Efficient Coding in Motor Planning

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Abstract

A paramount challenge for the brain is to precisely model the world and control behavior within the confines of limited encoding capacities. Efficient coding theory posits a unified framework for understanding how neural systems enhance encoding accuracy by tuning to environmental statistics. While this theory has been thoroughly explored within the perceptual realm, it is less clear how efficient coding applies to the motor system. Here, we probe the core principles of efficient coding theory through center-out reaching tasks. Our results reveal novel sequential effects in motor planning. Specifically, current movements are biased in a direction opposite to recent movements, and movement variance increases with the angular divergence between successive actions. These effects are modulated by the variability within the motor system: a larger repulsive bias is observed when movements are performed with the nondominant hand compared to the dominant hand, and in individuals exhibiting higher motor variance compared to those with lower variance. These behavioral findings align with the predictions of an efficient coding model, suggesting that the motor system rapidly adapts to the context to enhance 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

direction aligned with the prior will be more precisely encoded, and the variability in movement will escalate when its direction diverges from the prior (Fig 1d).

Moreover, the differential allocation of coding resources across the space will introduce an encoding bias[10,11]. In visual perception, efficient coding leads to aftereffects, where perception is biased in the direction opposite to previously viewed stimuli[19]. This mechanism reduces redundancy in sensory representation and enhances sensitivity to new information. Similarly, when encoding a specific movement direction, the efficient coding model suggests that the encoding resources are imbalanced on the two sides of the movement direction. As a result, the population distributional response to this movement direction will also be asymmetric, with a higher encoding accuracy on the prior side and a flat tail pointing away from the prior mean (Fig 1e). As such, the mean direction encoded by the neural population will be biased in a direction opposite the prior mean (Fig 1f).

Other models offer alternative frameworks for understanding how prior expectations improve encoding accuracy[10,20]. For example, Bayesian models suggest that perception arises from combining prior expectations with incoming sensory information to compute a posterior estimate. As a result, they predict that current movements or perceptions will be biased toward prior expectations. Importantly, this is opposite to the repulsive biases predicted by the efficient coding model. The Bayesian framework has been successful in explaining various perceptual and motor biases[11,21,22]. Therefore, we consider the Bayesian model as an alternative to compare with our efficient coding model in predicting sequential effects in motor tasks.

While the visual world is relatively stable and continuous, motor goals can vary significantly over short time scales[23]. Consider, for example, the actions required when shopping: reaching for a milk box, placing it in a cart, and pushing the cart away, all within a matter of seconds. Instead of relying on a static prior for motor planning, the sensorimotor system may continuously update its priors based on the current motor goal to facilitate efficient coding. In other words, priors for motor planning might be largely shaped by recent movements. Based on this assumption, the efficient coding theory will predict specific sequential effects on movement bias and variance in a center-out reaching task (Fig 1d&f). Other frameworks, such as Bayesian models, make different predictions. We aim to test these competing predictions in the following experiments.

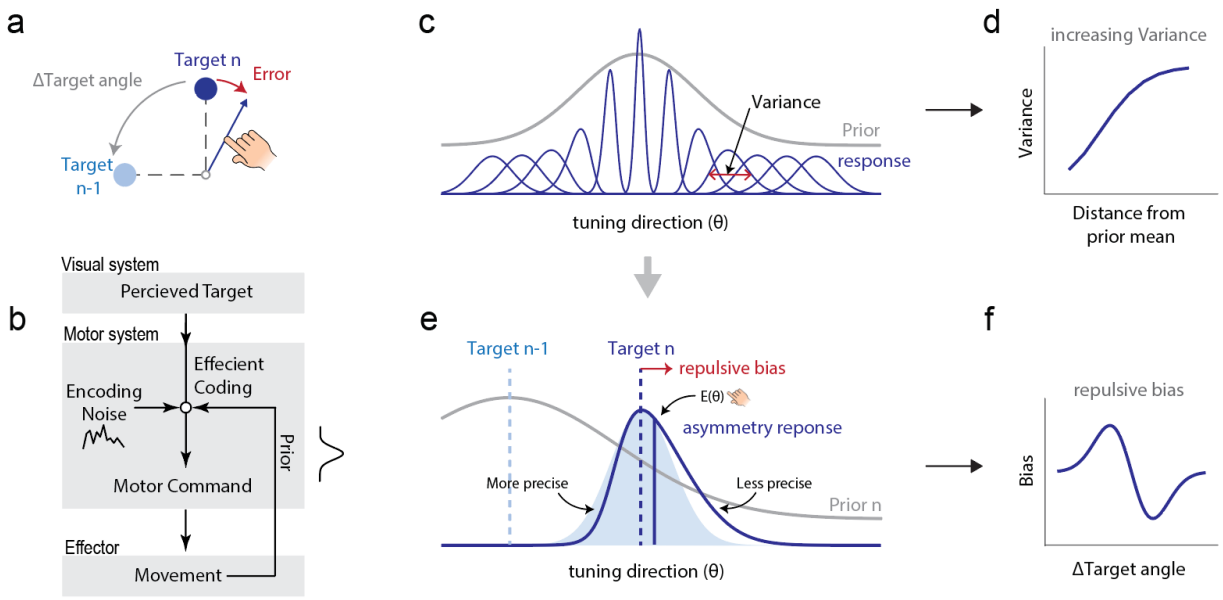

Figure 1. An efficient coding framework for motor control. a) Illustration of a reaching task. b) Schematic of an efficient coding framework. The motor system encodes a motor command based on the perceived target. The effector implements the motor command, which serves as a prior that drives the motor 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

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

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

prevent online corrections. Endpoint feedback was provided after the movement to indicate the hand position at the target radius.

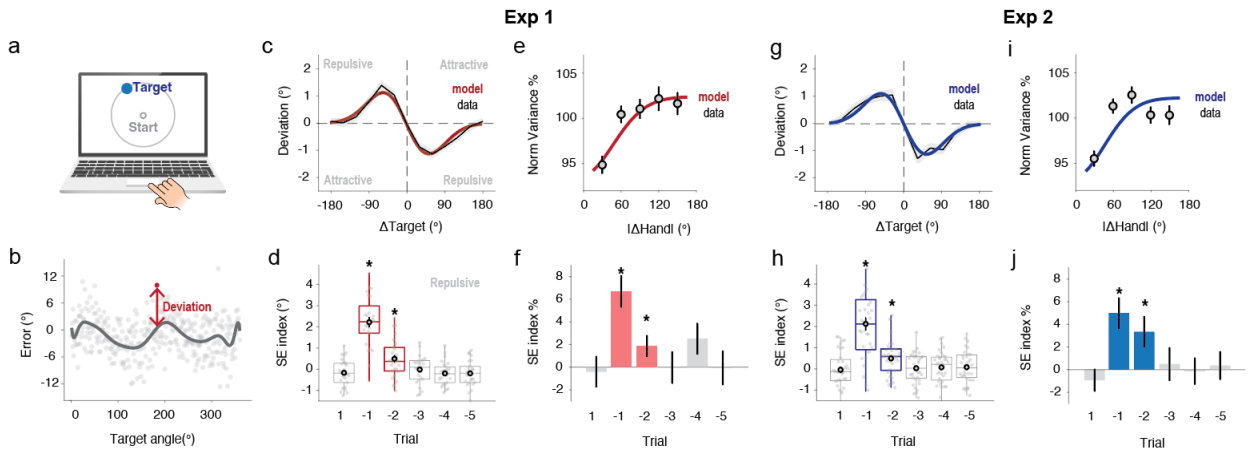

Figure 2. Sequential effects in reaching. a) An illustration of the repulsive bias predicted by the efficient coding model. b) The motor bias of a sample participant. The gray curve shows the smoothed motor bias function. The deviation was defined as the difference between the current response and the 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

the magnitude of this repulsive effect increasing with ΔTarget, peaking at 1.5° for a ΔTarget of approximately 60°. This bias function aligned well with predictions from an efficient coding model. To quantify the size of the sequential bias, we calculated a sequential effect (SE) index, defined as the difference between the average bias for Δ Target from -90° to 0° and 0° to 90°. A positive SE index signified 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) 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 median trial duration of 2.08s (SD: 1.05s), this result suggested rapid updating of prior expectations by the motor system.

We then measured the sequential effect as a function of movement variance. Again, consistent with the prediction of the efficient coding model, the movement variance increased with the distance between the directions of the two consecutive movements (Fig 2g-h). We quantified this effect by fitting a sigmoid function with motor variance as the dependent variable and the difference in hand angle as the independent variable, pooling data from all participants. The SE index was defined as the sigmoid amplitude predicted by the best-fit function (Fig 2e). Similar to what we have observed for the sequential bias, this SE index of the movement variance dropped rapidly across trials: a significant effect was found for trial N-1 ($p<0.001$, Bootstrap) and N-2 ($p=0.026$, Fig 2f), measured by bootstrap resampling. The effect disappeared for trial N-3 ($p=0.98$), which occurred only ~6 seconds prior.

In Exp 1, we showed that the sequential effects in the motor bias and movement variation are consistent with the efficient coding model. However, we noted that endpoint feedback was provided after reaching, facilitating the recalibration of the sensorimotor system. This recalibration process might be specific to areas near the recently reached positions, potentially contributing to the observed sequential effect in motor variance. To eliminate the potential influence of sensorimotor recalibration, we conducted a replication of Exp 1 without endpoint feedback (Exp 2). The results showed remarkably similar sequential effects in both movement bias and variance (Fig 2g-j), confirming that these effects were independent of visual feedback or sensorimotor recalibration.

The results in Exp 1-2 established a sequential effect in reaching movements that aligns with the predictions of the efficient coding model. In the following session, we considered two alternative models proposed to explain sequential effects. The first model we evaluated was the Bayesian model [20,21,27], which is widely used to explain how prior expectations influence behavior. According to Bayesian principles, the

system integrates prior knowledge with current observations to form a posterior estimate (Fig 3a). This process allows the system to reduce encoding noise. However, importantly, the posterior skews the average response toward the prior and leads to an attractive sequential bias (Fig 3b), which contradicts the repulsive bias as observed in behavioral results (Fig 2c).

Another alternative model we evaluated was the repeated suppression model[28,29]. This model suggests that after observing a stimulus or executing a movement, neurons tuned to that direction become less sensitive due to fatigue or active suppression, a mechanism that favors novel stimuli to avoid encoding redundancy. The suppression model predicts a repulsive sequential bias due to the asymmetric response of units on the suppressed and unsuppressed sides (Fig 3c). However, unlike the efficient coding model, which facilitates the processing of repeated stimuli, the suppression mechanism increases sensitivity to stimuli that change[30,31]. As a result, the model posits that movements closer to the previous one are encoded with less precision and exhibit greater variability compared to movements further away (Fig 3d). This prediction stands in opposition to the sequential effects observed in our experiments (Fig 2e). As such, the unique sequential effects in reaching suggest that motor planning follows efficient coding principles.

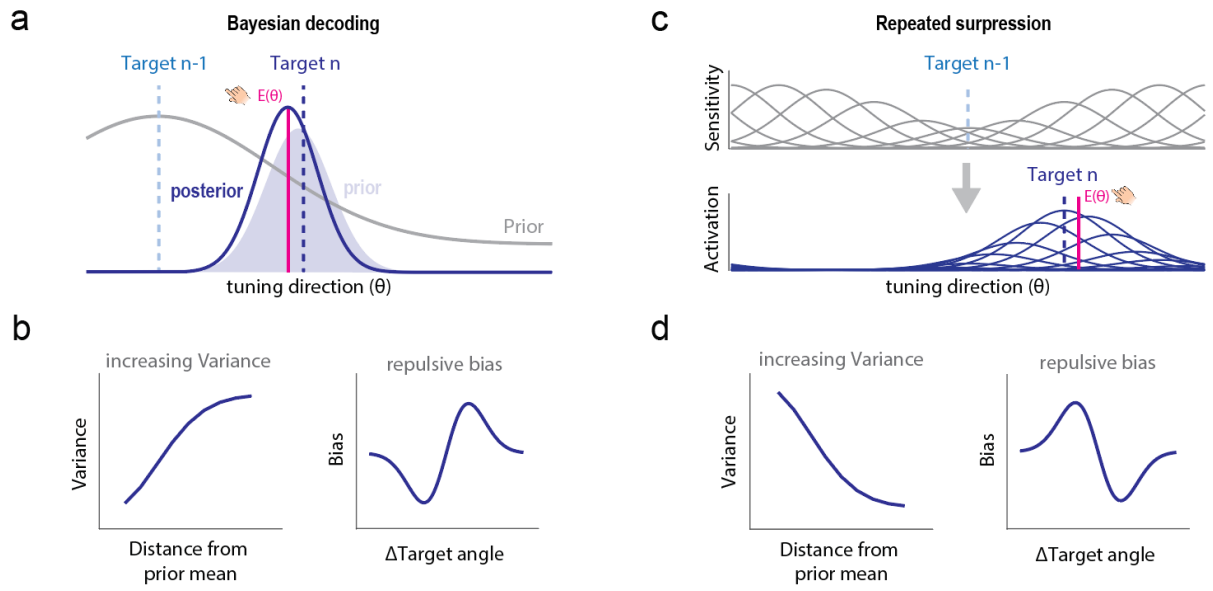

Figure 3. The repeated suppression model and Bayesian model cannot explain the sequential effects in reaching. a) Schematic of the Bayesian decoding model. b) This model predicts increasing variance and attractive bias. c) Schematic of the Repeated suppression model. The sensitivity of the unit tuned to the previous movement decreases, which causes an asymmetric representation of the subsequent movement direction. d) The Repeated suppression

model predicts decreasing variance and repulsive bias. Neither of these models were able to explain the sequential effects observed in behavioral results (Fig. 2).

Temporal dynamics of the sequential effect

In Exp 1-2, we observed a repulsive effect only from the 1-back and 2-back trials. This motivated us to further examine the temporal regulation of the repulsive sequential effect. We tested whether the rapid drop in the sequential effect solely depended on time, or whether it also depended on the number of trials. As such, in Exp 3, we extended the inter-trial interval (ITI) to either 6s or 18s for two groups of participants and compared the results with Exp 1 (0s ITI) (Fig 4). While the strength of the sequential effects decreased with time, both the repulsive bias ($t(26)=5.9$, $p<0.001$, d=1.2) and the variance modulation ($p<0.001$, Bootstrap) could be observed for trial N-1 if participants simply wait for 6s between two trials. This result contrasted with the N-3 trial in Exp 1, which was ~6s prior to the current movement (Fig 4b, d), but no sequential was observed. Moreover, the repulsive bias remained significant even in the 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 conditions showed a positive trend but did not reach significance ($p=0.16$, Fig 4d). These results suggested that the attenuation of the sequential effects depended on both passing time and intervening information.

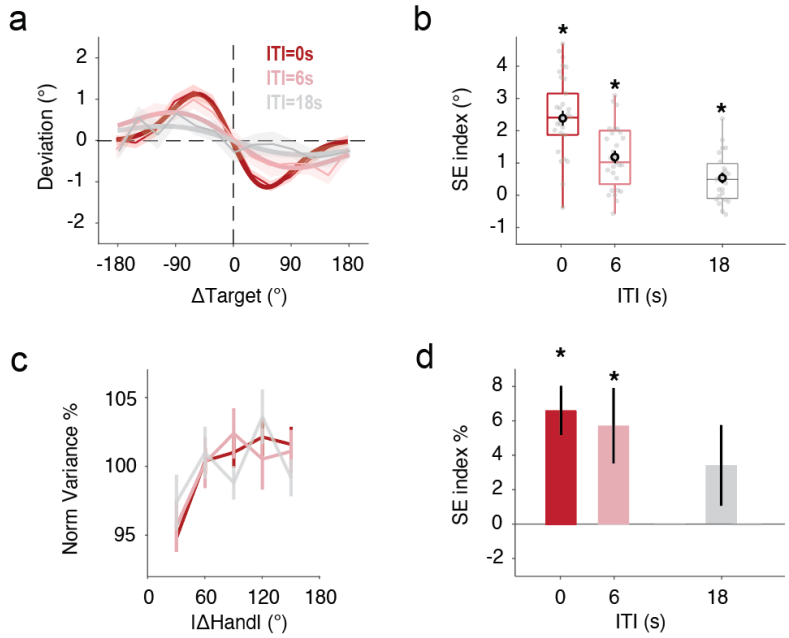

Figure 4. Temporal dynamics of the Sequential effects in reaching. (a) Sequential effect in movement direction for three ITI conditions. The thinner lines indicate the data, and the thicker lines indicate the prediction of the efficient coding model. (b) SE index with different ITI. Different from what has been observed in the 3-back condition in Exp

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<.002.

Dissociating sequential effect in movement and perception.

Sequential effects have been widely observed in perceptual tasks[22,32,33]. While we tried to minimize the role of visual uncertainty and perceptual working memory in Exp 1, a more rigorous examination was necessary to differentiate effects originating in the motor versus the perceptual systems[34]. To this end, in Experiment 4 we implemented a design where participants were instructed to either move directly towards the target (Standard condition, 75% of trials) or in the opposite direction (Opposite condition, 25% of trials). As a critical test of the source of these sequential effects in Exp 1, we analyzed scenarios where trial N-1 was an Opposite trial and trial N was a Standard trial (Fig 5a, bottom). In such cases, the inconsistency between movement direction and target in trial N allowed us to disentangle the influences of target location representation from the motor control itself. If the repulsive bias was primarily driven by motor factors, the direction in trial N would be repelled by the movement in trial N-1. Conversely, if perception of the target location was the cause, trial N's reaching direction would be repelled by the perceived location of the target in trial N-1.

When two consecutive trials were both Standard trials (Fig 5a, top), we observed a repulsive bias similar to that in Exp 1 (Fig 5b). Crucially, when trial N-1 was an Opposite trial and trial N was a Standard trial, the direction in trial N was repelled away by the previous *reaching movement* ($t(40)=4.4$, $p<.001$, d=0.68), not by the previous target location (Fig 5c). The magnitude of this repulsive effect from the previous movement was comparable to that observed when both trials N and N-1 were Standard conditions, indicated by the SE indexes ($t(40)=0.70$, $p=.49$, d=0.11; Fig 5d). Moreover, when examining the sequential effect on motor variance, we found that variance increased with the difference in hand angle ($p<.001$, Bootstrap, Fig 5e) rather than the difference in target angle ($p=.20$, Fig 5f-g). These results suggested that the sequential effects in Exp 1-2 were rooted in the motor system rather than the perceptual system.

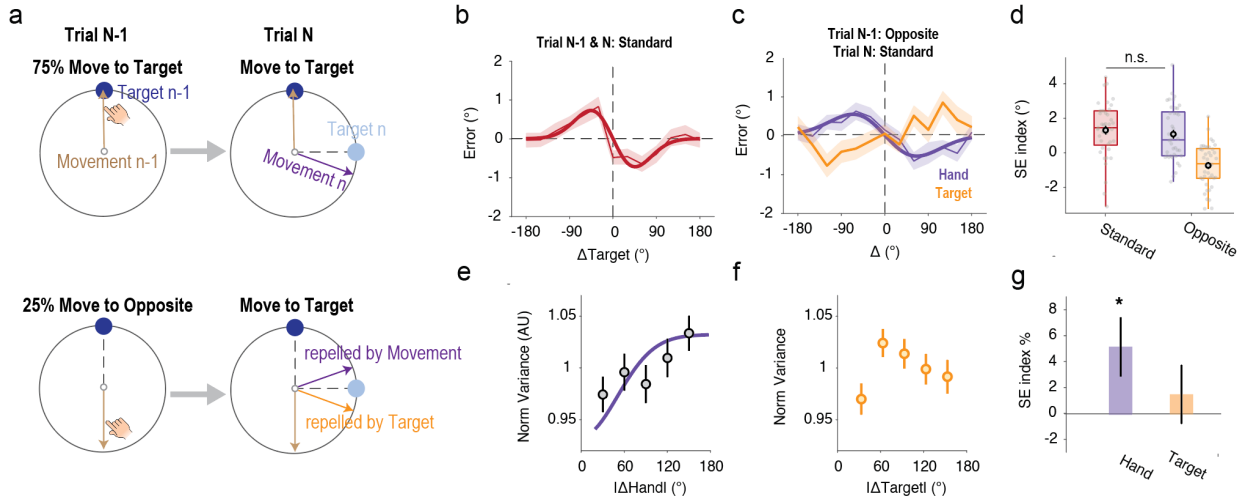

Figure 5. Sequential effects in reaching were associated with motor movement rather than perception. a) Design of Exp 3: In 75% of trials, participants were directed to move towards the target (Standard), and in 25% of trials, they were directed to move in the opposite direction of the target (Opposite). 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.

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

target/movement in N-1 (Fig S2b). Our findings aligned with the direct hypothesis (Fig S2c-d). Based on the results in Exp 4, we concluded that the current movement was directly influenced by the previous movement.

We also observed a priming effect in reaction time in Exp 1-4. Consistent with the notion of efficient coding, reaction times were shorter when the current target was close to the previous target (Fig S3a-b). However, this effect may pertain more to target detection than motor planning. The reaction time for the current trial was influenced by targets presented more than 10 trials in the past (Fig S3c-d), which was very different from the temporal dynamics of sequential effects in movement direction or motor variance (Fig 3e). Moreover, in Exp 4, the reaction time priming effect was similar after both Opposite and Standard trials (Fig S3e), suggesting the effect may be related to target detection rather than reaching, per se.

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

Another key prediction of the efficient coding theory is that the sequential bias should be modulated by encoding noise. Specifically, increased noise within the system should lead to a broader distribution of the response signal. Consequently, the average response of the system will exhibit a larger repulsive bias relative to the prior mean (Fig 6a). To examine this, we compared the sequential bias in reaching movements between the dominant hand and the non-dominant hand, with the premise that encoding a movement with the non-dominant hand incorporates more noise (Fig 6b), which should increase the repulsive bias. In Exp 5, we performed a similar center-out reaching task and participants were randomly instructed to use one hand per trial. To make sure that participants adhered to the instruction, we performed this experiment in a lab setup with the experimenter supervising the task (Fig 6c). Participants moved their occluded hand on a tablet, with the visual stimulus displayed on a monitor directly above (Fig 6c). Consistent with our assumption, participants showed significantly lower motor variability with the dominant hand compared to the non-dominant hand ($t(23)=4.9$, $p<.001$, d=1.0; Fig 6d).

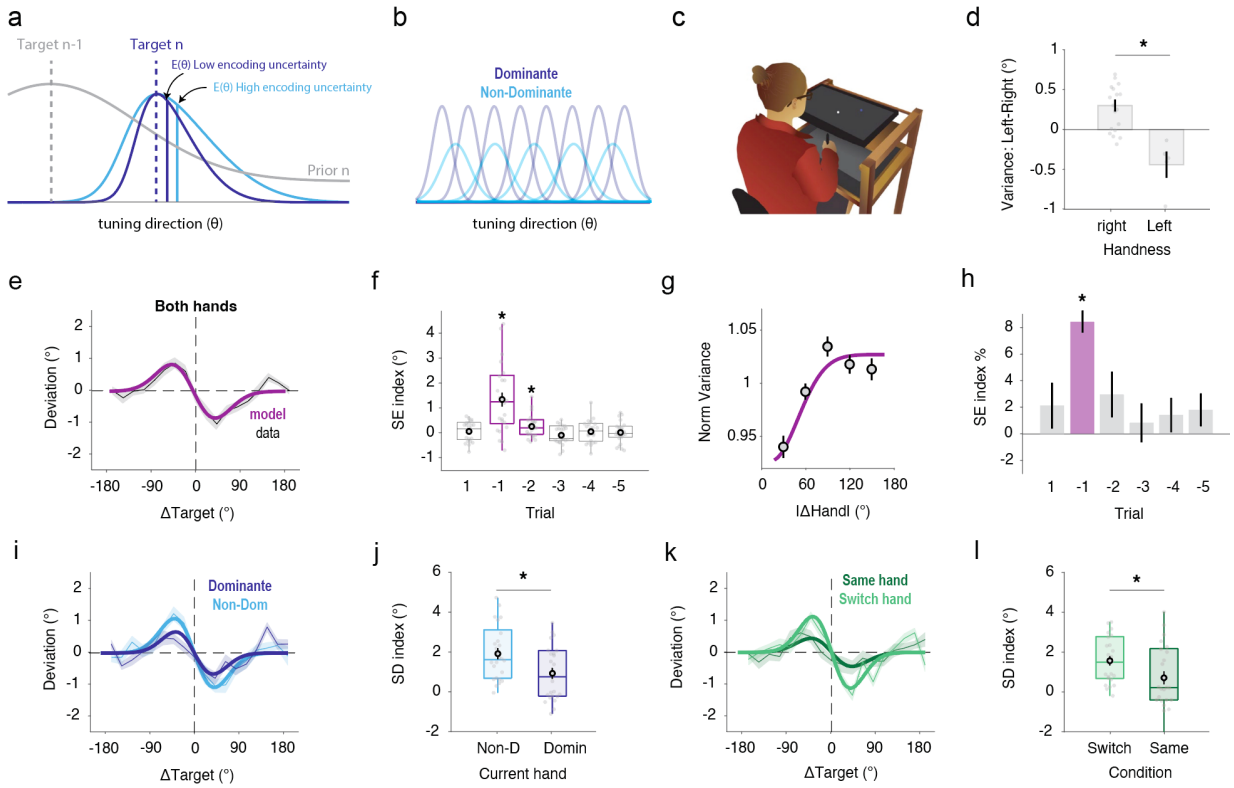

Figure 6. The repulsive sequential bias increased with the encoding noise in the motor system. a) Illustration of how encoding noise increases the repulsive bias based on the efficient coding model. b) We assumed that the non-dominant hand has fewer movement planning units with higher encoding uncertainty, 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

the efficient coding theory that bias escalates with encoding noise in the motor system. Interestingly, we also observed a larger sequential bias when participants switched their hands (namely using different 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 is likely due to dynamic allocation of encoding resources across hands, leading to increased encoding variability immediately after a hand switch and, consequently, a larger bias. Alternatively, more units might be recruited when repeating a movement with one hand, reducing encoding noise as well as the sequential bias.

To further examine how the variability in the motor system influences the sequential bias, we analyzed the correlation between motor variance and the SE index in Exp 5. Consistent with the prediction of the efficient coding theory, we found a positive correlation between individual differences in variance and the SE index for both hands (Fig 7a). A positive correlation was also found when we re-examined the data from Exp 1 and 4 (Fig 7b-c). Those results together further supported the hypothesis that motor planning follows the principles of efficient coding.

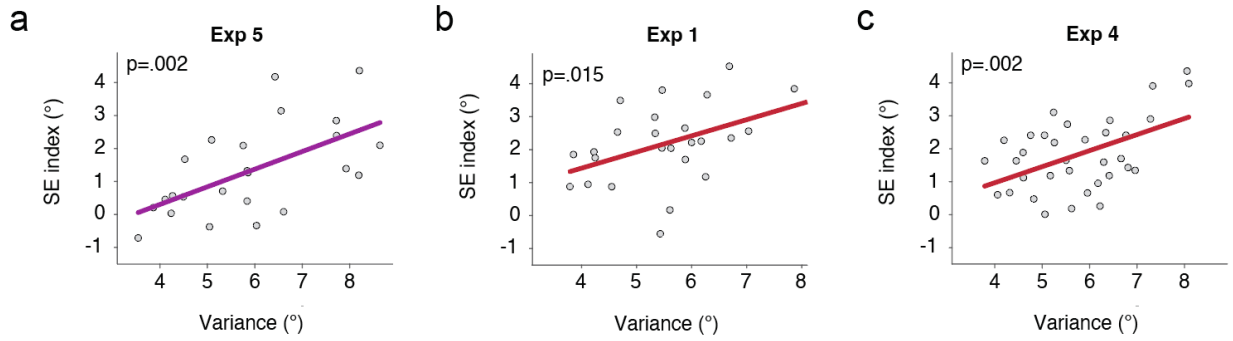

Figure 7. The repulsive sequential bias increased with the motor variability across participants. Correlation between the SE index and the motor variance for Exp 5 (a), Exp 1 (b), and Exp 4 (c). Each dot is one participant. The colored line shows the best-fitted linear model. The p-value was measured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

Discussion

Motor planning requires rapid computations in high-dimensional spaces[17,35,36]. Our study investigated whether the motor system employs efficient coding mechanisms to improve encoding accuracy. Efficient coding, a theory initially applied to perceptual systems, posits that neural systems allocate resources in a

manner that optimizes the overall information encoded[1,4,14]. Specifically, the system prioritizes encoding resources for more probable stimuli/movements over less frequent ones, leading to heterogeneous accuracy across the task space as well as systematic biases in the percepts/movements[10–13,15]. The current study confirmed these key predictions of efficient coding in a series of experiments using planar reaching tasks, suggesting that motor planning is indeed subject to efficient coding principles.

When testing the efficient coding model, we identified two novel sequential effects in reaching tasks. First, reaching variability increased when the current reaching direction deviated significantly from the previous direction. This modulation in variability suggests that the motor system dynamically adjusts its encoding resources based on recent movements, resulting in movements closer to prior expectations being encoded with higher precision. Second, the current reaching direction was biased away from the previous reaching direction. This repulsive bias is a by-product of the efficient coding model: due to the asymmetric representation of movement directions, the noise distribution causes movements to shift in the opposite direction from the prior.

Additionally, we observed that the strength of this bias increases with encoding noise. This correlation was evident both within participants, where the non-dominant hand showed a stronger sequential effect compared to the dominant hand, and between participants, where individuals with higher motor variability exhibited a stronger repulsive bias. Together, these results confirmed that efficient coding principles hold for motor planning.

The temporal dynamics of the sequential effect highlighted the flexibility in the motor system to dynamically reallocate resources. The principles of efficient coding have been tested through systematic biases shaped by long-term priors[14,15], often influenced by life-long experiences[10,11]. In our study, we extended this principle to explain trial-by-trial biases in movement. Remarkably, the repulsive effect extinguished after only 3 trials (or 6 seconds), suggesting that priors in the motor system updated rapidly. This rapid adaptability might be optimal for motor planning, given the frequent and swift variations in the goals and interactions of the motor system with objects over time[23]. In line with the notion of dynamic priors, the sequential effect decreased when participants consistently used one hand, as opposed to alternating between hands. This observation suggested that encoding resources are preferentially allocated to the active hand, thereby reducing encoding noise.

While previous studies suggest that uncertainty in visual perception can also generate sequential effects[22,37–39], our design specifically minimized the influence of those visual effects. Typical visual tasks embed high visual uncertainty: the targets are often vague, presented for a short duration, and disappear when participants make their response[33]. In contrast, our study presented a high-contrast target that remained visible during the movement. This design would minimize perceptual serial dependence, as previous studies found[24].

Our results also clearly dissociated the current motor sequential effects from the visual serial dependence reported in other studies. First, the direction of the motor sequential bias observed in our study is opposite to the serial dependence typically seen in visual tasks[22,24,33,39]. In our motor tasks, the current movement is repulsed away from the previous movement, whereas in visual perception tasks, the perceived target is usually attracted towards the previous target position. Second, the tuning properties of the sequential effects differ between visual and motor tasks; the repulsive bias in motor tasks peaks at around 60°, whereas the sequential effect in vision is usually narrower, peaking at less than 30°[33]. Third, our sequential effects are significantly modulated by handedness, further suggesting an association with movement rather than perception.

The opposite directions of the sequential biases in motor and visual systems might reflect their different functional purposes and underlying mechanisms. In visual perception, maintaining a stable and consistent representation of the world is crucial[40–42]. This stability is achieved through Bayesian decoding[13,43–45], where the system interprets current evidence based on prior knowledge. This mechanism ensures a coherent and reliable perception of the environment, albeit at the potential cost of an attractive bias. Because objects in the world are, typically, physically stable, these attractive biases can be beneficial[46,47].

While the objects of perception in the world have identities that are physically stable, the actions we need to make upon these objects can and do change from moment to moment. The motor system, therefore, operates under distinct constraints. Motor planning, at least by definition, is an encoding process rather than a decoding process[48,49], making the Bayesian decoding mechanism less applicable. Additionally, motor goals can vary quickly over time[23], so assimilation of past movements does not present a clear benefit for the motor system. Instead, a decorrelation mechanism can be beneficial for minimizing repetitive mistakes or biases induced by the perceptual system and other sources[50]. As such, the repulsive

effect observed in our study serves these purposes, promoting the exploration of diverse motor strategies in a dynamic environment while avoiding redundancy.

Interestingly, the sequential bias identified in our study contrasts with a history-influenced effect known as use-dependent learning in motor control. Use-dependent learning refers to a bias toward repeated movements in the same direction[51–53]. However, the time course of use-dependent learning is very different from the repulsive sequential bias we observed. First, use-dependent learning typically requires multiple trials to manifest[51,54,55], whereas the current repulsive effect emerges after a single trial. Moreover, use dependent learning usually last for tens of trials while the repulsive sequential effect lasted for only two trials.

Our results suggest that the differing timescales of use-dependent learning and efficient coding may reflect a progressive shift of motor control strategy in developing a skilled movement. The repulsive bias induced by efficient coding could be beneficial in a volatile environment for several reasons, such as reducing repeated errors and enhancing sensitivity to changes in the environment or target[17,50]. However, there are instances where repeated, stable movement is desirable, such as when hammering a nail while holding it steady with one's fingers. Initially, efficient coding may increase the precision of movements. Those movement might be slow and performed with caution so that the system can correct for undesired exploratory errors with online control. As the activity continues, use-dependent learning dominates to stabilize the movement, facilitating smooth and stable repetition without conscious control. Future studies should explore the intriguing possibility that there is a transition between efficient coding and use-dependent learning, which may reveal how the system balances the competing needs of flexibility and stability in motor planning.

Methods

Participants

Testing was conducted online for Exp 1, 2, 3, 4 and in the lab for Exp 5. For the online studies, 154 young adults (76 female, age: 26.7 ± 4.9 y) were recruited using the Prolific.io. The participants performed the experiment on their personal computers through a web-based platform for motor learning experiments. Based on a prescreening survey employed by Prolific, the participants were right-handed and had normal

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 Design and procedure
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

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

To start each trial, a letter “R” or “L” would be presented within the start circle to inform participant which hand to use on this trial. Participants used the instructed hand to hold the pen and put the other hand on the side. The experimenter supervised the whole experiment to make sure the participant applied the correct hand. After maintaining the cursor within the start circle for 500 ms, a target appeared. The participant was instructed to make a rapid slicing movement through the target. Right after their movement amplitude reached 8 cm, a cursor would be presented at that position for 1 s, providing feedback of the accuracy of the movement (angular position with respect to the target). After this interval, the target and cursor were extinguished. Another letter appeared at the start position and participants changed hand accordingly. To guide the participant back to the start position without providing angular information about hand position, a white ring appeared denoting the participant’s radial distance from the start position. Once the participant moved within 2 cm of the start position, the ring was extinguished, and a veridical cursor appeared to allow the participant to move their hand to the start position. If the movement time was >300 ms, the audio "Too Slow" was played right after the reaching.

The required hand was pseudorandomized so there were 4 left-hand and 4 right-hand trials within every 8 trials. Target locations were randomized in a way that both hands would visit targets from 1°-360° (with a step of 1°) within every 720 trials. The whole experiment included 2160 trials and took about 4 h. However, we allowed participants to end the experiment based on their convenience. 14 out of 24 participants finished all trials; other participants finished 1000~2000 trials.

Data Analysis

We calculated the error of hand angle as a difference between the hand position when it reached the target distance and the target position. A positive hand angle denoted that the hand position was more clockwise than the target at the target radius. Trials with a movement duration longer than 500 ms or an error larger than 60° were excluded from the analyses. For the web-based experiment, 1.5% trials were removed. For the lab-based experiment, 0.4% of trials were removed.

To analyze the sequential effect in movement, we regressed out the influence of systematic bias. 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:
546 $$variance = a + \frac{b-a}{e^{-c|\Delta\mathrm{Hand}|}} \quad [1]$$
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

RT changes as a function of |ΔTarget|. The RT SE index is the difference between the average normalized RT within 180°-90° |ΔTarget| and the average RT within 0°-90° |ΔTarget|. Simple t-tests were conducted to determine whether the SE indexes were significantly different from 0. We confirmed that the data met the assumptions of a Gaussian distribution and homoscedasticity for all tests. The significance level was set at $p < 0.05$ (two-tailed).

Model

Efficient coding model

We assumed that the motor system encodes a movement direction (m) based on an observed target direction (θ) following the rule of efficient coding. This model is based on previous models of efficient coding in perception[10,12,15]. A key assumption of the model is that the encoding system allocates its resources to maximize the mutual information $I[\theta,m]$ between input θ and output m. By imposing a constraint to bound the total coding resources of the system[10], this requires the Fisher information $J(\theta)$ to be matched to the stimulus prior distribution ($p(\theta)$): $p(\theta) \propto J(\theta)$. As such, coding resources are allocated such that the most likely movement direction is coded with the highest accuracy.

We next calculated the likelihood functions of how the system responds to different target directions with constraints of the prior distribution. Technically, the likelihood functions can be computed by assuming a symmetric Gaussian noise structure in a space where the Fisher information is uniform (the motor space, $\tilde{\theta}$), and then transforming those symmetric likelihood functions back to the target space (θ). To construct a motor space with uniform Fisher information based on the prior distribution of θ, one defines a mapping F from the target space (θ) to the motor space ($\tilde{\theta}$), following[10]:

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

Given an input θ, the output m is computed as follows[15]. We first calculated the response value r, which would be of the form $\theta + \epsilon$, where ϵ represents an error due to the intrinsic encoding noise of the system. Note that ϵ follows an asymmetric distribution in the target space (Fig 1b). Let $\tilde{\epsilon}$ represent the transformation of ϵ to the motor space. Since we were assuming $\tilde{\epsilon}$ has a symmetric Gaussian distribution, 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 response value in the target space of:

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

Next, we assumed that the system knows that its response r is noisy. Therefore, it generates a distribution of the form $r + \delta$, where δ follows the same distribution as ϵ. If $\tilde{\delta}$ represents the transformation of δ to the motor space, this distribution will be of the form $F^{-1}(r+\delta)$, where $\tilde{\delta} \sim N(0, \sigma^2)$. Finally, the system returns the expected value of this distribution as the output m:

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

where $E(\mathrm{X};\ \mathrm{z})$ means the expected X as z varies. We defined $\phi(\tilde{\theta}) = F^{-1}(\tilde{\theta})$. In the small-noise limit, we can take a second-order Taylor expansion:

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

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

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

To estimate the motor bias predicted by the model, we calculated the expected value of m ($\widehat{m}$) when ϵ varies can be expressed as:

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

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

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

Since the sequential effect in movement is influenced principally by the last movement, we assumed the prior of the motor planning system is a mix of a uniform distribution across the whole space and a Gaussian distribution centered at the last target direction (θ_{n-1}):

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

where *k* is a scale factor controlling the relative contribution of the two distributions; ρ indicates the width of influence from the previous trial. To simulate the bias and the variance predicted by this efficient coding model, we computed the numerical approximation of ϕ'' and ϕ' based on this prior function using an incremental approach.

<u>Repeated Suppression model</u>

We considered two alternative models to explain the sequential effects in the motor planning. The first model is a repeated suppression model, which assumes that neurons tuned to a specific direction become

less sensitive after repeating a similar movement. Those modulations can enhance the sensitivity to the changes in the environment or/and encourage exploration. Here we applied a population coding model with a group of neurons with Gaussian-shaped tunning functions. For a target direction θ, the unit tunned to i ($i \in [0, \pi]$) direction generates a response r_i as follow:

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

where $Norm(\theta, i, d)$ is the probability density function of a Gaussian distribution with a mean of i and standard deviation of d. The output of the system is determined by summing the activation of all neurons:

$$\boldsymbol{m} = \sum_i \mathrm{s}_i \mathrm{r}_i \boldsymbol{v}_i \quad [11]$$

where $\boldsymbol{v}_i$ is a vector representing the tuning direction of unit i, $\boldsymbol{m}$ is a vector pointing towards the movement direction, and s_i is the sensitivity of unit i. After a movement in trial n, s_i is updated based on the strength of the activation in unit i:

$$\mathrm{s}_i\ (n+1) = 1 - a\mathrm{r}_i(n) \quad [12]$$

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

<u>Bayesian Decoding model</u>

The second alternative model we applied is a classic Bayesian Decoding model that utilizes the prior distribution of θ to improve performance[20,21,61]. The system generates a response r based on a target direction θ. Considering Gaussian encoding noise, the relationship between r and θ can be expressed as follows:

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

Importantly, the model assumes that the system utilizes both the prior and this likelihood function to form a posterior estimation following Bayesian rules:

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

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 output of the system (m) is the posterior mean. For the Bayesian model, we used the same prior distribution (see [9]) as the efficient coding model.

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Competing interests

We have nothing to declare.

Data availability

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

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Supplementary figures

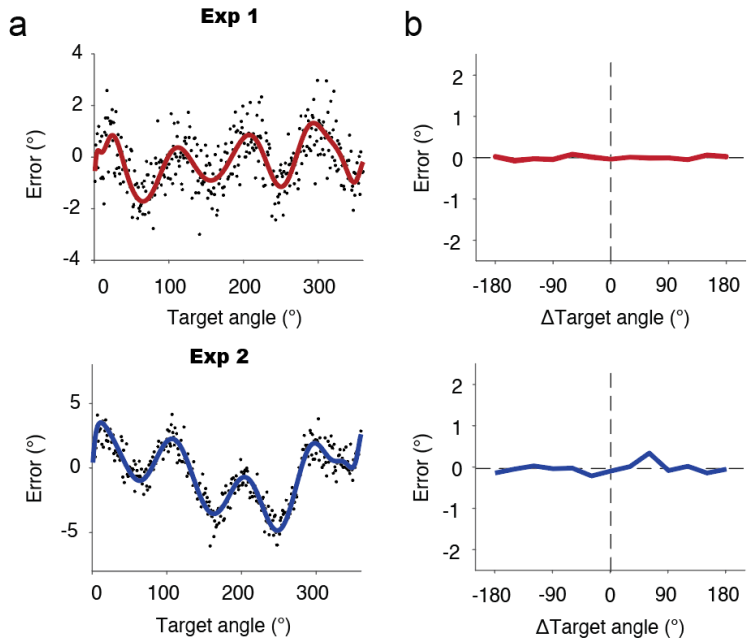

Figure S1. Systematic motor biases did not generate sequential effects. a) Systematic motor bias relative to target position in Exp 1 (upper panel) and 2 (lower panel). Participants exhibited greater bias in Exp 2, where feedback was absent. Black dots indicate data. The thick line represents a smoothed 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.

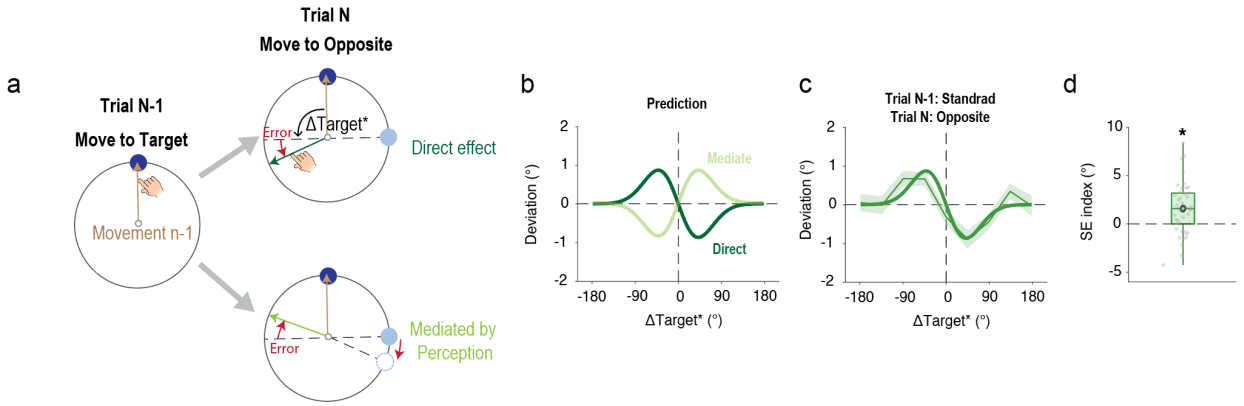

Figure S2. The current movement was directly influenced by the previous movement, with no mediation of perception. a) When trial N was an Opposite trial and trial N-1 was a Standard trial, it allowed for examination of whether the effect was directly caused by the previous movement repelling the current 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.

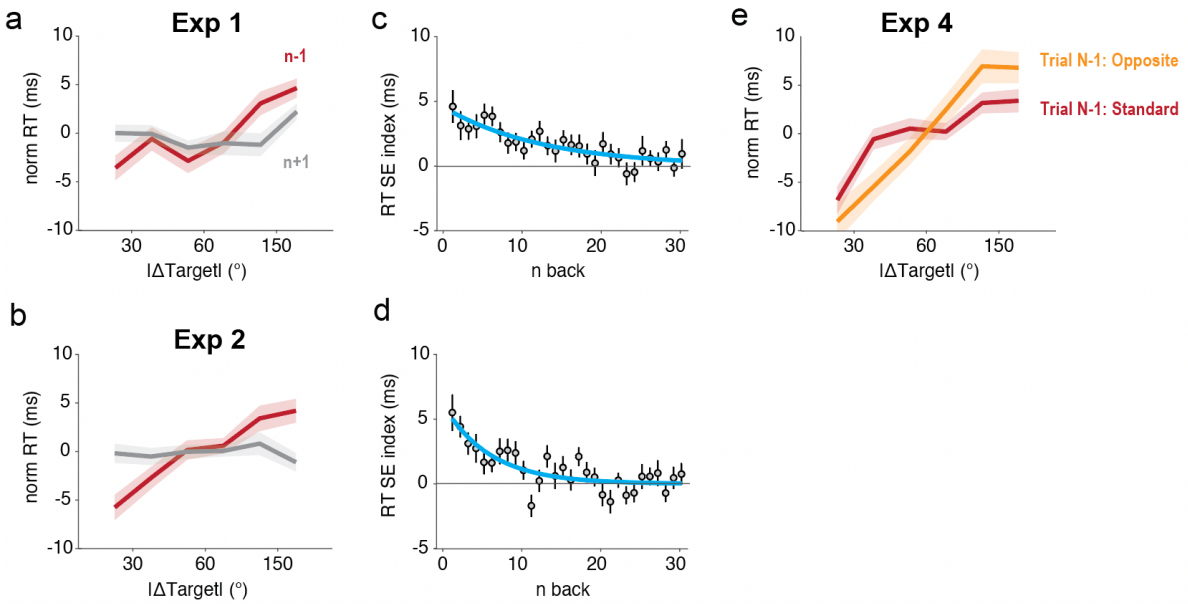

Figure S3. Priming of Reaction Times. a-b) Reaction time increased when the target in the previous (n-1) trial was further away from the current (n) trial in Exp 1-2. Reaction time was not correlated with the future trial (n+1). c-d) The SE index for reaction time lasted for more than 10 trials, differing 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.