**Introduction**

Practice, in the form of movement repetition, is widely recognized as an indispensable component of motor skill acquisition (Schmidt and Lee, 2005). Yet, even after acquiring a skill, repetition continues to play an important role. For example, repetition hastens 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 (Classen et al., 1998; Diedrichsen et al., 2010). These features of use-dependent learning may explain, in part, why a basketball player continues to practice her free throws years after she initially learned how to shoot. However, since no two movements can ever be identical, how consistent must the basketball players’ free throws be during practice to engage the use-dependent learning process?

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 UDP 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 in 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; Wood et al., 2020). In this study, visual targets were used to guide participants into walking with an asymmetry (i.e., a limp). Practicing this asymmetric walking pattern caused a use-dependent bias: when all visual feedback was removed and participants were instructed to “walk normally”, participants demonstrated a small, but persistent aftereffect resembling the practiced limp. Given that movement is intrinsically variable, a critical question remains unanswered: 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. We first provide two distinct computational accounts of how use-dependent learning may arise. In 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, the magnitude of use-dependent biases are directly related to the consistency of the environment, or target locations. Our second model involves two processes acting in parallel: A strategic learning process that is active when the goal is to match step lengths to visual targets, and in parallel, a slowly updating use-dependent learning process that biases movements in the direction of immediately preceding movements (Diedrichsen et al., 2010). Critically, our Strategy plus Use-Dependent model is much less sensitive to the consistency of the environment than the Bayesian model. Therefore, we have designed a set of walking experiments that systematically vary environmental consistency and assess the state of use-dependent biases during no-feedback 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.

*Power analysis:*

As our main hypotheses involve within-subjects comparisons of behavior during multiple epochs, as well as specific pair-wise comparisons, we performed power analyses for these statistical tests based on an alpha value of 0.05 and power of 0.90. Previous work examining use-dependent biases report standardized effect sizes effect sizes of 1.48 (French et al., 2018). This yields a sample size of 7. Based on these estimates, we expect to recruit 15-21 individuals for this study in order 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 for good statistical power relative to documented effect sizes 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 of all other participants in terms of either step asymmetry index or target accuracy.

If any data are replaced, we will perform our analyses both with and without the removed participant(s), reporting any qualitative differences in our findings.

*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, to be selected based on comfort by the participants. This range is to ensure that each participant walks at a speed that is comfortable 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). A step length is defined as the sagittal distance between the leading limb’s heel marker and the trailing limb’s heel marker at the moment of the leading limb heel strike.

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. Baseline step length will be calculated as the mean of the last 50 strides of the Baseline 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. One stride is defined as one left heel strike to the subsequent left heel strike. 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 day one 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). Participants will be asked to confirm they understand the relationship between their step length and the visual feedback after this phase. 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. 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.

*Conditions:*

Participants will perform three different conditions separated by 5-10 days. To prevent contamination from potential order effects, we will counterbalance the order of conditions across all participants. The independent variable will be the consistency of targets during the Learning phase. Going from the most to least consistent condition: 1) In the Repeated condition, the target positions will be set to 22% SAI throughout the Learning phase; 2) In the 5% σ condition, target SAI will be drawn from a normal distribution with a mean of 22% and standard deviation of 5%; and 3) In the Uniform condition, the targets will be drawn from a uniform distribution with a range of 5%-39% SAI (Figure 1C & D). 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 5% σ and Uniform conditions, targets will change, with equal probability, every 1-5 strides.

*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 retroreflective markers, one for each heel, each lateral malleolus, and each 5th metatarsal head. The seventh 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. Step lengths will be calculated as the sagittal difference between the leading and trailing heel markers at the moment of leading heel strike. Step lengths will be used to calculate our primary outcome, step asymmetry index (SAI):

(1)

Thus, SAI represents the difference between the two step lengths normalized by the stride length. We express this measure as a percentage where 0% is perfect symmetry and SAIs further away from 0% indicate greater asymmetry. We will correct for SAI baseline biases for each participant and each respective training session: the mean of the last 50 strides of the Baseline phase will be subtracted from all strides for that respective session. The baseline corrected measure will be used for the remainder of our analyses.

To assess how well participants perform on the learning task, we will calculate SAI accuracy as the mean absolute difference between the target SAI and the actual SAI during the Learning phase. We will also test our assumption that, during the learning phase, SAI mean will be similar across conditions, but the SAI standard deviation will be different across conditions by examining both for the entire Learning phase. We will determine how participants perform at the end of the Learning phase by averaging SAI for the last 30 strides.

Use-dependent bias will be calculated in two ways. First, to characterize the immediate use-dependent bias, we will calculate the mean SAI during the first 5 strides of the Washout phase (Initial Bias). Second, to characterize the state of use-dependent biases during the early 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). This procedure will allow us to determine differences between conditions at the Learning phase, Initial use-dependent bias, and the Early Washout. We will also analyze the rate of washout by regressing subsequent strides onto current strides for each stride of washout. The slope of this regression estimates the amount of SAI retained from one stride to the next. (Kitago et al., 2013; Wood et al., 2020).

*Statistical analysis:*

We will test for within-subjects differences across conditions for the mean and standard deviation SAI during the entire Learning phase to test our assumption that means will be the same but standard deviations will be difference between conditions with repeated measures analysis of variance (ANOVA). We will also perform separate repeated measures ANOVA for our key timepoints of interest: End of Learning, Initial Bias, Early Washout and washout rate and post-hoc pairwise comparisons if the ANOVA is significant. These comparisons are chosen because the two different models make distinguishable predictions specifically at these points of the experiment (see Figure 3 and simulations). 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 ƞp2 for analysis of variance). Alpha values will be set at 0.05 for F tests, pairwise comparisons alpha values will be set at 0.02 to correct for multiple comparisons. As one of our models (Strategy plus Use-Dependent) predicts similar aftereffects and washout across conditions (see Fig. 3), we will also report Bayes Factors to test for equality between conditions for Initial Bias and Early Washout. Equality will provide support for the null hypothesis: that SAIs are not differences between conditions during washout. Assumptions of normality and homoscedasticity will be tested with the Shapiro-Wilks test and Levene’s test, respectively. In cases where assumptions of normality 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 to assess potential SAI differences across 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 at each stride. The largest cluster of significant paired t-tests (p < 0.05) in a row 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.

**Modeling Based Analyses**

We have adapted two computational models of use-dependent learning that make dissociable predictions regarding the effect movement consistency has on use-dependent biases. We refer to the first model as the Strategy plus Use-Dependent model (Diedrichsen et al., 2010) and the second model as the Adaptive Bayesian model (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). 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, :

(5)

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

(6)

(7)

In this model, is a retention factor representing how much of the strategy () is retained from one trial to the next, and is the proportion of the error that is corrected for 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. Note that the update is a function of the motor output, as opposed to an error signal.

(8)

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

(2)

We assume the prior and likelihood are normally distributed, therefore is the variance for the posterior probability and is equal to . 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. The adaptive nature of the model is encapsulated by the stride-by-stride updating of the prior probability’s parameters :

(3)

(4)

,

Where is a free parameter representing the learning rate. Thus, 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 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.

*Planned Model Comparison:*

Model fitting and model selection will be the basis for our inferences regarding which model is more accurate, and thus, which hypothesis is supported. After 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. Next, we will simulate each model with the fitted parameters as a posterior predictive check. Simulating each model with the individual parameters for each condition of the experiment should yield similar observations as the empirical data. Therefore, we will analyze the simulated data in the same way we will analyze the empirical data. That is, we will statistically analyze the Initial Bias, Early Washout and washout rate values of the simulated data for differences between the conditions. We will use AIC to objectively compare the model fits and compare these AIC values between the two models using a t-test. We will also compare the number of subjects best fit by each model using the chi-squared test of independence.

**Completed work:**

*Confusion Matrices:*

To determine whether the models are distinguishable and the best method of objective comparison, we performed model recovery analysis (Hardwick et al., 2019; Wilson and Collins, 2019). By sequentially simulating data from each model and then comparing model fits of the simulated data, we show in the confusion matrices (Figure 2) that the models are distinguishable under these ideal circumstances. A confusion matrix provides the probability that a randomly generated, simulated model is fit better by itself or other models using objective model comparisons. Ideally, the model that generated simulated data will be better fit by itself than by the other model. This will result in values closer to 1 on the diagonals of the confusion matrix (brighter colors) and values closer to 0 off-diagonals (duller colors). 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).

*Simulations:*

We simulated both models to demonstrate how each accounts for the consistency of practiced target step lengths. For the Adaptive Bayesian model, the MAP estimate 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). In direct contrast to this framework, the Strategy plus Use-Dependent model is much more robust to environmental consistency in cases, as here, where there is a large asymmetry in one direction. The model assumes use-dependent learning is slow to learn and washout; 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.

We obtained parameters for model simulation by fitting the models to each individual from a previously collected dataset. 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 as the Learning block progresses, with much more marked differences between their predictions during the Washout phase.

We compared use-dependent biases during both Initial Bias and Early Washout (Figure 3C and D). Overall, the Strategy plus Use-Dependent model predicts more consistent use-dependent bias across conditions for both Initial Bias and Early Washout. However, the Adaptive Bayesian model demonstrates consistently decreasing aftereffects when the conditions become less stable during the Learning phase. We also analyzed the washout rates for each model. The Adaptative Bayesian model predicts slower washout as the conditions are less stable. The Strategy plus Use-Dependent model predicts a consistent washout rate across conditions. Based on these simulations, if the Adaptive Bayes model is appropriate, we should observe differences between conditions in our behavioral analyses; however, if the Strategy plus Use-Dependent model is more appropriate, we will observe an absence of differences between conditions.

*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 Uniform condition. These pilot results show that they were able to follow the feedback with a mean distance of 4.2 cm from the targets. 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). The pilot results are also consistent with our assumption that, during the Learning phase, SAI means will be similar across conditions, but SAI standard deviation will be different (Figure 4; 2/3 participants from the Uniform condition also completed the Repeated condition). 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 from November 15th to May 15th, 2021.

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**Figure Legends:**

**Figure 1:** Participants will walk on a treadmill while watching feedback of their step length (**A**). 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. During the Learning phase, the participant will aim for a pink horizontal target line which is derived from their baseline step length (**B** – both panels). 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). Target distribution for each condition (**C**): During the Repeated condition targets will not move from 22% SAI. During the 5% σ condition targets will be drawn from a normal distribution centered around 22% SAI and a standard deviation of 5% SAI. During the Uniform condition targets will be drawn from a uniform distribution between 5% and 39% SAI. Learning schedule for each condition (**D**): 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 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.

**Figure 3:** Simulated results. The experiment was simulated 1000 times using bootstrapped samples of parameter values (**A**). Results of the stimulation are plotted as means with shaded errors indicating standard deviation of bootstrapped sample means. The first 50 strides of the Washout phase are plotted in the insets. Learning plateau is the mean SAI of the last 30 strides of the Learning phase (**B**). Initial Bias is the mean of the first 5 strides of Washout (**C**) and Early Washout is strides 6-30 of the Washout phase (**D**). Filled circles represent the mean and error bars represent one standard deviation of bootstrapped sample means.

**Figure 4:** Pilot data. Mean values are represented as horizontal bars and individual participants as dots. SAI was averaged across the entire Leaning phase for each participant for the Repeated and Uniform conditions. SAI standard deviation was calculated across the entire Learning phase for each participant for the Repeated and Uniform conditions.