**Abstract**

Practice is widely recognized as an indispensable component of motor skill acquisition. However, it is unknown how consistent repeated movement patterns must be to engage a ‘use-dependent’ learning mechanism. In this Registered Report, we tackled this question by testing two competing computational frameworks of use-dependent learning. In the Strategy plus Use-Dependent (SU) model (Diedrichsen et al., 2010), use-dependent learning is viewed as a slowly updating and slowly decaying bias in the direction of repeated movements. The Adaptive Bayesian (AB) model (Verstynen and Sabes, 2011) frames use-dependent learning as an emergent property of quickly adapting prior probabilities of target step lengths. Critically, the AB model is much more sensitive to variable practice than the SU model. Eighteen healthy, young male and female participants completed 3 conditions of treadmill walking with visual feedback, each with a Baseline, Learning and Washout phase. During the Learning phase of each condition, visual step length targets were sampled from different distributions with the same mean, but different levels of variability. During the Washout phase participants were asked to ‘walk normally’, and visual feedback was removed from the screen which allowed us to probe any use-dependent bias. We found that the Initial Bias (mean of the first 5 strides of Washout) decreased as a function of practice variability, but a decay resistance bias persisted despite high levels of practice variability. Neither model could explain both these findings, so we performed post-hoc model adjustments. The adjusted models were able to better capture these two distinct use-dependent processes, one which is variability sensitive and decays quickly, and the other which is variability insensitive and is decay resistant.

**Significance Statement**

Use-dependent learning is when future movements are biased to be more like prior movements. In this Registered Report, we compare two computational models of use-dependent learning to determine the importance of movement variability to this repetition-based learning process. Using a visual locomotor learning paradigm, we show that movement variability during practice constraints use-dependent learning initially, but a decay resistant component of use-dependent learning continues despite high levels of movement variability. These findings represent two distinct use-dependent processes, one which is variability sensitive and decays quickly, and the other which is variability insensitive and is decay resistant.

**Introduction**

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

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

A recent study demonstrated that use-dependent learning explains step asymmetry aftereffects in visually guided treadmill walking (Wood et al., 2020), despite previous interpretations that aftereffects observed during this paradigm were primarily due to learning from sensory prediction errors, i.e., sensorimotor adaptation (Cherry-Allen et al., 2018; French et al., 2018; Hussain et al., 2013; Kim and Krebs, 2012; Kim and Mugisha, 2014; Statton et al., 2016). In the study by Wood et al. (2020), visual targets were used to guide participants into walking with an asymmetry (i.e., a limp). Critically, for one of the experimental groups, all visual feedback was veridical, and participants were fully aware that they were being guided by the targets to practice walking asymmetrically. Therefore, the small but persistent aftereffects observed during washout, when all visual feedback was removed and participants were instructed to “walk normally”, were highly consistent with use-dependent learning. As repetition of novel gait patterns is inherent to nearly all locomotor learning studies, these findings suggest that use-dependent learning may play an important yet underappreciated role in this body of literature. Thus, critical questions regarding use-dependent learning during locomotion remain: Given that movement is intrinsically variable, how consistent must the walking pattern be to engage use-dependent learning? Additionally, what are the computational principles underlying use-dependent learning in locomotion?

Here, through computational modeling, simulations, and a series of behavioral experiments, we directly tackle the question of how the consistency of movement patterns impacts use-dependent learning. Our competing hypotheses are formalized by two distinct computational models of how use-dependent learning may arise. In Model 1, the Strategy plus Use-Dependent model, two learning processes act in parallel: A voluntary, strategic learning process that is active when the goal is to match step lengths to visual targets, and an automatic, slowly updating use-dependent learning process that biases movements in the direction of immediately preceding movements (Diedrichsen et al., 2010). Due to the slow learning and slow forgetting nature of use-dependent learning in this model, the use-dependent bias is robust to changes in movement consistency. In Model 2, the Adaptive Bayesian model, adopted from a study of reaching (Verstynen and Sabes, 2011), use-dependent learning is framed as a process of combining quickly adapting prior probabilities of target (step) locations with current sensory estimates of where to step. Thus, in direct contrast to the Strategy plus Use-Dependent model, the magnitude of use-dependent biases is directly related to the consistency of the environment, or target locations. Concretely, the Adaptive Bayesian model predicts a progressive decrease in use-dependent bias magnitude with less consistent practice while the Strategy plus Use-Dependent model predicts similar use-dependent bias magnitude regardless of practice consistency.

Critically, while these two computational accounts provide putative explanations for use-dependent biases, they differ markedly in their theoretical underpinnings and, to our knowledge, have not been directly compared with each other. Therefore, we designed a set of walking experiments that systematically vary practice consistency during learning and assess the state of use-dependent biases during no-feedback washout trials in order to discriminate between these two competing theories on the underlying constraints of use-dependent learning.

**Materials and Methods**

This study was conducted as a Registered Report. First, we developed and simulated the models which drove our hypotheses (Figure 2). Next, we collected pilot data and performed model recovery analysis to ensure feasibility. We then submitted the Registered Report proposal and received in-principal acceptance on October 23, 2020. We then publicly posted the pre-registered report on Open Science Framework (<https://osf.io/qfw9z>) and initiated data collections and analysis.

**Behavioral Methods:**

*Participants:*

Young, healthy male and female individuals between the ages of 18-40 years were recruited to participate in this study. Participants were included if they were naive to locomotor learning tasks. Participants were excluded if they had a history of any neurologic, psychiatric or cognitive conditions, or had any cardiovascular or musculoskeletal problems that limit their walking. This study was approved by the [withheld due to double-blind reviewing] Institutional Review Board.

*Paradigm:*

Participants performed three sessions of walking spaced at least 5 days apart. During each session, they walked on a dual belt treadmill (with the belts tied throughout the experiment) at a speed between 1.0 and 1.2 meters per second, selected by the participants to ensure a comfortable walking speed based on their anthropometrics. Participants wore a ceiling mounted harness, which did not provide any body weight support, and held onto a handrail for safety during all walking phases. A computer monitor placed 60 cm in front of the treadmill provided real-time visual feedback of the participant’s step length (Figure 1A; The Motion Monitor Toolbox, Innovative Sports Training Inc., Chicago, IL, USA).

The visual feedback was in the form two bar graphs with a blue bar representing the left leg’s step length and a green bar representing the right leg’s step length (Figure 1B). The bars were time synchronized with each respective limb’s swing phase, increasing in height until the limb reached heel strike at which point the bar was held on the screen until the next swing phase began. There was also a pink horizontal target line for each leg which was derived from each participant’s baseline step length for each session and served as the target during that session’s Learning phase.

Each of the three sessions of walking involved a similar block schedule. Participants were first told to “look forward and walk normally” on the treadmill during the Baseline phase for 250 strides (i.e., 250 consecutive left heel strikes). No visual feedback was presented on the monitor during the Baseline phase. In order for participants to understand how changing each step length changes the height of the bars on the screen, they performed a short (25 strides) Orientation phase following Baseline during the first session only. During Orientation, the participants were guided by the experimenter in changing their step lengths (green and blue bars) relative to their baseline (pink horizontal target lines, one for each leg - Figure 1B, top panel). During the Learning phase, participants were told to hit the pink horizontal target lines exactly with each step for 500 strides. Both target lines were changed relative to their baseline step length, leading the participants to take a longer step with the left leg and a shorter step with the right leg (Figure 1B – bottom panel). The target lines had a width of ± 2% step length change from baseline. The researcher provided participants with a prompt to continue hitting the target lines every 100 strides during the Learning phase. During the Washout phase, the feedback was removed from the screen and participants were told to “look forward and walk normally” for 750 strides. The treadmill was stopped briefly between each phase so that instructions could be provided for the next phase.

Diagram, schematic

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**Figure 1**: **Experimental setup**. **(A)** Participants walked on a treadmill while watching feedback of their step lengths. Their step lengths were represented as a blue (left) and a green (right) bar which increased in height during the swing phase and was held on the screen at the moment of heel strike. **(B)** During the Orientation phase (top panel), participants were asked to change their step lengths (green and blue bars) relative to their baseline step lengths (pink horizontal target lines). During the Learning phase (bottom panel), the participant aimed for pink horizontal target lines which were derived from their baseline step length. **(C)** Example target distributions for each condition: During the Constant condition targets were set at 22% SAI (SAI is our measure of step asymmetry – see equation 1) during the Learning phase. During the Low Variability condition targets were drawn from a normal distribution centered around 22% SAI and a standard deviation of 5% SAI. During the High Variability condition targets were drawn from a uniform distribution between 5% and 39% SAI. Note the different scales for the y-axes. **(D)** Learning schedule for each condition: Each condition included a Baseline (Bsl), Learning and Washout phase. Shaded regions indicate no visual feedback was shown on the screen and participants were told to “walk normally”, so the target is effectively 0% SAI. During the Learning phase targets varied based on the condition.

*Conditions:*

We systematically manipulated the independent variable, the consistency of target positions, during the Learning phase. To accomplish this, participants completed three different conditions: 1) In the Constant condition, the target locations were set to a constant 22% step asymmetry throughout the Learning phase; 2) In the Low Variability condition, target locations were drawn from a normal distribution with a mean of 22% and standard deviation of 5%; and 3) In the High Variability condition, the targets were drawn from a uniform distribution with a range of 5%-39% step asymmetry (Figure 1C & D). Thus, all three conditions had a nearly identical average step asymmetry target of 22% (small discrepancies in the variable conditions due to drawing random samples), but the target variability for each condition was markedly different. This study design was intended to isolate the effects of target consistency on the use-dependent bias during Washout. Based on our pilot testing, changing the target on a stride-by-stride basis made the task too difficult for participants; thus, for both the Low Variability and High Variability conditions, targets changed, with equal probability, every 1-5 strides. To prevent contamination from potential order effects, we counterbalanced the order of conditions across all participants.

*Data Collection:*

Kinematic data was collected at a frequency of 100 Hz using a Vicon MX40 motion capture system with 8 cameras and Nexus software (Vicon Motion Systems, Inc., London, UK). We used a custom marker set with 11 total retroreflective markers, one for each greater trochanter, lateral knee, heel, lateral malleolus, and 5th metatarsal head. The eleventh marker was placed on the left 1st metatarsal head to ensure the tracking system can differentiate between the right and left feet.

*Data Analysis Pipeline:*

We performed all data analysis in custom-written MATLAB scripts (Mathworks, Natick, MA, USA). The code/software described in the paper is freely available online at [URL redacted for double-blind review]. The code is available as Extended Data. We used cubic spline interpolation to fill any gaps in the marker data with the MATLAB spline function. Next, kinematic data were low pass filtered at 10 Hz using a 4th order Butterworth filter. Kinematic marker data were used to select *heel strike* when the heel marker velocity transitioned from positive to negative and *toe off* when the 5th metatarsal head marker velocity transitioned from negative to positive (Zeni et al., 2008). Step lengths were calculated as the sagittal difference between the leading and trailing heel markers at the moment of leading heel strike. The step length during the last 50 strides of the Baseline phase was averaged and used to derive each legs’ respective target lines during that session’s learning phase. Step lengths were used to calculate our primary outcome, step asymmetry index (SAI):

(1)

Thus, SAI represents the difference between the two step lengths normalized by their sum. We express this measure as a percentage where 0% is perfect symmetry and SAIs further away from 0% indicate greater asymmetry. By convention, the SAI during learning was always positive. SAI was calculated on a stride-by-stride basis throughout all walking phases. We corrected for SAI baseline biases for each participant and each respective training session by subtracting the mean of the last 50 strides of the Baseline phase from all strides for that respective session. The baseline corrected measure was used for the remainder of our analyses.

We also calculated limb placement asymmetry. Leading limb foot placement was calculated as the sagittal distance between the hip and ankle marker during that limb’s heel strike and trailing limb placement was calculated as the sagittal distance between the same markers during that limb’s toe off. Leading and trailing limb placement asymmetry was calculated as the difference between the long and short leading and trailing limb placement, respectively (Finley et al., 2015; Long et al., 2016; Sánchez et al., 2020).

Our analyses of behavior during the Learning phase focused on checking our assumptions that the participants’ SAIs tracked the target SAI for each condition. That is, we assumed the mean SAI did not differ across conditions (Learning SAI mean), but the SAI standard deviation (Learning SAI σ) did. The purpose of the Learning phase was to provide the necessary task practice to develop potential use-dependent biases. The magnitude of use-dependent biases cannot be directly measured during Learning, since other processes are active during this period—cognitive strategies in the case of the Strategy plus Use-Dependent model and Bayesian estimation of visual target location in the case of the Adaptive Bayesian model. Thus, as expected, our models do not make qualitatively different predictions regarding behavior during the Learning phase (Figure 2A, learning insets).

Our hypotheses focused on use-dependent biases, probed during the no-feedback Washout phase. Use-dependent biases were analyzed at two different time points. First, to characterize the total magnitude of use-dependent learning, we calculated the mean SAI during the first 5 strides of the Washout phase (Initial Bias). Second, to characterize early changes in use-dependent biases during the Washout phase, we calculated the mean SAI of strides 6-30 of the Washout phase (Early Washout; Day et al., 2018; Leech et al., 2018). We also analyzed the rate of washout by regressing subsequent strides onto current strides for the first 50 strides of the Washout phase. We report 1-β (slope) as it quantifies the amount of unlearning per stride during the Washout phase (Kitago et al., 2013; Wood et al., 2020).

**Model-Based Methods:**

We adapted two computational models of use-dependent learning that can explain behavior following training with consistent targets (see Simulation section); however, the two models make dissociable predictions regarding the effect that changes in movement consistency during Learning have on use-dependent biases. We refer to the first model as the Strategy plus Use-Dependent model (Model 1). This model was inspired by a previously developed dual-process model of error-based and use-dependent learning (Diedrichsen et al., 2010). Unlike the force-field adaptation task used in the Diedrichsen et al. study, the learning paradigm in this study involves, in addition to use-dependent learning, explicit strategies, without contributions from sensorimotor adaptation (French et al., 2018, Wood et al. 2020). Therefore, we replaced the implicit adaptation process from the Diedrichsen model with a strategic process which learns quickly. The second model is referred to as the Adaptive Bayesian model (Model 2) and was adopted from a reaching study of use-dependent learning (Verstynen and Sabes, 2011).

*Strategy Plus Use-Dependent Model:*

The Strategy plus Use-Dependent model conceptualizes overall motor output as the sum of two parallel processes: cognitive strategy and use-dependent learning. This model attempts to capture the previously reported phenomenon that participants are able to explicitly control SAI in response to visual feedback, yet still demonstrate aftereffects (French et al., 2018; Long et al., 2016; Wood et al., 2020). Strategic learning accounts for the voluntarily controlled component of SAI, while use-dependent learning is insensitive to explicit task goals, and is instead an obligatory stride-by-stride biasing of motor output based purely on recent actions (Diedrichsen et al., 2010). In the context of the current study, the motor output is SAI (): the sum of the strategic process () and the use-dependent process () on each stride, :

(2)

The strategic process corrects errors () between the motor output () and the target ():

(3)

(4)

This model assumes that individuals remember some proportion, , of their explicit strategy. For example, when a participant aims for the target, they will remember, to some degree, where they aimed previously. Participants also correct a proportion of the error, , on each stride. As this is a strategic, or voluntary, process, we assume that is equal to zero when the visual feedback (VF) is turned off and the participants are instructed to walk normally.

Use-dependent learning () occurs in parallel with strategy and becomes biased towards the current motor output (). represents the retention factor for use-dependent learning and is the use-dependent learning rate. Here, the update is a function of the motor output which, in this experiment, changes based on the error signal, due to strategic learning (equation 3), and the slowly evolving use-dependent bias.

(5)

,

Strategic learning in humans is highly flexible and, under certain conditions, quite rapid (> 0.7 in Taylor and Ivry, 2011; Bond and Taylor, 2015). Yet the use-dependent process learns slowly (average learning rate of 0.038 in Diedrichsen et al., 2010). Therefore, we add the constraint that the strategic learning rate, , must be at least 5x faster than the use-dependent learning rate, . This model also assumes that this learning rate is fixed and thus, is not sensitive to the consistency of motor output (Diedrichsen et al. 2010). During washout, when the visual feedback is off and there is no strategy, motor output reflects the sole activity of use-dependent learning.

*Adaptive Bayesian Model:*

In the Adaptive Bayesian model, predicted step length is the weighted combination of expected target locations based on prior experience and current sensory estimates of target location.

Formally, this model follows from Bayes’ Theorem and combines the prior expectation of the SAI target () with the current sensory estimate of target position () to compute the posterior probability distribution. The model assumes that the motor output is a direct readout of the maximum a posteriori (MAP) estimate () of target location, as in Verstynen and Sabes (2011):

(6)

We assume the prior and likelihood are normally distributed. Therefore:

(7)

The mean of the likelihood is centered on the true target location, , on each stride, . The likelihood’s variance, is a free parameter representing the amount of sensory uncertainty regarding target location. During the Baseline and Washout phases, the target is the participant’s baseline walking pattern. We assume that the amount of uncertainty surrounding the participant’s baseline walking is similar to the uncertainty surrounding the visual targets. Therefore, we set the likelihood variance to be consistent throughout the experiment.

As beliefs about the consistency of targets during the Learning phase are likely to adjust as more evidence about target locations arrives, use-dependent learning has been more accurately modeled using adaptive priors as compared to a normative Bayesian model that does not include learning of priors (Verstynen and Sabes, 2011). Here, we also assume that the prior will change on a stride-by-stride basis. The adaptive nature of the model is captured by the stride-by-stride updating of the prior probability’s parameters :

(8)

(9)

,

is a free parameter representing the learning rate. The Adaptive Bayesian model has two free parameters, in comparison to the four free parameters of the Strategy plus Use-Dependent model.

Our two models provide distinct interpretations of how use-dependent biases evolve and the specific constraints acting on them. The Strategy plus Use-Dependent model assumes separate, yet parallel, explicit (strategy) and implicit (use-dependent) learning mechanisms. In this model, use-dependent learning is persistently active, but evolves slowly in response to the direction of the walking asymmetry. In direct contrast, the Adaptive Bayesian model does not invoke separate explicit and implicit learning processes, but frames the problem of changing an agent’s behavior in response to visual targets (or the absence of them, as during Washout) as one of Bayesian estimation (Ernst and Banks, 2002; Körding, 2007; Verstynen and Sabes, 2011; Wei and Körding, 2009). The MAP estimate may certainly result from contributions of implicit and explicit mechanisms, but the model does not distinguish between the two. In this study, the primary comparisons were between the two models differing predictions regarding use-dependent biases in response to varying degrees of practice consistency and the empirically observed biases. The Strategy plus Use-Dependent model predicted that the use-dependent bias will be similar across the three different conditions while the Adaptive Bayesian model predicts progressively smaller use-dependent bias as target consistency is reduced.

*Simulations:*

We simulated both models a priori to demonstrate how each accounts for the consistency of practiced target step lengths. The Strategy plus Use-Dependent model is robust to environmental consistency in cases, as here, where there is a large asymmetry in one direction. The model assumes use-dependent learning is slower to learn and washout than cognitive strategies; therefore, as long as the practiced asymmetry is much larger than the current state of use-dependent learning, the consistency of target step lengths has minimal impact on its output. The Adaptive Bayesian model stands in direct contrast to this framework. In this model, the MAP estimate, and thus the observed use-dependent bias during Washout, is sensitive to environmental consistency: The more consistent (i.e. less variable) the schedule of target step lengths, the more biased towards the prior (i.e., away from the likelihood) the MAP becomes; conversely, the more variable the schedule, the less weight is given to the prior and the more the MAP is pulled towards the likelihood (i.e., the actual target location).

Preliminary model parameters were obtained by fitting the models to walking data (n=16 participants) from [withheld due to double-blind reviewing], which used a protocol most similar to the Constant condition that we currently propose. (R-squared values: Adaptive Bayesian model = 0.895 ± 0.019; Strategy plus Use-Dependent = 0.870 ± 0.021 [mean ± SEM]). We then simulated our proposed experiment 1000 times with the mean learning function from each bootstrapped sample of the individual parameter fits. Figure 2 details the simulated data from these parameters for each condition. The panels in Figure 2A show each model simulation for the entire experiment. Across all 3 conditions, the models diverge in their predictions regarding use-dependent biases during the Washout phase.

We plotted the simulated use-dependent biases during both Initial Bias and Early Washout (Figure 2B and C). Overall, the Strategy plus Use-Dependent model predicts more consistent use-dependent biases across conditions for both Initial Bias and Early Washout. However, the Adaptive Bayesian model demonstrates consistently decreasing bias when the conditions become less stable during the Learning phase. For our third point of direct comparison between model predictions, we also analyzed the Washout Rates for each model (Figure 2D). The Strategy plus Use-Dependent model predicts a consistent Washout Rate across conditions, whereas the Adaptative Bayesian model predicts slower washout as the conditions during Learning increase in variability. Based on these simulations, if the Strategy plus Use-Dependent model is a more accurate model, we would have observed similar use-dependent biases between conditions; however, if the Adaptive Bayesian model is more accurate, we would have observed different use-dependent biases between conditions.

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**Figure 2: Simulated results. (A)** The experiment was simulated 1000 times using bootstrapped samples of parameter values from a previously collected dataset [citation redacted for double blind reviewing]. Results of the simulation are plotted as means with shaded errors indicating standard deviation of bootstrapped sample means. The first 10 strides of the Learning phase and the first 50 strides of the Washout phase are plotted in the insets. **(B)** Initial Bias is the mean of the first 5 strides of the Washout phase and **(C)** Early Washout is strides 6-30 of the Washout phase. **(D)** Mean and standard deviations of Washout Rates of each model across conditions. For panels B-D, filled circles represent the mean and error bars represent one standard deviation of bootstrapped sample means. Some error bars are not visible as their values are small and thus obscured by dots representing mean values.

**Statistical Analysis:**

Model fitting and model selection, in conjunction with behavioral analyses, formed the basis for our inferences regarding which of the two models (hypotheses) is more strongly supported.

*Behavior:*

As stated above, we did not have competing hypotheses regarding the Learning phase, and we expected participants to accurately follow the visual targets. If this assumption is correct, it would result in Learning SAI mean values that do not differ across conditions, but larger Learning SAI σ values when going from Constant to Low Variability and High Variability conditions. These assumptions were assessed using repeated measures ANOVA and in the case of a significant test, we performed post-hoc Bonferroni-corrected pairwise comparisons.

As the Adaptive Bayesian model predicts differences in use-dependent bias across conditions, we performed statistical analyses of Initial Bias, Early Washout and Washout Rate using separate repeated measures ANOVAs. In cases of a significant ANOVA, we performed post-hoc pairwise comparisons with Bonferroni-corrected t-tests. Because the Strategy plus Use-Dependent model predicts similar use-dependent biases across conditions, we also performed equivalence tests on Initial Bias, Early Washout and washout rate using the two one-sided tests (TOST) procedure (Lakens, 2017). Briefly, the TOST procedure involves two composite null hypotheses that an observed effect is either below or above chosen equivalence bounds (Cohen’s *d* of ± 0.3; see Lakens, 2013), and thus provides a rigorous means of inferring the lack of a meaningful effect.

We report t- and F- statistics, exact p-values, means, 95% confidence intervals and standardized effect sizes (Cohen’s *d* for t-tests and ƞp2 for ANOVAs). For equivalence testing, we also report the empirical equivalence bounds for which we would be able to reject the null hypothesis that there is an effect of condition. Bonferroni corrected p-values were used for tests involving multiple comparisons. Assumptions of normality and equality of variances were confirmed for all data with the Shapiro-Wilks test and Levene’s test, respectively.

In addition to our parametric analyses of pre-selected epochs, we also employed a cluster permutation analysis in order to assess SAI differences across the entire Washout phase for each condition (Holmes et al., 1996; Maris and Oostenveld, 2007). In this analysis, we compared SAI differences between two conditions at a time with paired t-tests between bins of 3 strides. Binning, in this case, was used to mitigate the effects of stride-to-stride SAI variability on the analysis and thereby reduce the probability of a Type II error. The largest cluster of consecutive significant paired t-tests (p < 0.05) was determined and the t-statistics for this cluster were summed. The summed t-statistics were then compared to a null distribution of summed t-statistics. The null distribution is built from resampling each group without replacement 10,000 times and computing the largest cluster’s t-statistic for each sample. This null distribution serves as the null hypothesis which states that each group is sampled from the same distribution. The cluster size from the empirical data is then compared to the null distribution of 10,000 samples. This comparison provides a probability that the empirical cluster is different from the null distribution while controlling for type I error (Maris and Oostenveld, 2007; Nichols and Holmes, 2002). This analysis was performed three times to compare differences between each condition.

*Computational Models:*

Our competing hypotheses are encapsulated by our two computational models, the Strategy plus Use-Dependent model (Model 1) and the Adaptive Bayesian model (Model 2), and their corresponding predictions regarding use-dependent biases: The Strategy plus Use-Dependent model predicted no difference in use-dependent bias across conditions while the Adaptive Bayesian model predicted reduced use-dependent bias during less consistent conditions. We fit both models to individual participant data from all three conditions combined, using the fmincon function in MATLAB. This allowed us to obtain one set of parameter values for each individual participant and model. We will provide a figure containing individual and group fits for each model and comparisons of simulated biases (using best-fit model parameters) with the behavioral data to further bolster support for one model over the other.

Additional objective support for one model over the other was formally assessed using model selection criteria, specifically Akaike Information Criterion (AIC) scores (See Model Recovery section for rationale). We compared these AIC values between the two models using a paired t-test. Quality of model fits were assessed using R-squared values. To provide confidence intervals on parameter estimates, we bootstrapped parameter values 10,000 times and report the empirical 2.5th and 97.5th percentile values.

*Model Recovery:*

Due to the central importance of model selection in the proposed study, we performed a priori model recovery analysis in order to 1) confirm that the models are distinguishable under ideal circumstances (Hardwick et al., 2019; Wilson and Collins, 2019) and 2) identify the ideal method of model comparison for this situation (between Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC); Wilson and Collins, 2019). We first sequentially simulated data 1000 times per condition with both models using randomized parameter values obtained by fitting data from a similar study (details in Simulations section). We then fit the simulated data with each model, calculating AIC scores for each model fit and directly compared the two values. A confusion matrix summarizes this process, providing the probability that the model which generated the simulated data was better fit by itself or the other model. Ideally, the model that generated simulated data will be better fit by itself than by the other model, resulting in values closer to 1 when comparing the simulations and fits from the same models (lighter colors on main diagonals in Figure 3) and values closer to 0 when comparing simulations and fits from opposing models (duller colors on off-diagonals in Figure 3). In Figure 3, we show one confusion matrix for each condition and a combined confusion matrix which reveals that the models are distinguishable under these ideal circumstances when using AIC as an objective model comparison criteria. We performed the same procedure for BIC, however this analysis revealed reduced model discriminability (i.e., smaller range between on- and off-diagonal values in the confusion matrix). Therefore, this analysis demonstrates that the two models are distinguishable under these constraints and that AIC is better-matched for the current experiment.

Chart, treemap chart

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**Figure 3: Confusion matrices**. Four different confusion matrices for each condition and all conditions combined. Lighter colors indicate higher percentages of better fits for each simulated model. Model fits were compared using AIC. AB is the Adaptive Bayesian model, S+U is the Strategy plus Use-Dependent model.

**Results:**

**Behavioral Results**

We sought to determine how the consistency of movement patterns impacts use-dependent locomotor learning. Our two computational models made different predictions about the relationship between use-dependent biases and amount of practice consistency (Figure 2). We tested these predictions behaviorally by varying step length targets during the Learning phase and measuring the amount of use-dependent bias during the Washout phase. Eighteen participants (10 Female, mean age ± SD = 23.2 ± 3.6 years) completed the Constant, Low Variability and High Variability conditions an average of 7.4 ± 3.2 days apart. Figure 4A shows individual and group averaged SAI data for each condition. As expected, the step length targets during the Learning phase prompted changes in SAI relative to participants baseline SAI.

Graphical user interface, application

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**Figure 4: Step asymmetry index. (A)** Group averaged (circles) and individual (lines) step asymmetry data for each condition. For plotting purposes, we truncated each phase (Baseline, Learning and Washout) to match the participant with the fewest strides and binned the data by 5 strides. **(B)** Histograms of SAI values for all Learning strides separated by condition. **(C)** Mean (think lines) and individual (thin grey lines) Learning SAI mean (purple) and Learning SAI σ (green). The mean and standard deviation of the SAI targets during the Learning phase are plotted as black dashed lines for reference.

To demonstrate how individuals made changes in SAI during this strategic learning, we calculated leading and trailing limb position. Figure 5A displays the left and right leading and trailing limb positions during the Learning phase for the High Variability condition. We removed 3 participants from this analysis due to unusable hip or ankle marker data (marker fell off or became covered during part of the Learning phase). To hit the (longer) left step length target, participants quickly lengthened both the leading position of their left limb and the trailing position of their right limb relative to the hip (red functions in Figure 4A). The opposite is true for the (shorter) right step length target, where participants quickly shortened both the leading position of the right limb and trailing position of the left limb relative to the hip (blue functions in Figure 4A). These changes resulted in an asymmetry in both the leading and trailing limb placement (Figure 5B and 5C). These results highlight the explicit nature of the task: Participants quickly made changes in foot position to hit the targets during the Learning phase. This is in contrast to the slower changes in foot position observed during the split belt adaptation paradigm (Malone et al., 2012; Sánchez et al., 2020).

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**Figure 5: Foot position. (A)** Group averaged (circles) and individual (lines) foot position for the Learning phase of the High Variability condition. For all panels, we truncated each phase (Baseline, Learning and Washout) to match the participant with the fewest strides and binned the data by 5 strides. The Left leg **(A - left panel)** depicts leading foot position in red and trailing foot position in blue. The right leg **(A - right panel)** depicts the leading foot position in blue because this corresponds to the left toe off when calculating a step length. Similarly, the right panel of A depicts the trailing foot position in red because this corresponds to the left heel strike when calculating step length. Specifically, the difference between red functions are analogous to left step length, and the difference between the blue functions are analogous to right step length. **(B)** Group averaged (circles) and individual (lines) leading foot placement symmetry for the High Variability condition. **(C)** Group averaged (circles) and individual (lines) trailing foot placement symmetry for the High Variability condition.

Our primary comparison hinges on the ability for participants to quickly make changes in step length in line with the visual targets. Because the SAI target distributions for each condition were centered around 22% SAI, the Learning SAI mean should yield similar results (Figure 4B and C). Indeed, Learning SAI mean was not different across conditions (Figure 4C – purple; F2 17 = 1.07, p = 0.35, ƞp2 = 0.06; mean [95% CI] Constant = 21.36 [20.60 22.13], LV = 21.69 [20.45 22.94], HV = 22.09 [21.06 23.13]). Successfully following the SAI targets should also yield greater variability in SAI behavior across conditions. In line with this assumption, Learning SAI σ increased across each condition (Figure 4C - green; F2 17 = 64.69, p < 2e-12, ƞp2 = 0.79; Constant = 3.48 [2.86 4.10], LV = 5.21 [4.64 5.78], HV = 7.98 [7.31 8.616]). Learning SAI σ was greater in the LV condition compared to the Constant condition (t17 = -4.99 pbonf = 3.4e-4, Cohens dz = -1.18), greater in the HV condition compared to the LV condition (t17 = -7.10 pbonf =5.3e-6, Cohens dz = -1.67) and greater in the HV condition compared to the Constant condition (t17 = -9.93 pbonf = 5.2e-8, Cohens dz = -2.34). As predicted, Learning SAI mean was similar across conditions, but the Learning SAI σ was different across conditions. These results demonstrate that our perturbation was effective in inducing different amounts of SAI variability during the Learning phase and allowed us to compare use-dependent bias during the Washout phase.

We measured use-dependent bias during the Washout phase when participants were asked to walk normally, and no visual feedback was on the screen. On average, participants were not immediately able to return to walking normally, instead they demonstrated a bias in the direction of the repeated movements made during the Learning phase (Figure 6A). We found that the Initial Bias (Figure 6B, mean of the first 5 strides) decreased from the Constant (2.45 [1.58 3.32]) to LV (1.67 [1.00 2.35]) to HV (1.24 [0.54 1.95]; F2 17 = 4.23, p = 0.02, ƞp2 = 0.20) with reliable differences between the Constant and High Variability conditions (t17 = 2.78, pbonf = 0.04, Cohens dz = 0.65), but not between the Constant and Low Variability (t17 = 1.83, pbonf = 0.25, Cohens dz = 0.43) or the Low and High Variability conditions (t17 = 1.06 pbonf = 0.91, Cohens dz = 0.25). These results demonstrate that immediate use-dependent bias measured in the first 5 strides of normal walking depends on the amount of practice consistency.

Diagram

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***Figure 6: Washout data. (A)*** *Group averaged SAI data during the Washout phase of each condition. Shaded error bars represent standard error of the mean. For plotting purposes, we truncated each individual’s Washout phase to match the participant with the fewest strides and binned the data by 3 strides. The dots and error bars in the grey shaded region represent the mean and standard error of the mean of the first 5 strides of Washout for each condition (not binned) which is the same as the Initial Bias measure.* ***(B)*** *Mean Initial Bias (mean SAI of strides 1-5 during Washout) for each condition (purple line) with individual Initial Bias for each condition (grey lines).* ***(C)*** *Mean Early Washout (mean SAI of strides 6-30 during Washout) for each condition (purple line) with individual Early Washout for each condition (grey lines).* ***(D)*** *Mean Washout Rate (using the autoregression calculation) for each condition (purple line) with individual Washout Rates for each condition (grey lines).* ***(E)*** *Individual regressions of Learning SAI σ and Initial Bias (grey lines). We used the mean of the individual betas to calculate the mean regression line (purple). The individual and mean betas are plotted in the inset.* ***(F)*** *Individual regressions of Learning SAI σ and Early Washout (grey lines). We used the mean of the individual betas (grey dots in inset) to calculate the mean regression line. The individual and mean betas are plotted in the inset.* ***(G)*** *Mean Washout Rate (using the Exponential Fit calculation) for each condition (purple line) with individual Washout Rates for each condition (grey lines).*

While the Initial Bias depended on practice consistency, this effect was quickly diminished. Early Washout (Figure 6C, mean of strides 6 to 30; Constant = 1.82 [1.28 2.37], LV = 1.61 [1.16 2.07],

HV = 1.33 [0.86 1.80]) did not reliably depend on condition (F2 17 = 1.26, p = 0.30, ƞp2 = 0.07). When there were no significant differences between the conditions, we ran equivalence testing between each condition using the TOST procedure with equivalence bounds set at Cohens dz = ± 0.3 because a similar study (Wood et al., 2020) showed SAI differences of Cohens d = 0.25 were not different. Using this equivalence bound, we found no evidence of equivalence between the three conditions (largest t value = 0.19, smallest p = 0.29). We additionally performed cluster permutation analyses to determine if there were differences between conditions across the entire Washout phase. However, none of the three comparisons resulted in cluster sizes greater three. These results show that despite an initial reliance on practice consistency, use-dependent biases have a decay resistant component that does not rely as heavily on practice consistency.

*Exploratory Analysis. Relationship between Initial Bias and Learning SAI σ:* After the data were collected, we performed exploratory analysis to determine the impact of practice consistency on use-dependent biases irrespective of condition. We performed a simple regression between Learning SAI σ and Initial Bias for each individual (Figures 6E). We found a consistent inverse relationship between Learning SAI σ and Initial Bias (mean beta = - 0.31 [-0.53 -0.09], t17 = -2.94, p = 0.01). We found a similar but muted relationship between Learning SAI σ and Early Washout (Figure 6F, mean beta = -0.11 [-0.22 0.01], t17 = -2.02, p = 0.06). We performed the same regression analysis for Learning SAI mean to determine if the mean asymmetry during learning was a significant factor in aftereffect. However, we found no consistent relationship between the Learning SAI mean and Initial Bias (mean beta = 0.15 [-0.95 1.24], t17 = 0.28, p = 0.78) or Learning SAI mean and Early Washout (mean beta = -0.45 [-1.29 0.39], t17 = -1.14 p = 0.27). This additional exploratory analysis further demonstrates an inverse relationship with practice consistency and use-dependent bias.

The two models also diverge with their predictions of Washout Rate across conditions. We assessed Washout Rate over the first 50 strides to isolate the part of the Washout phase with the fastest decay. We found differences in Washout Rate across conditions (Figure 6D; Constant = 0.86 [0.78 0.94], LV = 0.84 [0.77 0.90], HV = 0.98 [0.92 1.04]; F2 17 = 7.21, p = 0.002, ƞp2 = 0.30), with a faster washout occurring in the HV condition compared to the LV condition (t17 = -3.46, pbonf = 0.01, Cohens dz = -0.82). There were no differences between the Washout Rate of the Constant and LV (t17 = 0.86, pbonf = 1.21, Cohens dz = 0.20) or Constant and HV conditions (t17 = -2.47, pbonf = 0.07, Cohens dz = -0.58). This result is the opposite of what the Adaptive Bayesian model predicted (Figure 2D) and indicates that less practice consistency causes faster washout of use-dependent biases.

*Exploratory analysis. Washout Rate does not depend on practice consistency:* When we inspected our measure of Washout Rate, we found that this measure does a poor job of describing the data. Because the use-dependent bias seems to take a much longer time to washout than the unlearning per stride values indicate, we fit an exponential function to the same data using the equation:

Where is each stride of the Washout phase, is the gain, is the decay constant and is the plateau (Sánchez et al., 2020). We fit this exponential function to each individual’s first 50 strides of Washout and found it consistently fit the data better than the autoregression data (Autoregression AIC = 117.6 [76.75 158.51], Exponential function AIC = 30.4 [25.47 35.31], t53 = 4.36, p = 6.0e-5). Using the exponential decay constant, we found no differences in Washout Rate across conditions (Figure 6G; Constant = 17.81 [8.26 27.37], LV = 21.86 [13.65 30.07], HV = 15.08 [6.56 23.61], F2 17 = 0.14, p = 0.87, ƞp2 = 0.008). Additionally, we fit the exponential function to all the strides in the Washout phase and found similar results (F2 17 = 0.21, p = 0.81, ƞp2 = 0.01). While this was not our planned analysis, the decay constants were much more consistent with what we visually observe in the data (Constant = 236.02 [133.30 338.74], LV = 210.49 [100.94 320.04], HV = 188.19 [91.11 285.28]). This exploratory analysis revealed that practice consistency did not affect the decay rate of use-dependent biases.

**Model Based Results**

Overall, the behavioral findings support the hypothesis that use-dependent locomotor learning relies on practice consistency. This is consistent with the Adaptive Bayesian model predictions (Figure 2). To provide objective support for one computational model over the other, we directly compared the Adaptive Bayesian and the Strategy plus Use-Dependent model. We first concatenated binned SAI data for all three conditions for each participant. We then fit both models to each participant’s data to obtain a single set of parameters values for each model for each participant. We then simulated each model with the parameter values. For visualization purposes, we averaged these simulations across subjects against the averaged empirical data for all strides (Figure 7A) and for the Initial Bias and Early Washout (Figure 7C and D). Both models demonstrated good fits to individual data (AB mean ± SD r2 = 0.93 ± 0.02, S+U r2 = 0.90 ± 0.02). The Adaptive Bayesian model demonstrated consistently better fits compared with the Strategy plus Use-Dependent model (Figure 7E; AB model AIC = 2850 [2612 3088], S+U model AIC = 3478 [3286 3671], t17 = -5.92, p = 1.6e-5, Cohens dz = -1.40). These results seem to support the Adaptive Bayesian model, however, on visual inspection, we noticed that while the Adaptive Bayesian model adequately captures the dependence on practice consistency, it does a poor job of capturing the slow return to baseline SAI. Conversely, the Strategy + Use-dependent model does not capture the dependence on practice consistency, but it predicts the decay resistant component of use-dependent learning. These discrepancies motivated post-hoc adjustments to each model to offer additional support for the models and explanatory power.

Diagram

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**Figure 7: Model Based Results.** We fit each model to each individual’s data from all conditions and simulated the models using the parameter values. We plot the simulated models against the mean data (purple function). Shaded regions indicate standard error. **(A)** Original Adaptive Bayesian (top row) and Strategy + Use-Dependent (bottom row) averaged model simulations. Grey regions are the regions indicate no visual feedback phases. Insets are the first 100 strides of the Washout phase. **(B)** Adjusted Adaptive Bayesian (top row) and Adjusted Strategy + Use-Dependent (bottom row) averaged model simulations. **(C)** Simulated Initial Bias for each model across conditions. The diamonds and dotted lines represent the Adjusted models. The inset shows the difference between each model simulation and the data for the Constant (blue), Low Variability (red) and High Variability (yellow) conditions with grey dots representing individual differences. **(D)** Simulated Early Washout for each model across conditions. **(E)** Individual and mean differences between AICs for each model plotted as AB model minus SU model, so smaller values favor the AB models.

*Exploratory analysis. Adjusted models:*We made post-hoc adjustments to each model to provide improved explanations for both the sensitivity to practice consistency and the slow resistant return to baseline asymmetry. The Strategy plus Use-Dependent model failed to capture the sensitivity to practice consistency observed in the empirical data. We reasoned that the use-dependent learning rate (*F*) might be sensitive to practice consistency. Therefore, we added a gain parameter (γ) to the use-dependent learning rate *F*:

Where

This gain is set at 1 during the Constant condition but is allowed to vary during the Low and High Variability conditions.

The Adaptive Bayesian model failed to capture the decay resistant component of the use-dependent bias we see in the empirical data. Here, our modification was predicated on the idea that there is greater visual uncertainty when there is no visual feedback of step lengths. This greater uncertainty might lead a wider variance surrounding the likelihood (greater during Washout vs Learning) and a more slowly updating prior (smaller during Washout vs Learning). Therefore, we fit different and parameters for the experiment phases with and without visual feedback.

We performed the same fitting and plotting procedure for the adjusted models (Figure 7B). The adjusted models were able to explain more of the behavior observed during the experiment (Adjusted AB r2 = 0.95 ± 0.02, Adjusted S+U r2 = 0.91 ± 0.02). The Adjusted Adaptive Bayesian Model demonstrated overall better objective fits to the data compared with the Adjusted Strategy + Use Dependent model (Figure 7D; Adjusted AB model AIC = 2571 [2318 2825], Adjusted S+U model AIC = 3461 [3271 3651], t17 = -8.91, p = 8.2e-8, Cohens dz = -2.10). Despite better objective fits to the overall data, the Adjusted Adaptive Bayesian model still had difficulty explaining the use-dependent process during the Washout phase (Figure 7B insets – first 100 strides of Washout). The Adjusted Strategy + Use-Dependent model was able to capture the overall Washout data more consistently (Figure 7B insets). Indeed, the Adjusted Strategy + Use-Dependent model predicted aftereffects more closely resemble the empirical Initial Bias and Early Washout data (Figure 7C and D). Overall, the behavioral data and the model adjustments highlight two distinct processes of use-dependent locomotor learning: a process that is sensitive to practice consistency that decays quickly, and another that is variability insensitive and is decay resistant.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Model** | **β (VF)** | **σlikelihood (VF)** | **β (no VF)** | **σlikelihood (no VF)** | **C** | **A** | **E** | **F** | **γ LV** | **γ HV** |
| **AB** | 0.25  [0.18 0.31] | 27.76  [17.99 40.72] | 0.25  [0.18 0.31] | 27.76  [17.99 40.72] |  |  |  |  |  |  |
| **AB2** | 0.28  [0.20 0.42] | 39.07  [26.50 55.40] | 2.85e-3  [1.27e-3 6.36e-3] | 3.81  [1.07 13.12] |  |  |  |  |  |  |
| **SU** |  |  |  |  | 0.46  [0.43 0.50] | 0.98  [0.97 0.99] | 0.93  [0.66 0.99] | 1.31e-3  [8.04e-4 2.94e-3] |  |  |
| **SU2** |  |  |  |  | 0.46  [0.43 0.51] | 0.98  [0.95 0.99] | 0.96  [0.88 0.99] | 1.04e-2  [1.07e-3 2.92e-2] | 0.53  [0.34 0.71] | 0.60  [0.42 0.76] |

**Table 1: Model parameters.** Means and bootstrapped 95% confidence intervals.

**Discussion:**

Here we determined that movement variability, in the form of practice consistency, constrains use-dependent locomotor learning. We compared two computational models by systematically varying practice consistency during learning and assessed the state of use-dependent biases during no-feedback washout trials. We found that use-dependent learning was dependent on practice consistency initially, but this dependence faded quickly, and a decay resistant component emerged. Each of the original computational models explained one of these features better than the other: The Adaptive Bayesian model explained the initial sensitivity to practice consistency while the Strategy + Use-Dependent model explained the decay resistant component of use-dependent learning. We therefore performed post-hoc adjustments to each model to improve their explanatory power. A more slowly updating prior during the Washout phase due to lack of visual feedback allowed the Adaptive Bayesian model to capture the slow return to baseline asymmetry, and a gain specific use-dependent learning rate allowed the Strategy + Use-Dependent model to adopt a greater initial sensitivity to practice consistency. These findings highlight two distinct use-dependent locomotor learning processes: A variability sensitive component which depends on practice consistency and decays quickly, and a variability insensitive component which does not depend on practice consistency and is decay resistant.

One alternative explanation to the idea that aftereffects are due to repetition is that they are instead due to the reinforcement of successful actions. Aftereffects have been observed during reward based learning paradigms in reaching (Codol et al., 2018; Holland et al., 2018). Unlike these studies, we did not provide any explicit reward in our task, but we were still unable to control for target hitting as a reinforcement signal. While we view corrections based on target error as a strategic aiming component of learning (Bond and Taylor, 2015; French et al., 2018; Taylor and Ivry, 2011; Wood et al., 2020), it is possible that an implicit target hitting signal could influence learning (Kim et al., 2019; Leow et al., 2020). If aftereffects were due to reinforcement of successful actions, we would expect less target hits in the High Variability condition compared to the others and a consistent positive relationship between the number of target hits and Initial Bias. Participants did hit the targets with less frequency during the High Variability condition compared to the others, but there was no consistent relationship between target hits and Initial Bias for each condition indicating the aftereffects are due to repetition, not reinforcement of successful actions.

Perhaps the reduced aftereffects during the High Variability condition are due to reduced SAI at the end of the Learning phase. Use-dependent locomotor learning scales with the size of the practiced asymmetry in walking (Wood et al., 2020) and with distance from the target in upper extremity movements (Marinovic et al., 2017; Verstynen and Sabes, 2011) and saccades (Reuter et al., 2019) so consistently reduced SAI at the end of Learning could result in a smaller Initial Bias. Reduced SAI at the end of Learning could occur due to a systematic sampling bias of SAI targets. This effect should be mitigated by averaging out the group data since each participant received a different set of targets. Another possibility that could result in reduced SAI at the end of learning is that individuals in the High Variability condition were more fatigued over the course of learning due to the rapidly changing targets. However, when we averaged SAI over the last 50 strides of Learning for each participant, we found no differences between conditions. Furthermore, we split the Learning phases for each condition into 3 quantiles and found that the number of target hits and average distance from the targets was similar across each of these epochs, indicating fatigue did not play a role. These findings, along with the consistent relationship we observed between Learning SAI σ and Initial Bias indicates that practice variability was the driving factor behind the reduced Initial Bias across conditions, not target sampling bias or fatigue.

Our primary finding is that movement variability constrains use-dependent locomotor learning such that more practice consistency leads to greater use-dependent biases. This finding represents a use-dependent process that is sensitive to variability, consistent with prior findings in reaching where there are greater biases after reaching to more probable targets (Marinovic et al., 2017; Verstynen and Sabes, 2011). In both the original and adjusted Adaptive Bayesian models, this variability sensitive process is framed as less confidence in prior expectations of target locations when targets are more variable and greater certainty in the current target of 0 SAI during the Washout phase. The original Strategy + Use-Dependent model, which has a fixed use-dependent learning rate, cannot explain this finding, but the Adjusted Strategy + Use-Dependent model uses a gain on the use-dependent learning rate that is sensitive to practice variability. In this model, two gains for the Low and High Variability condition are free parameters which represent sensitivity to movement variability. In this case, the use-dependent process learns based on the mean movement direction but is also influenced by the variability of movement direction. Both models provide distinct but reasonable explanations for how movement variability constrains use-dependent locomotor learning.

An unexpected finding in our study is that even with highly inconsistent practice, use-dependent biases persisted over the Washout phase. This continued bias reflects a process that is insensitive to movement variability and updates based on the mean movement direction. This low-level bias has also been observed when reaching to a redundant target (Diedrichsen et al., 2010), repeating consistent force production (Selvanayagam et al., 2016) and during eye movements (Reuter et al., 2019). In both the original and adjusted Strategy + Use-Dependent model, the process is reflected in a slow forgetting rate on the use-dependent process that is insensitive to practice consistency. The original Adaptive Bayesian model cannot account for this finding, but the Adjusted adaptive Bayesian model considers the variability insensitive process a product of a more slowly updating adaptive prior when there are no visual targets on the screen. Each model provides plausible explanations for both variability sensitive and variability insensitive use-dependent process.

Despite both models being reasonable explanations for how use-dependent locomotor learning arises, the models that perform better during the Washout phase are the Strategy + Use-Dependent models (Figure 7A and B insets), yet the Adaptive Bayesian models provide better objective fits in both comparisons (Figure 7E). We believe this discrepancy can be explained in how each model accounts for behavior during the Learning phase. The Adaptive Bayesian models combine the target expectation with current sensory information of the current target location. The sensory information is centered around the exact target location, so depending on the weight on the prior and likelihood, these models can predict highly accurate behavior. Conversely, the Strategy + Use-Dependent models correct for error between the target and the behavior based on the Strategic Correction rate (C). Because the strategic learning process also has a forgetting rate (A), the overall behavior will reach a plateau somewhere below the actual target. Furthermore, the mean strategic correction rate in our sample is 0.46 making it difficult for the Strategic component of the model to make rapidly changing, accurate movements. Both models are plausible explanations for how the brain might strategically aim for targets, but the Adaptive Bayesian model has the advantage of quickly combining current information and expectation.

These distinctions between the models might themselves reflect the variability sensitive and variability insensitive process. For example, the variability insensitive process, like the use-dependent component of the Strategy + Use-Dependent model, can be viewed as a low-level bias based purely on the mean movement direction that is slow to learn and slow to washout and is insensitive to movement variability. This is a process that has been consistently observed in upper extremity movements (Classen et al., 1998; Diedrichsen et al., 2010; Marinovic et al., 2017) and reflects an unconscious bias in the mean movement direction and is slow to washout.

The variability sensitive process might be viewed, like the Adaptive Bayesian model as a high-level decision-making process which is based on a combination of past and current targets and is sensitive to movement variability. A high-level, decision making use-dependent process has also been observed in prior studies. In Marinovic et al., (2017), the authors observed a process that depends on action prediction which is constrained by reaction time. Additionally, reaching path biases can develop as fast as a single trial (Jax and Rosenbaum, 2007). The variability sensitive process in the current study can be viewed as a decision-making process.

Repetition of movement patterns is ubiquitous across motor learning literature. Repetition is often well controlled in reaching studies due to the variety of target locations often employed in reaching experiments. However, the impact of repetition should still be considered when designing these experiments, especially when considering a low-level use-dependent process that is biased based on average movement direction. In walking studies, repetition is likely a more significant factor as repeating movement patterns in one direction of asymmetry generally occurs throughout learning experiments. Repetition can be more consistent in walking studies with visual feedback (Cherry-Allen et al., 2018; French et al., 2018; Kim and Mugisha, 2014; Wood et al., 2020) because visual feedback allows participants to perform consistent movements using fast aiming strategies. In paradigms that elicit slower learning processes, such as split belt adaptation, the role of repetition is less clear. There is evidence that repetition of similar movement patterns during split belt adaptation impacts savings (Roemmich and Amy J. Bastian, 2015), but the interaction between repetition and split belt adaptation itself remains unclear. Use-dependent learning interacts with sensorimotor adaptation in reaching (Diedrichsen et al., 2010; Huang et al., 2011) indicating that this interaction should be studied in locomotion.

This study also provides two plausible computational accounts of use-dependent locomotor learning. The ability for computational accounts of motor learning processes to generalize across reaching and locomotion is not new. Specifically, the dual rate state space model adequately describes sensorimotor adaptation in both reaching and walking (Roemmich et al., 2016; Smith et al., 2006). Here we show that computational accounts of use-dependent learning developed in reaching can account for similar behavior in locomotion. The generalizability of these models show that computational models can be used to make predictions and design locomotor learning experiments, as we did in the current study.

Here we show that practicing inconsistent movements can affect use-dependent learning shortly after practice. Therefore, to take advantage of use-dependent learning during practice movements in sport, it is important that these movements are consistent. Use-dependent learning also has a variability insensitive component which could be helpful during rehabilitation practices. Individuals after neurologic injury often experience more variable movement patterns (sources). This might diminish their ability to take advantage of the variability sensitive component of use-dependent learning, but they could still take advantage of the variability insensitive component of use-dependent learning. Indeed, individuals with stroke, using the visual locomotor learning paradigm, demonstrate, use-dependent aftereffects similar to that of healthy individuals (French et al., 2021).

Here we demonstrate that use-dependent locomotor learning is constrained by practice consistency. However, a separate use-dependent learning process is resistant to decay and does not depend on practice variability. The two original computational models each explained one of these processes better than the other, so we adjusted each model after data were collected. The adjusted models were able to better capture these two distinct use-dependent processes, one which is variability sensitive and decays quickly, and the other which is variability insensitive and is decay resistant.

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**Figure Legends:**

**Figure 1**: **Experimental setup**. **(A)** Participants walked on a treadmill while watching feedback of their step lengths. Their step lengths were represented as a blue (left) and a green (right) bar which increased in height during the swing phase and was held on the screen at the moment of heel strike. **(B)** During the Orientation phase (top panel), participants were asked to change their step lengths (green and blue bars) relative to their baseline step lengths (pink horizontal target lines). During the Learning phase (bottom panel), the participant aimed for pink horizontal target lines which were derived from their baseline step length. **(C)** Example target distributions for each condition: During the Constant condition targets were set at 22% SAI (SAI is our measure of step asymmetry – see equation 1) during the Learning phase. During the Low Variability condition targets were drawn from a normal distribution centered around 22% SAI and a standard deviation of 5% SAI. During the High Variability condition targets were drawn from a uniform distribution between 5% and 39% SAI. Note the different scales for the y-axes. **(D)** Learning schedule for each condition: Each condition included a Baseline (Bsl), Learning and Washout phase. Shaded regions indicate no visual feedback was shown on the screen and participants were told to “walk normally”, so the target is effectively 0% SAI. During the Learning phase targets varied based on the condition.

**Figure 2: Simulated results. (A)** The experiment was simulated 1000 times using bootstrapped samples of parameter values from a previously collected dataset [citation redacted for double blind reviewing]. Results of the simulation are plotted as means with shaded errors indicating standard deviation of bootstrapped sample means. The first 10 strides of the Learning phase and the first 50 strides of the Washout phase are plotted in the insets. **(B)** Initial Bias is the mean of the first 5 strides of the Washout phase and **(C)** Early Washout is strides 6-30 of the Washout phase. **(D)** Mean and standard deviations of Washout Rates of each model across conditions. For panels B-D, filled circles represent the mean and error bars represent one standard deviation of bootstrapped sample means. Some error bars are not visible as their values are small and thus obscured by dots representing mean values.

**Figure 3: Confusion matrices**. Four different confusion matrices for each condition and all conditions combined. Lighter colors indicate higher percentages of better fits for each simulated model. Model fits were compared using AIC. AB is the Adaptive Bayesian model, S+U is the Strategy plus Use-Dependent model.

**Figure 4: Step asymmetry index. (A)** Group averaged (circles) and individual (lines) step asymmetry data for each condition. For plotting purposes, we truncated each phase (Baseline, Learning and Washout) to match the participant with the fewest strides and binned the data by 5 strides. **(B)** Histograms of SAI values for all Learning strides separated by condition. **(C)** Mean (think lines) and individual (thin grey lines) Learning SAI mean (purple) and Learning SAI σ (green). The mean and standard deviation of the SAI targets during the Learning phase are plotted as black dashed lines for reference.

**Figure 5: Foot position. (A)** Group averaged (circles) and individual (lines) foot position for the Learning phase of the High Variability condition. For all panels, we truncated each phase (Baseline, Learning and Washout) to match the participant with the fewest strides and binned the data by 5 strides. The Left leg **(A - left panel)** depicts leading foot position in red and trailing foot position in blue. The right leg **(A - right panel)** depicts the leading foot position in blue because this corresponds to the left toe off when calculating a step length. Similarly, the right panel of A depicts the trailing foot position in red because this corresponds to the left heel strike when calculating step length. Specifically, the difference between red functions are analogous to left step length, and the difference between the blue functions are analogous to right step length. **(B)** Group averaged (circles) and individual (lines) leading foot placement symmetry for the High Variability condition. **(C)** Group averaged (circles) and individual (lines) trailing foot placement symmetry for the High Variability condition.

**Figure 6: Washout data. (A)** Group averaged SAI data during the Washout phase of each condition. Shaded error bars represent standard error of the mean. For plotting purposes, we truncated each individual’s Washout phase to match the participant with the fewest strides and binned the data by 3 strides. The dots and error bars in the grey shaded region represent the mean and standard error of the mean of the first 5 strides of Washout for each condition (not binned) which is the same as the Initial Bias measure. **(B)** Mean Initial Bias (mean SAI of strides 1-5 during Washout) for each condition (purple line) with individual Initial Bias for each condition (grey lines). **(C)** Mean Early Washout (mean SAI of strides 6-30 during Washout) for each condition (purple line) with individual Early Washout for each condition (grey lines). **(D)** Mean Washout Rate (using the autoregression calculation) for each condition (purple line) with individual Washout Rates for each condition (grey lines). **(E)** Individual regressions of Learning SAI σ and Initial Bias (grey lines). We used the mean of the individual betas to calculate the mean regression line (purple). The individual and mean betas are plotted in the inset. **(F)** Individual regressions of Learning SAI σ and Early Washout (grey lines). We used the mean of the individual betas (grey dots in inset) to calculate the mean regression line. The individual and mean betas are plotted in the inset. **(G)** Mean Washout Rate (using the Exponential Fit calculation) for each condition (purple line) with individual Washout Rates for each condition (grey lines).

**Figure 7: Model Based Results.** We fit each model to each individual’s data from all conditions and simulated the models using the parameter values. We plot the simulated models against the mean data (purple function). Shaded regions indicate standard error. **(A)** Original Adaptive Bayesian (top row) and Strategy + Use-Dependent (bottom row) averaged model simulations. Grey regions are the regions indicate no visual feedback phases. Insets are the first 100 strides of the Washout phase. **(B)** Adjusted Adaptive Bayesian (top row) and Adjusted Strategy + Use-Dependent (bottom row) averaged model simulations. **(C)** Simulated Initial Bias for each model across conditions. The diamonds and dotted lines represent the Adjusted models. The inset shows the difference between each model simulation and the data for the Constant (blue), Low Variability (red) and High Variability (yellow) conditions with grey dots representing individual differences. **(D)** Simulated Early Washout for each model across conditions. **(E)** Individual and mean differences between AICs for each model plotted as AB model minus SU model, so smaller values favor the AB models.