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, ~~it~~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 have designed a set of walking experiments that systematically vary environmental 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

Behavioral Methods:

Participants:

Young, healthy male and female individuals between the ages of 18-40 years will be recruited to participate in this study. Potential participants will be included if they are naive to locomotor learning tasks. Potential participants will be excluded if they have a history of any neurologic, psychiatric or cognitive conditions, or have any cardiovascular or musculoskeletal problems that limit their walking. This study has been approved by the (university name redacted until approved for publication) institutional review board.

Paradigm:

Participants will perform three sessions of walking spaced 5-10 days apart. During each session, they will walk 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 will wear a ceiling mounted harness, which does not provide any body weight support, and hold onto a handrail for safety during all walking phases. A computer monitor placed 60 cm in front of the treadmill will provide 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 will be in the form of a bar graph 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 will be time synchronized with each respective limb's swing phase, increasing in height until the limb reaches heel strike at which point the bar will hold on the screen until the next swing phase begins. There will also be a pink horizontal target line for each leg which will be derived from each participant's baseline step length for each session and serve as the target during that session's Learning phase.

Each of the three sessions of walking will involve a similar block schedule. Participants will first be 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 will be 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 will undergo a short (25 strides) Orientation phase following Baseline during the first session only. During Orientation, the participant will perform guided practice in changing their step lengths (green and blue bars) relative to their baseline (pink horizontal target lines, one for each leg). During the Learning phase, participants will be asked to hit the pink horizontal target lines exactly with each step for 500 strides. Both target lines will be 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. The target lines will have a width of ± 2% step length change from baseline. The researcher will provide participants with a prompt to continue hitting the target lines every 100 strides during the Learning phase. During the Washout phase, the feedback will be removed from the screen and participants will be asked to “look forward and walk normally” for 750 strides. The treadmill will be stopped briefly between each phase so that instructions can be provided for the next phase.

Conditions:

We will systematically manipulate the independent variable, the consistency of target positions, during the Learning phase. To accomplish this, participants will complete three different conditions: 1) In the Constant condition, the target locations will be set to a constant 22% step asymmetry throughout the Learning phase; 2) In the Low Variability condition, target locations will vary, being drawn from a normal distribution with a mean of 22% and standard deviation of 5%; and 3) In the High Variability condition, the targets will vary more widely, being drawn from a uniform distribution with a range of 5%-39% step asymmetry (Figure 1C & D). Thus, all three conditions will have 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 will be markedly different. This study design is 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 will change, with equal probability, every 1-5 strides. To prevent contamination from potential order effects, we will counterbalance the order of conditions across all participants.

Data Collection:

~~Kinetic data will be collected at a frequency of 1000 Hz from the dual belt treadmill instrumented with two force plates, one under each belt (Bertec, Columbus, OH, USA).~~ Kinematic data will be 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 will use a custom marker set with ~~7~~11 total retroreflective markers, one for each ~~heel, each~~greater trochanter, lateral knee, heel, lateral malleolus, and ~~each~~ 5th metatarsal head. The ~~s~~e~~l~~eventh marker will be placed on the left 1st metatarsal head to ensure the tracking system can differentiate between the right and left feet. ~~Kinematic data will be time-synchronized with kinetic data in Nexus.~~

Proposed Analysis Pipeline:

First, any gaps in the kinematic data will be filled using a Woltring filter for small gaps (1-4 frames) and Pattern Fill for larger gaps (>4 frames) in Nexus. The remainder of the data analysis will be performed with 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. ~~Kinematic and kinetic data will be low pass filtered at 10 Hz using a 4th order Butterworth filter. Kinetic data will be used to detect heel strike events when the force plate reads greater that 20 N and toe off events when the force plate reads less than 20 N. Erroneous force plate events will be removed and replaced with kinematic events. For heel strikes this is the most anterior position of the heel marker in the sagittal plane, and for toe offs this is the most posterior position of the 5th metatarsal head in the sagittal plane.~~Kinematic data will be low pass filtered at 10 Hz using a 4th order Butterworth filter. Kinematic marker data will be used to select *heel strike* when the heel marker velocity transitions from positive to negative and *toe off* when the 5th metatarsal head marker velocity transitions from negative to positive (Zeni et al., 2008). Step lengths will be 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 will be averaged and used to derive each legs' respective target lines during that session's learning phase. Step lengths will be used to calculate our primary outcome, step asymmetry index (SAI):

$$SAI = \frac{\cancel{(Step\ Length_{LEFT} - Step\ Length_{RIGHT})}(Step\ Length_{LONG} - Step\ Length_{SHORT})}{(\cancel{Step\ Length_{LEFT}}Step\ Length_{LONG} + Step\ Length_{\cancel{RIGHT}SHORT})} * 100\% \quad (1)$$

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 will always be positive. SAI will be calculated on a stride-by-stride basis throughout all walking phases. We will correct 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 will be used for the remainder of our analyses.

We will also calculate limb placement asymmetry. Leading limb foot placement is the sagittal distance between the hip and ankle marker during that limb's heel strike and trailing limb placement is the sagittal distance between the same markers during that limb's toe off. Leading and trailing limb placement asymmetry is calculated as the difference between the long and short leading and trailing limb placement, respectively. A visualization of this analysis will be provided in a figure (Finley et al., 2015; Long et al., 2016; Sánchez et al., 2020).

Our analyses of behavior during the Learning phase will focus on checking our assumptions~~,~~ ~~based on the task design and our pilot data (see Figure 4), that~~ that the participants' SAIs will track the target SAI for each condition. That is, the mean SAI will not differ across conditions (Learning SAI mean), but the SAI standard deviation (Learning SAI σ) will~~.~~ (Figure 4D). The purpose of the Learning phase is 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 3A, learning insets).

Our hypotheses focus on use-dependent biases, probed during the no-feedback Washout phase. Use-dependent biases will be analyzed at two different time points. First, to characterize the total magnitude of use-dependent learning, we will calculate 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 will calculate the mean SAI of strides 6-30 of the Washout phase (Early Washout; Day et al., 2018; Leech et al., 2018). We will also analyze the rate of washout by regressing subsequent strides onto current strides for the first 50 strides of the Washout phase. We will report $1-\beta$ (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 have 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 we are proposing 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 (x): the sum of the strategic process (s) and the use-dependent process (w) on each stride, n:

$$x_{n+1} = s_{n+1} + w_{n+1} \qquad (2)$$

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

$$e_n = t_n - x_n \qquad (3)$$

$$s_{n+1} = \begin{cases} A * s_n + C * e_n, & with\ VF \\ 0, & without\ VF \end{cases} \qquad (4)$$

$0 < A < 1,$

$0 < C < 1$

~~In this~~This model assumes that individuals remember some proportion, A ~~is a retention factor representing how much~~, of ~~the~~ their explicit strategy ~~(s) is retained from one trial~~. For example, when a participant aims for the target, they will remember, to ~~the next, and C is the proportion~~some degree, where they aimed previously. Participants also correct a proportion of the error ~~that is corrected for~~ , C, on each stride. As this is a strategic, or voluntary, process, we assume that s is equal to zero when the visual feedback (VF) is turned off and the participants are instructed to walk normally.

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

$$w_{n+1} = E * w_n + F * x_n \qquad (5)$$

$0 < E < 1,$

$0 < F < C$

~~We assume the use-dependent process learns much slower than a strategic process (Diedrichsen et al., 2010) and thus constrain F to be at least 5 times less than C.~~

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, C, must be at least 5x faster than the use-dependent learning rate, F. This model also assumes that this learning rate F 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 ($\bar{\theta}$) with the current sensory estimate of target position (θ) to compute the posterior probability distribution. The model assumes that the motor output is a direct readout of the maximum a posteriori (MAP) estimate (θ_{MAP}) of target location, as in Verstynen and Sabes (2011):

$$\theta_{MAP} = \cancel{\frac{\sigma^2_{posterior}}{\sigma^2_{prior}}}\frac{\sigma^2_{likelihood}}{\sigma^2_{prior} + \sigma^2_{likelihood}} * \bar{\theta} + \cancel{\frac{\sigma^2_{posterior}}{\sigma^2_{likelihood}}}\frac{\sigma^2_{prior}}{\sigma^2_{prior} + \sigma^2_{likelihood}} * \theta \qquad (6)$$

We assume the prior and likelihood are normally distributed~~,~~. ~~t~~Therefore ~~$\sigma^2_{posterior,n}$ is the variance for the posterior probability and is equal to $(\sigma^{-2}_{prior,n} + \sigma^{-2}_{likelihood})^{-1}$.~~:

$$\sigma^2_{posterior} = \frac{\sigma^2_{likelihood} * \sigma^2_{prior}}{\sigma^2_{likelihood} + \sigma^2_{prior}} \qquad (7)$$

The mean of the likelihood is centered on the true target location, θ, on each stride, n. The likelihood's variance, $\sigma^2_{likelihood}$, 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 $N(\bar{\theta}_n, \sigma^2_{prior,n})$:

$$\bar{\theta}_{n+1} = (1-\beta) * \bar{\theta}_n + \beta * \theta_n$$ (~~7~~8)

$$\sigma^2_{prior,n+1} = (1-\beta) * \sigma^2_{prior,n} + \beta * (\bar{\theta}_n - \theta_n)^2$$ (~~8~~9)

$0 < \beta < 1,$

$0 < \sigma^2_{likelihood} < 100$

β 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 are 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 predicts 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.

Statistical Analysis:

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

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~~. Relative support for one model over the other will be formally assessed using model selection criteria, specifically Akaike Information Criterion (AIC) scores. ~~: The Strategy plus Use-Dependent model predicts no difference in use-dependent bias across conditions while the Adaptive Bayesian model predicts reduced use-dependent bias during less consistent conditions. After the data are collected, we will fit both models to individual participant data from all three conditions combined, using the fmincon function in MATLAB. This will allow us to obtain one set of parameter values for each ~~model for each individual participant~~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.

~~We will use AIC to objectively compare the model fits and~~

Additional objective support for one model over the other will be formally assessed using model selection criteria, specifically Akaike Information Criterion (AIC) scores. We will compare these AIC values between the two models using a paired t-test. Quality of model fits will be reported using R-squared values. The number of subjects best fit by each model will be reported and presented in visual format in a figure. As fits to individual data can be noisy (Wilson and Collins, 2019), we will also calculate AIC scores on fits to the average learning functions across conditions. To provide confidence intervals on parameter estimates, we will fit the average learning function for each of 10,000 bootstrapped samples and report the empirical 2.5th and 97.5th percentile values.

Behavior:

As stated above, we do not have competing hypotheses regarding the Learning phase, and we expect 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 (see Pilot Data section and Figure 4D). These assumptions will be assessed using repeated measures ANOVA and in the case of a significant test, we will perform post-hoc Bonferroni-corrected pairwise comparisons ~~if necessary~~.

As the Adaptive Bayesian model predicts differences in use-dependent bias across conditions, we will perform statistical analyses of Initial Bias, Early Washout and washout rate using separate repeated measures ANOVAs. In cases of a significant ANOVA, post-hoc pairwise comparisons will be performed with Bonferroni-corrected t-tests. Because the Strategy plus Use-Dependent model predicts similar use-dependent biases across conditions, we will also perform 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 will report t- and F- statistics, exact p-values, means, 95% confidence intervals and standardized effect sizes (Cohen's *d* for t-tests and η_p^2 for ANOVAs). For equivalence testing, we will 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 will be used for tests involving multiple comparisons. Assumptions of normality and equality of variances will be tested with the Shapiro-Wilks test and Levene's test, respectively. In cases where these assumptions are not met, we will perform non-parametric permutation tests. For pairwise comparisons, we will use the difference between group means as our test statistic, to be compared to a null distribution created by random shuffling of group assignment in 10,000 Monte Carlo simulations (resampling with replacement), to obtain an exact p-value. For comparisons involving more than two conditions, we will implement a similar approach but use the F-value obtained from a repeated-measure ANOVA as our test statistic.

In addition to our parametric analyses of pre-selected epochs, we will also employ a cluster permutation analysis in order to assess potential 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.

Power Analysis:

We performed a power analysis to determine the sample size required to detect differences in use-dependent biases across conditions, with alpha of 0.05 and power of 0.90. Based on an estimated standardized effect size (Cohen's *d*) of 0.91 from a prior study comparing locomotor use-dependent biases across different magnitudes of induced stepping asymmetries during an abrupt learning phase~~s~~ (Wood et al., 2020), we will require 15 subjects. We therefore expect to recruit 15-21 individuals for this study in order to account for possible attrition and to exceed the minimum acceptable power. This sample size will also ensure appropriate counterbalancing of practice schedules across participants while also being well-above the threshold of statistical power documented in comparable motor learning studies (Diedrichsen et al., 2010; French et al., 2018; Long et al., 2016; Verstynen and Sabes, 2011; Wood et al., 2020).

Data Replacement:

Data will only be replaced under the following conditions:

1) If a participant does not complete the entire learning task for all 3 conditions due to a technical error or equipment failure in the middle of data collection or if the participant chooses to drop out of the experiment.

2) If the experimenter deems the participant unsafe to continue the study, which may occur if there is an injury or illness after the participant has been enrolled.

3) If a participant does not meet a threshold of performance on the task, which will be defined as falling outside of 3 standard deviations from the mean performance in terms of target accuracy. Target accuracy will be defined as the mean absolute difference between the target SAI and the actual SAI measured across the entire Learning phase.

Completed Work:

~~*Confusion Matrices:*~~

~~To determine whether the models are distinguishable and~~*Model Recovery*

Due to the central importance of model selection in the ~~best method of objective comparison~~proposed study, we performed model recovery analysis in order to 1) confirm that the models are distinguishable under ideal circumstances (Hardwick et al., 2019; Wilson and Collins, 2019)~~. By~~ 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 ~~simulating~~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~~ and then comparing model fits of the simulated data, we show in the confusion matrices (Figure 2) that~~, calculating AIC scores for each model fit and directly compared the ~~models are distinguishable under these ideal circumstances.~~two values. A confusion matrix ~~provides~~summarizes this process, providing the probability that ~~a randomly~~the model which generated~~,~~ the simulated ~~model is fit~~data was better fit by itself or the other ~~models using objective model comparisons~~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 2) and values closer to 0 when comparing simulations and fits from opposing models (duller colors on off-diagonals in Figure 2). ~~We fit the simulated data from each model using the same fitting procedure as above and found that comparison using Akaike Information Criterion (AIC) distinguishes between the models better than Bayesian Information Criterion (BIC).~~In Figure 2, 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.

Simulations:

We simulated both models 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).

~~We obtained~~ Preliminary model parameters ~~for model simulation~~ were obtained by fitting the models to ~~each individual~~walking data (n=16 participants) from [withheld due to double-blinding], which used a ~~previously collected dataset~~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 3 details the simulated data from these parameters for each condition. The panels in Figure 3A 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 3B 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 3D). 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 ~~differences~~different use-dependent biases between conditions~~ in our behavioral analyses~~.

Pilot Data:

To assess the feasibility of our behavioral methods, and specifically, to determine if individuals are able to follow frequently changing step length targets, we collected pilot data from 3 individuals for the High Variability condition, with 2/3 of these individual also completing the Constant condition (see Figure 4). The pilot results show that participants were able to follow the feedback during the High Variability condition with a mean absolute distance of 4.2 cm from the targets~~.~~ (Figure 4A). Furthermore, we correlated step length targets with actual step lengths for each subject during the Learning phase: mean R-value = 0.59 and 0.78 for the right and left step lengths, respectively ($p < 0.0001$ for all). We also calculated the Initial Bias and Early Washout for those participants who completed both the Constant and High Variability conditions (Figure 4B & C). The pilot results are also consistent with our assumption that, during the Learning phase, SAI means will be similar across conditions (Learning SAI mean), but SAI standard deviation (Learning SAI σ) will be different (Figure 4D). These pilot data will not be included in the final analysis.

Timeline for Completion:

We have received IRB approval from our university for this project. However, all labs have been shut-down due to the COVID-19 pandemic. Data collections are ready to be initiated as soon as human research resumes at the university. Given uncertainty around when labs will be reopened, we offer a proposed resubmission window between January 15th, 2021 and June 15th, 2021.

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Figure Legends:

Figure 1: Experimental setup. (A) Participants will walk on a treadmill while watching feedback of their step length. Their step lengths will be represented as a blue (left) and green (right) bar which increases in height during the swing phase and holds on the screen at the moment of heel strike. **(B)** During the Learning phase, the participant will aim for a pink horizontal target line which is derived from their baseline step length. On the first stride of learning the target will be offset from their baseline (**B** – top panel), and the subject will have to adjust their step length on subsequent strides to hit the target (**B** – bottom panel). **(C)** Target distribution for each condition: During the Constant condition targets will always be at 22% SAI during the Learning phase. During the Low Variability condition targets will be drawn from a normal distribution centered around 22% SAI and a standard deviation of 5% SAI. During the High Variability condition targets will be 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 will include a Baseline (Bsl), Learning and Washout phase. Shaded regions indicate no visual feedback will be shown on the screen and participants are told to “walk normally”, so the target is effectively 0% SAI. During the Learning phase targets will vary based on the condition.

Figure 2: 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 3: Simulated results. (A) The experiment was simulated 1000 times using bootstrapped samples of parameter values from a previously collected dataset. Results of the simulation are plotted as means with shaded errors indicating standard deviation of bootstrapped sample means. ~~The~~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 for 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 4: Pilot data. ~~Mean values are represented as horizontal bars and individual participants as dots.~~**(A)** Stride-by-stride data for individual participants and the mean for the Constant (top) and High Variability (bottom) conditions. Two participants completed both conditions, while one participant performed the High Variability condition only.* Each phase (Baseline, Learning, Washout) was truncated to match the length of the participant with shortest time series and strides were averaged in bins of 3. Note that the *Mean Target* locations are shown, which in the case of the *High Variability* condition is a smoothed version of the actual target locations, in order to aid visualization of the behavioral data. **(B-C)** Use-dependent bias for the two participants who completed both conditions. **(B)** Initial bias is the mean of the first 5 strides of the Washout phase and **(C)** Early Washout is the mean of strides 6 – 30 of the Washout phase. **(D)** SAI was averaged across the entire Leaning phase for each participant for the Constant and High Variability conditions (Learning SAI mean). SAI standard deviation was calculated across the entire Learning phase for each participant for the Constant and High Variability conditions (Learning SAI σ). *Only the Learning Phase of this latter participant's data is included due to a technical error that occurred after this point.