Manuscript title: How movement variability constrains locomotor use-dependent learning

Responses to Reviewers:

We thank the reviewers for their many helpful comments which have strengthened this Registered Report. We have edited the manuscript accordingly. Below, please find our point-by-point responses to all the comments in bold. We also identify the location (lines) of all edits in the tracked-changes version of the manuscript.

Responses:

Main Request:

It would be helpful to see the learning and washout time series for the 2 subjects that they tested in the constant condition and the 3 in the high variability condition. The preliminary data that are shown only give the mean and std during of SAI during learning. This does not illustrate the time course of learning and the time course of washout trials, the latter of which is their main outcome measure based on model predictions.

We agree with the reviewers with regard to the necessity of the stride-by-stride data and thank the reviewers for this comment. We have now expanded the Pilot Data Figure (Figure 4) to include binned stride-by-stride data for all participants. This figure now provides a clear illustration of the time courses of the Learning and Washout phases. We provide all individual data and the mean for each condition across strides. Each phase (Baseline, Learning and Washout) has been truncated to match the length of the participant with the shortest time series. Two participants completed both the high variability and the stable condition. One participant completed the high variability condition only; however, there was a bug in our experiment code, which has since been fixed (the condition changed from Highly Variability to Consistent in the middle of the Learning phase), and therefore we have included the data for this participant up to the point where the technical error occurred. We also added further description of this figure in the Pilot Data section (lines 504-505) and the Figure 4 legend (lines 628-642).

Reviewer #1:

1. Authors need to indicate more explicitly in the methods in what way their theory is distinct from the one proposed in Diedrichsen et al. 2010. In other words, is it the exact same theory but just adapted to locomotion?

   We agree with the reviewer that there should be more explicit description of how our theory is distinct from that of Diedrichsen et al 2010 and have now added further description in the Model-Based Methods section (lines 209-213). The original model from the Diedrichsen et al. 2010 paper combines two processes: use-dependent and motor adaptation. The adaptation component is in response to a force field, a task that is qualitatively different from the one we plan to use in the current study. Previous work has demonstrated that participants learn the walking task we are proposing through primarily explicit, or strategic, means and that this task does not provide a robust sensory prediction error for eliciting motor adaptation even when the bars are distorted (French et al., 2018; Wood et al., 2020). For these reasons, we replaced the adaptation component with a strategic learning process. The use-dependent plasticity component remains the same as in Diedrichsen et al. 2010.

2. Authors need to indicate more clearly what are the distinct predictions from these two models upon changes in the consistency of the task.

   We appreciate the reviewer's comment and have attempted to clarify the text in the suggested areas. Specifically, we have now added a sentence in the Introduction (lines 50 & 56-59) to make the specific model predictions relative to the current proposed study clear. To address R1's comments #17 and #18, we added similar clarifications to the Model-Based Methods section (lines 317-322) and the Statistical Analysis section (lines 333-335), respectively. We also added further explanation to the Simulation section (lines 492-493). The two competing model predictions will be tested by comparing the size of the use-dependent biases across conditions. The Adaptive Bayesian model predicts the bias that depend on the consistency of the Learning phase. Therefore, the model predicts a progressive reduction in bias from the Consistent condition to the High Variability condition. However, the Strategy plus Use-Dependent model predicts no significant differences in the bias between the three conditions.

3. This is not a good idea. The authors should overlay the kinetic and kinematic events to realize that they are not equivalent time points.

   We agree with the reviewer and now plan to perform event detection with kinematic markers only using the velocity-based tracking algorithm described in Zeni et al (2008). This method detects heel strike and toe off events using the velocity of kinematic tracking markers. We now plan to detect a heel strike when the heel marker velocity moves from positive to negative and a toe off when the toe marker velocity moves from negative to positive. We have removed references to kinetic data collection, post-processing, and analysis and modified the Proposed Analysis Pipeline section to include this velocity-based tracking method (lines 152-155).

4. Authors should consider reporting the asymmetry in leading and trailing legs. This will help the reader gain an insight on their use-dependent learning task. Many people have done this decomposition. As an example see Sanchez et al. 2020 Using asymmetry to your advantage: learning to acquire and accept external assistance during prolonged split-belt walking. doi: https://doi.org/10.1101/2020.04.04.025619

   We agree, and we have now added this analysis to our Proposed Analysis Pipeline section (lines 173-178). Based on the reviewer's suggestions, we now plan to provide this analysis and a related figure, so that the reader can gain a greater intuition regarding the use-dependent learning task. Although we are unable to perform this analysis for the pilot data because of the marker set we used, we will add markers for the bilateral greater trochanter and the bilateral lateral knees (lines 136-137) so we can accomplish this analysis once experimental data have been collected.

5. Consider defining SAI in terms of long and short step length to help the reader contrast the authors results to previous findings.

   This change has been made to equation 1 (line 161).

6. Authors should indicate that by design, the asymmetry is always positive.

   This has been added to the Proposed Analysis Pipeline section (lines 166-167).

7. Authors should zoom in the early part of the learning period for the reviewers to appreciate this. Also, authors should present the learning results under the different conditions during the early period to evaluate the extent to which the predictions from the model equally match the learning and washout periods.

We agree with the reviewer and have now added insets to Figure 3 for the initial Learning phase to demonstrate that the models do not make qualitatively distinct predictions for this phase. We added a description to the Figure 3 legend (line 620).

To address the second part of this comment, we have added stride-by-stride data to the Pilot Data Figure (Figure 4; please see our response to the main request for more details). To view individual data with the model fits and predictions, we have added a figure in this document (Supplemental Figure 1, below). This figure demonstrates the model fits to binned (bins of 3) individual data for the 2 participants who completed both conditions. We fit the models by concatenating each condition for one participant and fitting each model as described in the Statistical Analysis section (lines 335-337). This figure demonstrates that the models adequately describe the individual data during Learning and Washout for the Consistent and High Variability conditions (r^2 range 0.89 to 0.95). Furthermore, we added plots of the pilot data and model predictions for both our measurements of use-dependent bias in the same figure (note that the Initial Bias of Pilot Subject 2 – blue circle – is hidden behind the AB model prediction – purple diamond). We plan on creating a similar figure when we resubmit for a potential phase 2 report (lines 338-341).

Supplemental Figure 1:
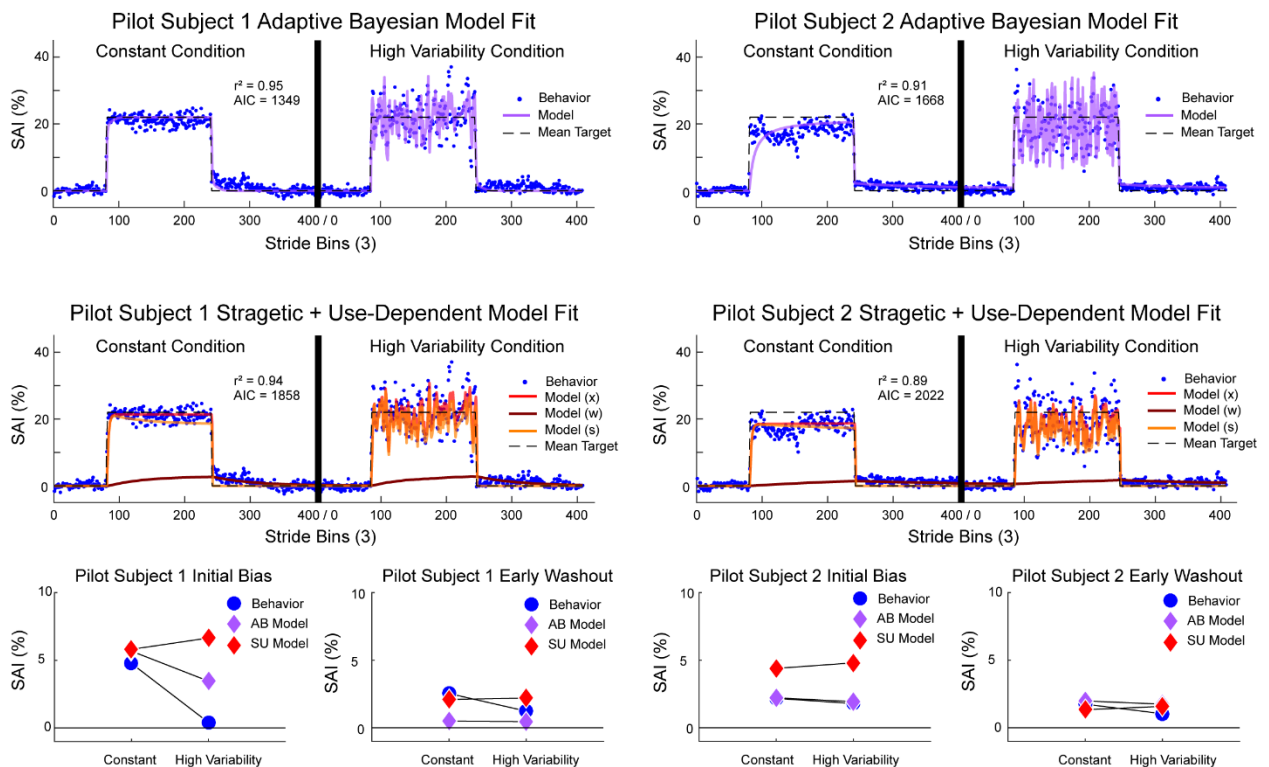
8. Authors should indicate explicitly that they are fitting one single set of parameters to the learning and washout periods.

   We have added this description to the Computational Models section of Statistical Analysis (lines 337-338).

9. Aren't errors and motor output directly related according to eq. 3? It is unclear why the authors indicate that the use-dependent component is not updated as a function of the error signal.

   We thank the reviewer for this comment and have now clarified this statement in the Model-Based methods section (lines 247-249). In the Strategy + Use-Dependent model, use-dependent learning depends on previous motor output and occurs in parallel to updates based on an error signal (Diedrichsen et al., 2010). The error signal directly drives strategic learning, and due to the interactions between strategic and use-dependent learning, impacts the use-dependent process. However, in the absence of an error signal (e.g., an individual chooses to walk asymmetrically without a specific goal or external target), the use-dependent learning process would still be active, given that it learns from previous motor output, regardless of whether the motor output changed due to an error signal or not.

   As the phenomenon we are trying to capture in the use-dependent process is the pure repetition effect absent any error, we chose to emphasize that component in the text. However, we see how the way we stated the unique features of the model could be improved and adjusted the Model-Based Methods section (lines 247-249) to address this comment. It now reads "...*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.*".

10. Unclear why authors chose a fixed sensitivity (learning rate F) to the update rule, given literature indicating that the update of motor memories depends on the consistency of the task. For example, see the work of Maurice Smith (Gonzalez-Castro LN*, Hadjiosif AM*, Hemphill MA & Smith MA (2014). Environmental Consistency Determines the Rate of Motor Adaptation. Current Biology 24, 1050-1061.) or Reza Shadmehr (Herzfeld and Shadmehr. A memory of Errors in Sensorimotr Learning 2014). While this literature focuses on adaptation processes, it is unclear why use-dependent plasticity won't be also affected by consistency in the "teaching" signal, in this case motor output.

   The reviewer raises an interesting point, one which we have addressed in the main text now in lines 262-263. With regard to the Strategy plus Use-Dependent model, we believe the lack of an extra sensitivity term in the use-dependent process is a core feature of the model and is why we have pit this model directly against the Adaptive Bayesian model, which is sensitive to consistency. The basis for a fixed learning rate comes directly from Diedrichsen et al 2010, where data from experiment 3 of their paper is particularly instructive. There, participants demonstrated a robust use-dependent bias in parallel with adaptation to a velocity-dependent force field (Fig. 3H). Because of the force field, movements were highly variable across the early trials, yet the use-dependent process demonstrated robust changes in response to the variable movement angles. Indeed, the use-dependent learning rate was not lower during this experiment than in the other two experiments from the paper, which induced use-dependent learning through more consistent movement patterns. While

this evidence is indirect, this suggests that under certain conditions, such as force field adaptation, use-dependent learning may not be sensitive to consistency. Of course, the work of Verstynen and Sabes presents a counter example under different task demands. Thus, we believe that this question of how sensitive use-dependent learning during walking is to the consistency of movement is best tackled directly and forms the primary motivation of our study and our choice of models.

11. Unclear stability of the model

   To obtain stable model parameters we bootstrapped parameter values from the acquired dataset 1000 times. We explain this fitting process, in the Simulations section (lines 475-477). Also, see Supplemental Figure 1 and our next response to comment #12.

12. This seems arbitrary. Authors should provide a better justification or sensitivity analysis.

   We appreciate the reviewer's comment and have provided a clearer justification in the Model-Based Methods section (lines 258-262) for why we chose this constraint and the empirical evidence for a slower use-dependent versus strategic learning rate (F and C, respectively). Briefly, humans can quickly adjust strategic aiming (Bond and Taylor, 2015; Haith et al., 2015; Morehead et al., 2015) and with appropriate instruction, even demonstrate "one trial learning" (Mazzoni and Krakauer 2006; Taylor and Ivry, 2011). Given that strategic aiming is much faster than implicit adaptation, which typically has estimated learning rates between 0.10-0.30, and that implicit adaptation is much faster than use-dependent learning (which is somewhere on the order of 0.05, as shown in Diedrichsen et al. 2010), we took a similar approach to parameter constraints as several papers in the field (e.g., Smith et al. 2006, Taylor and Ivry 2011, Roemmich et al. 2016) and reasoned that strategy must be many times faster than use-dependent learning. We also note that when we remove this constraint, the model fitting procedure produces similar parameter estimates and fits for binned data as with the constraint; however, the constraint provides the additional benefits of more rapid optimization and increased numerical stability.

13. Authors should reformulate this equation such that it only depends on the prior and likelihood variances. This will make it easier for the reader to relate to prior maximum likelihood frameworks such as the paper by Ernst and Banks (for example). More importantly, how is target location and motor output related?

   We have now reformulated equation 6 accordingly (line 277).

   In the Adaptive Bayesian model, we assume that the maximum a posteriori (MAP) represents the brain's estimate of the target location. We assume that the motor output is a direct readout of this estimate as in Verstynen and Sabes, 2011. We describe this assumption in the Model-Based Methods section (lines 273-275).

14. This is unclear.

   We have reformulated this equation in similar fashion to equation 6. We have also removed it from the main text so that it is featured in its own equation to improve clarity (now equation number 7; line 283).

15. Is the likelihood variance the same during the learning and washout period? If so, authors need to justify why given that the sensory information is quite distinct during these two experimental periods.

This is an excellent point. Yes, we assume the likelihood variances to be the same during Baseline, Learning and Washout. We have added a justification for this assumption in the main text (lines 287-290). To summarize, the likelihood function represents the sensory estimate of where to step, based on the visual target information provided during Learning. During Baseline and Washout, there is no visual target provided, instead, the "target" step length is the participants' normal baseline (a)symmetry. Although possible to fit two separate likelihoods to the different conditions, if we assume that sensory uncertainty around target step lengths is similar during both conditions, then it is more parsimonious to fit only one likelihood function. (We note here that if we had asked participants to do anything other than return to normal walking during Washout, we would want to fit separate likelihoods). Given that the target step length is their usual walking pattern, we believe this assumption is justified. Concretely, if the participants were able to see the baseline target lines on the screen during the Washout phase (without the feedback of their step lengths) we would not expect behavior to be different as compared to a condition in which the visual targets were not visible, nor would we expect the level of uncertainty about where to step to change.

16. Authors need to provide a rational for their proposed update rules for the prior distribution of the target step length

We have added a rationale for the adaptive priors in the Model-Based Methods section (lines 292-296). We now make clear that the adaptive priors express one way that the brain may adjust its belief about the consistency of the environment as more data (evidence) arrives—in other words, how the brain learns new priors. As empirical support for this view, Verstynen and Sabes 2011 showed that use-dependent learning is more accurately modeled using adaptive priors versus their normative Bayesian model in which prior variances were "hand-tuned" to match the target variance, an assumption the authors explicitly state as likely to be incorrect.

17. While authors explain in here the computational differences between the two hypothesis, the distinct predictions from each of these models need to be explained more explicitly.

Please see our response to R1 comment #2.

18. Authors need to indicate more clearly, what are the distinct predictions from the two models in this section.

Please see our response to R1 comment #2.

19. Authors should validate their models by contrasting the distinct predictions from each against empirical data. This will be more convincing than AIC.

We agree with the reviewer and now plan to contrast model predictions against empirical data by simulating use-dependent bias for each model with parameter values obtained from individual model fits. We will visualize the differences between each model prediction and empirical data in a figure once data are collected. This

figure will be similar to Supplemental Figure 1 we show in this document. This plot should bolster support for one model over the other. We have added a description of this proposed plot to lines 338-341. We will continue to use AIC to provide additional objective support for one model over the other (lines 343-344).

20. While this is ok for quantifying the fit of the data, authors should consider a different approach if they are truly interested in contrasting the two hypothesis that they present. In principle they have two contrasting theories that provide distinct predictions. Authors will presumable test these predictions experimentally. The results will match one theory better than the other. This will be more convincing for selecting the model that underlies use-dependent plasticity in locomotion, as opposed to AIC.

    Please see our response to R1 comment #19 above.

21. I might have missed this, but I did not see the rational for this expectation.

    We have bolstered our rationale in the Conditions section (lines 121-125) and the Proposed Analysis Pipeline section (lines 181-183). We believe changes to these areas will improve understanding when we discuss the analysis of the Learning phase in the Statistical Analysis section. To summarize, we state that the variability of SAI behavior during the Learning phase should change as a function of the target variability. More concretely, we expect behavior to follow the on-screen targets during Learning. If this is true, the mean SAI behavior for the entire Learning phase should be almost identical across all conditions (as the distributions of target location are centered around the same value across conditions), but the standard deviation of the SAI behavior measured for the entire Learning phase should be different across phases. Participants should demonstrate the smallest SAI standard deviation during the Constant condition, the second largest SAI standard deviation during the Low Variability condition and the largest SAI standard deviation during the High Variability condition. Validating that there are indeed different amounts of training consistency (centered around similar means) will allow us to confidently say that aftereffects either do or do not depend on that training consistency.

22. Revise. As of now it is unclear if Authors have done (or will) correct for multiple comparisons.

    We have revised to indicate that post-hoc comparisons will take place in the event of a reliable ANOVA (lines 358-360), and that we plan on correcting for multiple comparisons (lines 376-377).

23. Authors should submit their paper once they can validate their models. Even if this is a Stage 1 Registered Report, as of now, the study is not complete and does not add to the current theories of processes underlying use-dependent learning.

    We hope our additional analyses and previous responses have changed the reviewer's mind regarding the validity of our models. To the reviewer's points, we have provided more details in our explanation of model fitting to prior data in the Simulations section (lines 471-474). Specifically, we have now adjusted this sentence to read "Preliminary model parameters were obtained by fitting the models to walking data (n=16 participants) from [withheld due to double-blinding], which used a protocol most similar to the Constant condition that we currently propose". We plan on

replacing this placeholder with the citation to the study once the Stage 1 submission is accepted.

Regarding the completeness of the study, this is a Stage 1 Registered Report and we are proposing to collect experimental data to help determine which of our two models of use-dependent learning is more accurate. We have provided the results of fitting both models to previously collected data during a different walking paradigm in order to validate the rationale of pitting the two directly against each other. The proposed experiments, modeling, and analyses will serve as the discriminative test of the Adaptive Bayesian versus Strategy Plus Use-Dependent models.

24. This section is appropriate for a grant, not for a journal paper! Please revise.

If we understand correctly, based on their comment, the reviewer seems to be saying that it is inappropriate to include a Completed Work section in a journal article. We politely point out to the reviewer that this interpretation is inaccurate, however, because the journal's instructions for preparing a Registered Report includes instructions for how to format Completed Work. Specifically, instructions for stage 1 Registered Reports in eNeuro state that it is important to clearly delineate what has been completed and what has not. Indeed, the instructions state that failing to do so is one of the top 10 reasons for why stage 1 Registered Reports are rejected. Based on these instructions, we believe we should clearly state that we have performed simulations, model recovery analysis, and pilot testing, all of which are included in the submitted manuscript.

However, if we have misinterpreted this comment and, in the reviewer's mind, it is the section title that is inappropriate rather than the section itself, we are open to suggestions as to how to label this section.

25. Authors should consider removing this analysis. It is more convincing to observe distinct predictions from each model.

We appreciate the reviewer's comment and hope we have addressed the overall concern regarding model recovery analysis. Our rationale for including the model recovery analysis, in addition to the more direct analyses of our models' predictions, is to ensure that the models can indeed be differentiated under ideal circumstances (i.e. when the models themselves generated the data). It can also help determine which method of objective model comparison is best to use under specific circumstances (i.e. with these specific models and experimental paradigm). We have now adjusted the description of this section and also changed the name of the section to "Model Recovery" (lines 428-455).

26. Model fits implies that the parameters were fit to data. It is unclear if this was the case.

We have adjusted the phrasing in this section (lines 437 & 441-442) to make it clear that we are fitting models to *simulated* data, as suggested by Wilson and Collins (2019).

27. What "objective model comparisons"?

We now make clear in the revised manuscript that we were referring to AIC and BIC as possible objective model comparisons (lines 433-435 & 451-452).

28. Typo

   This typo has been removed.

29. Not always true. This statement is not substantiated.

   The reviewer is correct in their assertion that AIC is not always better than BIC. We now realize we should have been more direct about the point we were trying to make here and have adjusted our language accordingly (lines 433-435 & 452-455). We were attempting to communicate that we performed model recovery analysis with both AIC and BIC. In this specific instance, assessing this experiment with these two models, AIC did a better job than BIC of discriminating the models during model recovery analysis. We believe the adjustments made to this section now make this point clear.

30. This seems incorrect. While the authors have made the point regarding the slow dynamics of the use-dependent process in their S+U model, they fail to explain why the sensitivity to previous motor output (F parameter in eq. 5) will not be affected by variable targets.

   Please refer to our response to R1 comment #10.

31. Authors need to expand this explanation. What kind of data, how many samples, same protocol as this one or not, etc?

   We have now adjusted this sentence to read "Preliminary model parameters were obtained by fitting the models to walking data (n=16 participants) from [withheld due to double-blinding] which used a protocol most similar to the Constant condition that we currently propose." (lines 471-474). We plan on replacing this placeholder with the citation to the study, once the Stage 1 submission is accepted. We further plan to report the model fits to these data in a figure either in the main manuscript or supplemental material.

32. What about the aftereffects for these two conditions?

   We now provide the aftereffect data in Figure 4 and in Supplemental Figure 1. We added a description of the figure to the Pilot Data section (lines 503-505) and in the figure legend (lines 628-642).

33. While this is a stage 1 submission for a registered report in eNeuro, the manuscript is not ready for publication. I suggest that authors include preliminary data of the aftereffects. Since as of now, it is quite challenging to evaluate the merit of the proposed theories.

   As stated above, we now provide pilot data of the aftereffects. We believe that the changes we have made in response to the reviewer's requests and comments have substantially improved this Stage 1 Report, and we sincerely hope the reviewer now views it as acceptable for publication.

Reviewer #2:
This is a well written stage 1 registered report that proposes a design to test whether and how movement variability (here variability in step asymmetry) affects a form of use dependent locomotor learning. The paper largely relies on a behavioral paradigm that was described in a recent article by Wood et al. 2020 and two different computational models. The two models are shown to respond differently to increased variability-one is a use dependent model with a strategic component added on, and the other is a Bayesian model.

I have no major concerns about the hypothesis being tested-- it is interesting and timely. However, there are a few things that would be worth thinking through a bit more, or justifying a bit better, within the design.

We thank the reviewer for their encouraging words regarding our study and for their insightful comments.

1. The Wood et al. 2020 paradigm used a gradual introduction of a perturbation during learning and the experimental design proposed here uses an abrupt change during learning. These can result in different after-effects in other types of motor learning paradigms for walking (e.g. adaptation). Are there reasons to think that these types of perturbations would be equivalent in this use-dependent experiment? This may influence the power analysis since it is being done using gradual learning data and applied to abrupt conditions. It might not be a problem, but it seems worth thinking about.

    The reviewer brings up an important point. We were unclear in our original submission that, for the power analysis, the aftereffect magnitudes are based on the Washout phase from Wood et al. (2020), which was performed after a 5-minute abrupt (not gradual) learning phase (we have now changed this point in lines 407-408). Therefore, the power analysis was indeed based on a similar perturbation (abrupt). However, we appreciate the reviewer's point and would, in the future, like to explore this question of gradual versus abrupt perturbations, especially because gradual perturbations have even been used as a proxy for less repetition in upper extremity studies (Leow et al., 2016; Orban de Xivry et al., 2011; Orban de Xivry and Lefèvre, 2015). We suspect that the modeling results of the proposed study may shed some light on this question, albeit indirectly. For example, if variability does impact use-dependent bias, a gradual change in motor output, being less consistent, should then elicit reduced bias if the plateau phase is not sufficiently long.

2. I also assume that you switched to an abrupt change so that the model fitting would include both adaptation and de-adaptation. You state that you will model individual subject data, which is appropriate, but I am not clear why you will model all three conditions combined? Wouldn't it be a stronger test if you model one condition for each subject (e.g. the high variability condition where you expect the greatest differences) and then see how those model parameters apply to the other conditions? Can you clarify?

    We switched from a gradual to an abrupt change for two main reasons: The first is to maintain a high level of asymmetry for as long as possible to maximize our chance of observing reliable aftereffects. Second, we wanted to change the consistency of the task in only one way. For example, performing a gradual target change and increasing variability would make it difficult to determine if it was the gradual change or increased variability that caused differing aftereffects, unless we were to go to a full 2 x 3 perturbation matrix (gradual or abrupt versus 3 levels of variability). Based on the

primary research question—the effect of movement consistency on use-dependent learning—assessing all 6 conditions did not seem necessary.

With regard to why we are choosing to fit the models to all three conditions combined, your suggestion was one we had considered. However, we concluded that fitting all three conditions at once was best because we feared that fitting a reference condition could unduly privilege that condition. For instance, on one hand, we could argue that the High Variability condition is the most discriminative test of the two models and therefore fit that condition first; but one could alternatively argue that the Consistent condition is the most standard means to induce use-dependent learning of the three, and therefore, we should fit that condition first since it may induce the most use-dependent learning. Thus, in order to avoid a potential risk of bias, we decided to use the simultaneous fitting procedure. An additional benefit of this method is that it maximizes the chances for both models to minimize the error between model fit and data; as such, the results of comparing the models this way will, we believe, increase the robustness of our findings in support of one model over the other.

3. The use-dependent + strategic model seems to be based on the use-dependent model from the Diedrichsen et al. 2010 paper. Correct me if I am wrong, but it adds in an assumption about a strategic component that was not in the Diedrichsen paper-namely that there is a retention factor for the strategy that is assumed to be used from one stride to the next. I would like some more intuitive justification for the need for the strategy component and for fitting the A parameter. In walking, subjects may easily have time to modify the gait pattern online and hit a target, thus they might only need the C*en part of that equation. It would be nice to understand the basis for the A*sn component. It is not entirely intuitive. Perhaps it just biases the model in the direction of the abrupt perturbation? More explanation would be useful. Perhaps even a plot showing how the different components of the model change as a function of stride, which might help the reader intuit.

   The reviewer is correct regarding the changes we made to the model from Diedrichsen et al. We provide a detailed explanation in our response to R1 comment #1, and added to the Model-Based Methods section (lines 209-213). Briefly, the error-based learning component from Diedrichsen et al. is based on a force field adaptation task. This adaptation task is qualitatively different from the one we plan to use in the current study. Previous work has demonstrated that participants learn the walking task we are proposing through primarily explicit or strategic means and that this task does not provide a robust sensory prediction error to drive adaptation, even when the bars are distorted (French et al., 2018; Wood et al., 2020). For these reasons, we replaced the error-based learning component with a strategic component. The use-dependent learning component remains the same as in Diedrichsen et al. 2010.

   With regard to an intuition behind the different parameters, we have now included the Supplemental Figure 1 below to demonstrate the different processes fit to individuals from our pilot data. This figure shows how the component processes of the Strategy plus Use-Dependent model change on a stride-by-stride basis. The models are fit to binned (bins of 3) individual data for the 2 participants who completed both conditions. We fit the models by concatenating each condition for one participant and fitting each model as described in the Statistical Analysis section (lines 335-337). This figure demonstrates that the models provide good fits to the individual data during Learning and Washout for the Consistent and High Variability conditions (r^2 range

0.89 to 0.95). We also added plots of the pilot data and model predictions for both our measurements of aftereffects in the same figure (note that the Initial Bias of Pilot Subject 2 – blue circle – is hidden behind the AB model prediction – purple diamond). A similar figure is planned for a potential phase 2 submission (lines 338-341).

We have also added details of our description of the *A* term in the Model-Based Analysis section (lines 237-241). The *A* term represents the proportion of the prior strategy that is retained from one stride to the next. One justification for its inclusion is the assumption that participants remember a proportion of their explicit action selection. For example, when a participant aims for a target, they would remember the general area where they aimed previously. The fact that this retention factor is less than 1 indicates that the memory is not perfect, as it may be corrupted by noise or decay over time. In a previous model of strategic learning during reaching (Taylor and Ivry, 2011), the memory term was a core feature of the model and demonstrated sensitivity to the quality of visual feedback, something that we believe makes intuitive sense given our example of trying to remember where you last directed your step.

Supplemental Figure 1:
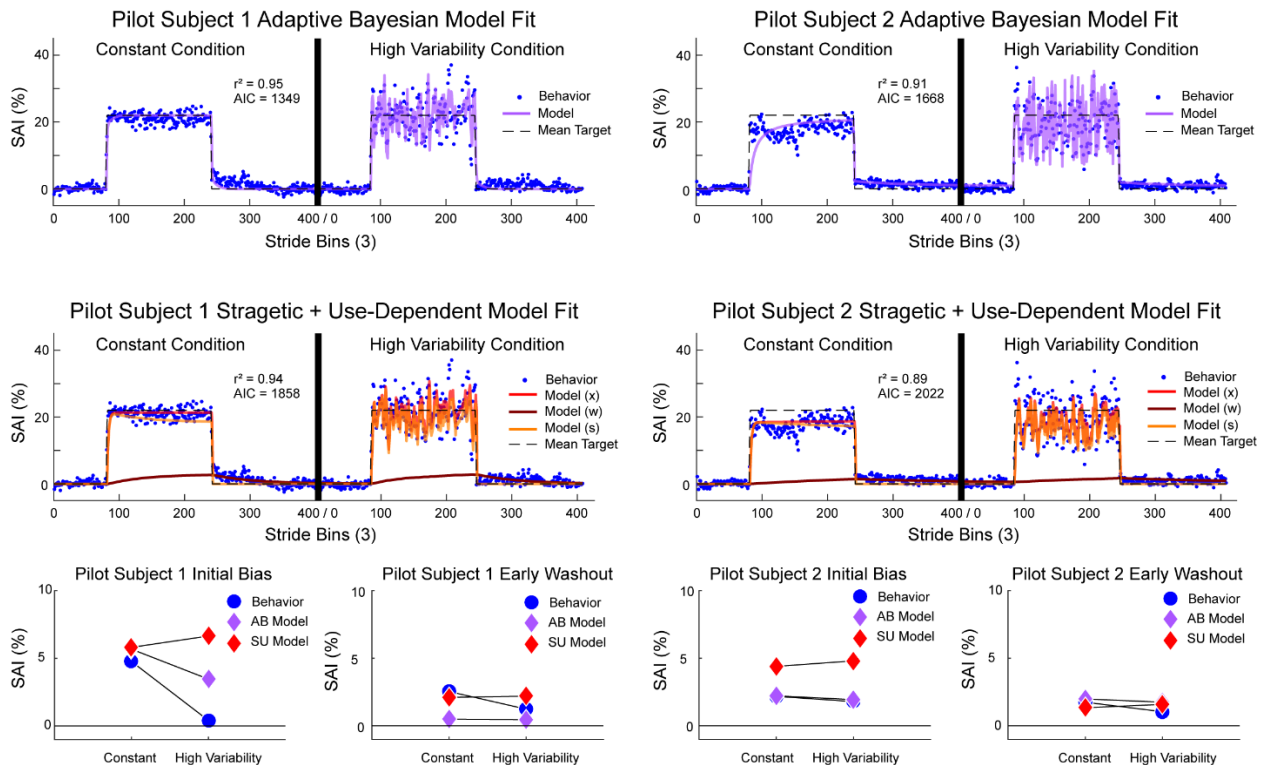
4. The simulations that you show have a high SD for the learning phase in the groups where variability was added. It makes me wonder what the individual fits might end up looking like? The fit relies so heavily on the learning portion of the data since it is nearly half the data for each condition. Do you have individual subject examples? Perhaps I am missing something?

We have now provided Supplemental Figure 1 to address this and previous reviewer comments (R1 comments #7 and R2 comment #3 above). To aid visualization (especially in the High Variability condition) as the reviewer suggested, Supplemental

Figure 1 includes stride-by-stride data of the pilot subjects who completed both conditions along with separate model fits. The reviewer is correct in noting the high SD during learning for the variable conditions. However, the new figure makes clear that the variability in Figure 3 is primarily due to the variability of target locations across strides, as each simulation has a unique target set drawn from the distributions for each of the respective conditions. Importantly, in Supplemental Figure 1 we can see that the models fit the data quite well across all conditions (r^2 range 0.89 to 0.95).