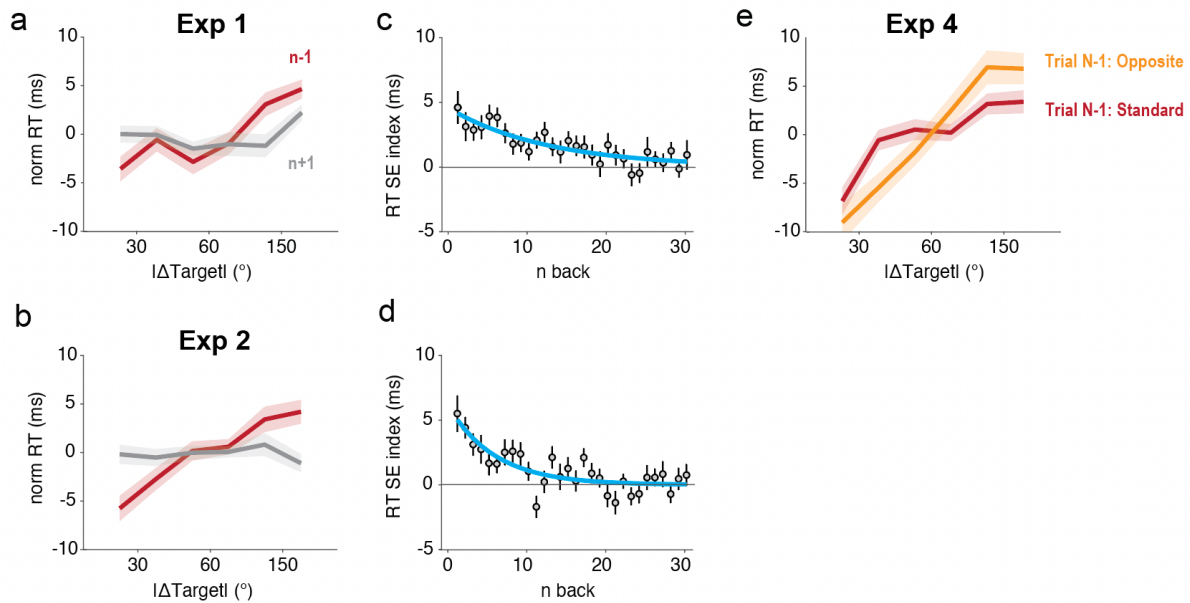
798 indicate data, and the thick curve indicates the prediction of the efficient coding model. Shaded areas indicate

799 standard error. d) SE index indicates that the current movement was significantly repelled away from the previous

800 movement. *, p<.001.

801

Figure S3. 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.