**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. We tackled this question by testing two competing computational frameworks of use-dependent learning and comparing them to human walking data. Eighteen healthy, young male and female participants completed 3 conditions, 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’ which allowed us to probe any use-dependent bias. We found that the Initial Bias decreased as a function of practice variability. Objective AIC scores also marginally favored the AB model over the SU model. However, although the AB model captured the effect of movement variability on the Initial Bias, the SU model more accurately predicted the very slow, and incomplete, return to baseline over the 750 stride Washout. This finding motivated adjustments to the and motivate development of an alternative model, one which can capture both the sensitivity of Initial Biases to practice variability as well as the decay-resistant component of use-dependent learning Combined, these findings show that movement variability constrains locomotor use-dependent learning,.

**Significance Statement**

**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 (Figure 1B, top panel - pink horizontal target lines, one for each leg). 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 relative to their baseline step lengths. 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). 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 a 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 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 will observe similar use-dependent biases between conditions; however, if the Adaptive Bayes model is more accurate, we should observe different use-dependent biases between conditions.

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**Figure 3: 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 left and right insets, respectively. **(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 (first 50 strides of Washout) 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. This should 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 reported 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 will be used for tests involving multiple comparisons. Assumptions of normality and equality of variances were confirmed with the Shapiro-Wilks test and Levene’s test, respectively.

In addition to our parametric analyses of pre-selected epochs, also employed a cluster permutation analysis in order to assess SAI differences across the entire Washout phases for each condition (Holmes et al., 1996; Maris and Oostenveld, 2007). In this analysis, we will compare SAI differences between two conditions at a time with paired t-tests between bins of 3 strides. Binning, in this case, is 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) will be determined and the t-statistics for this cluster will be summed. The summed t-statistics will be 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 will be 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.

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). We compared these AIC values between the two models using a paired t-test. Quality of model fits were assessed using R-squared values. The number of subjects best fit by each model are reported and presented in Figure X. To provide confidence intervals on parameter estimates, we fit the average learning function for each of 10,000 bootstrapped samples 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.

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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:**

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. 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.

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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.

These changes observed in step asymmetry can occur due to changes in different gait parameters (sources). To gain a better intuition for how individuals were making changes in SAI, we calculated leading and trailing limb position. Figure 5A displays the left and right leading and trailing limb positions during the Learning phase of 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 help provide an intuition for how changes in SAI are made in this learning task and 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 behavior should yield similar results. In line with this assumption, Learning SAI mean was not different across conditions (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]). 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 4B & C; F2 17 = 64.69, p < 2e-12, ƞp2 = 0.79). Learning SAI σ was greater in the LV condition compared to the Constant condition (LV = 5.21 [4.64 5.78], Constant = 3.48 [2.86 4.10]; p = 3e-4, Cohens dz = -1.18), greater in the HV condition compared to the LV condition (HV = 7.98 [7.31 8.616]; p = 5e-6, Cohens dz = -1.67) and greater in the HV condition compared to the Constant condition (p = 5e-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 significant differences between the Constant and High Variability conditions (p = 0.04, Cohens dz = 0.65), but not between the Constant and Low Variability (p = 0.25, Cohens dz = 0.43) or the Low and High Variability conditions (p = 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. 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 errors 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)*** *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. The individual and mean betas are plotted in the inset.* ***(F)*** *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 Early Washout (grey lines). We used the mean of the individual betas to calculate the mean regression line. The individual and mean betas are plotted in the inset.* ***(F)*** *Mean Washout Rate (using the autoregression calculation) for each condition (purple line) with individual Washout Rates for each condition (grey lines).* ***(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 than 3 bins. 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.

After the data were collected, we performed exploratory analysis to determine the impact of practice variably on use-dependent biases irrespective of condition. We performed a simple regression between Learning SAI σ and Initial Bias (Figures 6D). We found a consistent inverse relationship between Learning SAI σ and Initial Bias (mean beta = - 0.31, one sample t-test: p = 0.01). We found a similar but muted relationship between Learning SAI σ and Early Washout (Figure 6E, mean beta = -0.11, 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 or Early Washout (stats). This additional exploratory analysis further demonstrates the relationship with practice consistency and the use-dependent learning process.

A characteristic of a use-dependent bias is a relatively longer return to baseline (Diedrichsen et al., 2010; Wood et al., 2020). Therefore, it is possible that greater amounts of practice consistency would result in more robust use-dependent biases. We calculated 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 6F; 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 (p = 0.01, Cohens dz = -0.82). There was no difference between the Washout Rate of the Constant and LV (p = 0.40, Cohens dz = 0.20) or Constant and HV conditions (p = 0.07, Cohens dz = -0.58).

On inspection of our measure of Washout rate, we found that this measure does a poor job of describing the data. The Washout Rate parameter calculated using Autoregression, unlearning per stride, had a value greater than one for some participants indicating that SAI was increasing during the first 50 strides of Washout. To determine if this prediction was accurate, we simulated the first 50 strides of Washout using the unlearning per stride parameter and initialized the simulation at the mean of the first five strides of the Washout phase. On visual inspection, we found that the autoregression rate analysis was unable to adequately reproduce the behavioral data. We believe this is an artifact of noisy stride by stride data which biases the regression slope to be small, resulting is larger Washout Rates (for example, a Washout rate of 0.86 means SAI decreases by 86% from one stride to the next). Because, on visual inspection, the bias seems to take a much longer time to washout than these 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 consistently better fits to the data (Autoregression AIC = 117.6, Exponential function AIC = 30.4, p < 6.0e-5). We found no differences in the decay constant between conditions (Figure 6G; Constant = 13.16 [3.92 22.41], LV = 13.83 [5.00 22.66], HV = 10.08 [1.84 18.32], F2 17 = 0.14, p = 0.87, ƞp2 = 0.008). Additionally, we performed the same calculations of Washout rate for all the strides in the Washout phase which led to 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 observed (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 the use-dependent biases.

The behavioral findings support the hypothesis that practice consistency improves use-dependent locomotor learning. According to our simulations (Figure 2), this is consistent with the Adaptive Bayesian model. 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 (3) 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 empirical data for all strides (Figure 7A) and for the Initial Bias and Early Washout (Figure 7B and C). Both models demonstrated good fits to the data (AB 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 7D; AB model AIC = 2865 ± 456, S+U model AIC = 3587 ± 361, p = 2e-6). 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 walking. 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, timeline

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**Figure 7: Model Based Results.** We fit each model to each individual’s data from all conditions. These plots show the mean model fits to the mean data (purple function). Shaded regions indicate standard error. **(A)**

We made post-hoc adjustments to the Strategy plus Use-Dependent model to determine if it can provide a better account of the use-dependent process reflected in the data. Our modification was predicated on the idea that the use-dependent learning rate might be sensitive to practice consistency. Therefore, we added a gain parameter the use-dependent learning rate *F*. We also made post-hoc adjustments to the Adaptive Bayesian model to determine if it provides a better account of the use-dependent process reflected in the data. Our modification was predicated on the idea that there is greater visual uncertainty when there is no visual feedback of step lengths (specifically, during the Washout phase). This greater uncertainty leads to both a wider variance surrounding the likelihood (greater during Washout vs Learning) and a more slowly updating prior (smaller during Washout vs Learning).

We performed the same fitting and plotting procedure for the adjusted models (Figure 7E)

Statistical table

|  |  |  |
| --- | --- | --- |
| Data Structure | Type of Test | Confidence intervals |
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**Discussion:**

Here we determined the importance of practice consistency on use-dependent locomotor learning.

1. Overview of main findings
2. Go back to the hypotheses: provide an intuitive explanation for why each model performed the way it did and relate it to the current findings
3. Discuss the new models
4. Support for the use-dependent nature of this aftereffect including
5. Quickly decaying process that depended on variability
6. Slowly decaying process that did not depend on variability

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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 relative to their baseline step lengths. 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 3: 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 left and right insets, respectively. **(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 (first 50 strides of Washout) 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.

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