**Responses to Reviewers:**

Manuscript number: eN-RGR-0265-20

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

Date:

**We thank both reviewers for their helpful comments. 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 respect 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. We have truncated the data so that each phase (Baseline, Learning and Washout) is of equal length. 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 code (the condition changed from Highly Variability to Consistent towards the end of the Learning phase), which has since been fixed, and therefore we have included the data for this participant up to the point where the technical error occurred. We also include separate plots of the aftereffects for these individuals.**

**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 199-202). The original model from the Diedrichsen et al. 2010 paper combines two processes: use-dependent learning and error-based learning. The error-based learning component is based on a force field adaptation task. The force field adaptation task in Diedrichsen et al. 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 elicit 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 plasticity component remains the same as in Diedrichsen et al. 2010.**

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

**We thank the reviewer for this comment and have now added more clarity to the text in the suggested areas. We have now added a sentence in the introduction (lines 44-45, & 52) 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 283-284) and the statistical analysis section (lines 290-292), respectively. The two competing model predictions will be tested by comparing the size of the use-dependent aftereffects across conditions. The Adaptive Bayesian model predicts aftereffects that depend on the consistency of the Learning phase. Therefore, the model predicts a progressive reduction in aftereffects from the Consistent condition to the High Variability condition. However, the Strategy plus Use-Dependent model predicts no significant differences in the aftereffect between the three conditions.**

1. 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 (lines 129-130 & 145-150) and modified the Proposed analysis pipeline section (lines 144-145).**

1. 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 thank the reviewer for this suggestion, and we have now added this analysis to our Proposed analysis pipeline section (lines 150-153). Although we are unable to perform this analysis for the pilot data because of the marker set we used (see lines 133-134), we will add markers for the bilateral greater trochanter and the bilateral lateral knees (lines 133-134) so we can accomplish this analysis when we perform the experiment. We now plan to report this analysis so the reader can gain insight on the use-dependent learning task in a figure as the reviewer suggests.**

1. 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.**

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

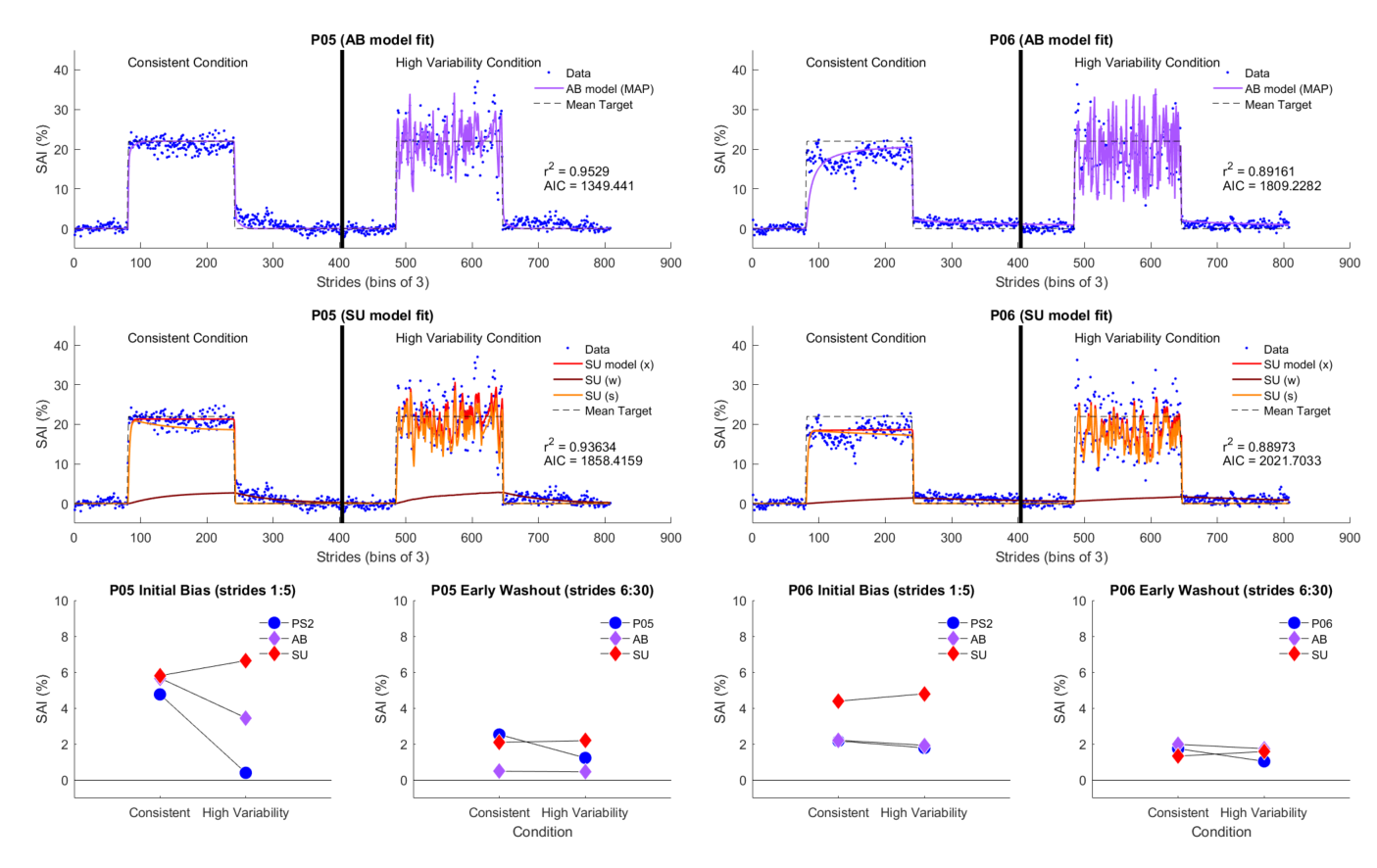
**This has been added to the Proposed analysis pipeline section (lines 165-166).**

1. 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 the simulations plot (Figure 3) for the initial Learning phase to demonstrate that the models do not make qualitatively distinct predictions for this phase.**

**To address the second part of this comment, we have added a 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 Model Based Methods (lines…). This figure demonstrates that the models adequately describe the individual data during Learning and Washout for the Consistent and High Variability conditions (R2 range 0.89 to 0.95). Furthermore, we added plots of the pilot data and model predictions for both our measurements of aftereffects in the same figure. We plan on reporting a similar figure when we resubmit for phase 2 (lines…).**

*Supplemental Figure 1*



1. 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 371-373).**

1. 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.

**This is an excellent point and the reviewer is correct with regard to how use-dependent learning is impacted by the error signal in the context of this study. We have now clarified this statement in the Model Based methods section (lines...). 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 was not clear and adjusted the Model Based Methods section (lines 233-234) to address this comment. It now reads “...the update is a function of the motor output which changes based on the error signal…”.**

1. 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 … 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 initially highly variability, 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, even though the other experiments 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 controversy over 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.**

1. 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 459-461). Also see the supplemental figure 1 and our response to comment #12**

1. 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 240-244) for why we chose this constraint and the empirical evidence for a slower use-dependent learning rate than strategic learning (F and C, respectively). Briefly, Taylor and Ivry (2011) showed that humans can quickly adjust strategic aiming and can reach learning rates that are even close to 1 (“one trial learning”). 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 (somewhere on the order of 0.05, as shown in Diedrichsen et al. 2010), we reasoned that strategy must be many times faster than use-dependent learning. Constraints are also used in models by Smith et al. 2006 and Roemmich et al. 2016 to describe the fast and slow adaptation processes. We also note that when we remove this constraint the model produces similar parameters without a reduction in fits with binned data.**

1. 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 have reformulated equation 6 accordingly (line 256). We also remove the equation for the posterior variance as this is now incorporated into equation 6.**

**In the Adaptive Bayesian model, we assume that the maximum a posteriori (MAP) estimate 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 253-255).**

1. This is unclear.

**Please see the first part of our response to R1 comment #13***.*

1. 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.

**Yes, and we have now added a justification for assuming the same variances in the main text. To summarize, the likelihood function represents the sensory estimate of where to step which is based on the visual target information provided during Learning. During washout, there is no visual target provided, instead, the “target” step length is the return to normal walking (i.e., baseline (a)symmetry). While it would be possible to fit two separate likelihoods to the different conditions, parsimony dictates that only one likelihood function is necessary if we assume that sensory uncertainty around target step lengths is similar during both conditions. (We note here that if we had asked participants to do anything other than return to normal walking during the 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. Put another way, 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. We have added further justification to the Model Based Methods section (lines 264-265).**

1. 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 265-266). 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, we cite Verstynen and Sabes 2011, where they show 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 not being correct.**

1. 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.**

1. 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.**

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

*We thank the reviewer for this suggestion. We now plan to visualize differences between the model predictions and empirical data for each individual participant (in a supplemental figure) and for our two aftereffect epochs (in a main figure). This plot will be similar to the supplemental figure we show in this document. This plot should provide support for one model compared to the other. We have added this a description of this plot to lines…*

1. 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.*

1. 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 119-122). There, we state that the variability of SAI behavior during the Learning phase should change as a function of the target variability. Put more simply, 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 similar across all conditions (as the mean target location is the same 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 least amount of SAI standard deviation during the Constant condition, the second highest amount of SAI standard deviation during the Low Variability condition and the highest amount of 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.*

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

*We have revised to indicate that we plan on correcting for multiple comparisons (lines 350-351).*

1. 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 have provided more detail in our explanation of model fitting to prior data in the Simulations section to demonstrate that fitting these data help validate the models. Specifically, we have now adjusted this sentence to read "**preliminary model parameters were obtained by fitting the models to data from [withheld due to double-blind reviewing]". We plan on replacing this placeholder with the citation to the study once the Stage 1 submission is accepted. We would also like to emphasize that these models were either borrowed (Verstynen and Sabes, 2011) or inspired (Diedrichsen et al, 2010) by previously published work demonstrating that these are valid models of use-dependent learning. We contend that once data are collected and the procedures and analysis we describe are completed as proposed, this study will add to current theories underlying use-dependent learning by providing a definitive account regarding the effect of task consistency on the use dependent process.*

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

*Our understanding of the instructions for stage 1 registered reports in eNeuro is that it is important to clearly delineate what has been completed and what has not. Indeed, the instructions state that this is one of the top 10 reasons why stage 1 registered reports are rejected. Therefore, we felt it important to include an entire section called Completed Work (rather than just, say, use past/future tense) because we have completed possibly more work than other registered reports. Based on the instructions, we felt that most registered reports might include only pilot data, but since we have performed simulations, model recovery analysis and pilot testing we wanted to clearly demonstrate to reviewers what has been completed and what has not.*

*If we are understanding the reviewer’s comments correctly, it is the section title that is inappropriate, rather than the section itself. We feel strongly that is important to include the section itself, but if the reviewer feels the title “Completed Work” is inappropriate we will remove the title.*

1. 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 testing distinct predictions in our responses to comment #’s 29-27. 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 in a given circumstance (i.e. with these specific models in this specific experimental paradigm). We have now adjusted the description of this section and also changed the name of the section to model recovery.*

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

*We thank the reviewer for this comment. We adjusted the phrasing in this section (lines 417 &422) to make sure it is clear that we are fitting models to simulated data as described in Wilson and Collins (2019).*

1. What "objective model comparisons"?

*Here, we were referring to AIC and BIC as possible objective model comparisons, but we realize this was not clear in the text. We are now more specific about what objective model comparisons we are using throughout this section.*

1. Typo

*This typo has been removed.*

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

*We thank the reviewer for addressing this point. The reviewer is correct regarding the fact the AIC is not always better than BIC. We were vague about the point we were trying to make here and have adjusted our language accordingly (lines …). We were attempting to communicate that we performed model recovery analysis with both AIC and BIC and in this specific case, with this specific experiment and these specific models, AIC distinguished the between models better than BIC. We believe the adjustments made to this section now communicate our point more clearly.*

1. 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.*

1. 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 data from [withheld due to double-blinding]..." 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.

1. What about the aftereffects for these two conditions?

*Please refer to our response to the main request.*

1. 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.

*Please refer to our response to the main request.*

**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.*

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 failed to mention 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. Therefore, we do not believe that the fact the first learning phase during Wood et al. was initiated gradually would affect the power analysis in the current proposed behavioral experiment.*

1. 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 thank the reviewer for this thoughtful comment. Switching from a gradual to an abrupt paradigm was mainly so that we could systematically vary the targets over a wide, but still achievable range of step asymmetries. A gradual Learning phase would constrain the amount of target variability we could provide. The learning of this paradigm is primarily strategic (see the response to R#1 comment 1) so observing the learning process itself (beyond the behavior following the targets reasonably well) is not our primary goal.*

*The reviewer also asks why we are choosing to fit the models to all three conditions combined rather than fitting the models to a ‘reference’ condition and then testing those parameters with the other condition. This thought had crossed our mind when considering the best way to fit the models to behavioral data. We decided to model all three conditions combined because we felt that choosing a condition as our reference condition would unduly favor that condition. Put differently, using one specific condition as our reference condition means we believe that the model fit to condition acts as a ‘gold standard’ for the use-dependent process. We do not want to assume that any one of these conditions reflects the use-dependent process better than any others. For example, the High Variability condition may not reflect a use-dependent process (if the Adaptive Bayesian hypothesis is correct). By fitting a model to this condition as our reference condition we believe we would be assuming this condition involves a use-dependent process. As a result, we decided to take an unbiased approach and determine which model fits all three conditions the best.*

1. 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 about the changes we made to the model from Diedrichsen et al., 2010. We explain this change further in our response to R#1 comment 1.*

*The reviewer also asks for clarity on the retention parameter of the strategic model. To address this concern, we have added clarification to these points in the Model Based Analysis section (lines 226-228) and we have included a figure in this response document to demonstrate the different processes fit with individuals from our pilot data. We now further describe the A\*sn term with more clarity. The A\*sn term represents the ability for the brain to remember or retain prior strategies, not just correct for errors. This is added because when a participant aims for a target, they would remember the general area where they aimed previously. This memory of the previous strategy is not perfect, so they remember only a portion of the previous strategy. The A parameter, specifically, retains a portion of the strategy from one trial to the next. This term has also been added to previous studies of upper extremity reaching studies to model strategy* (Taylor and Ivry, 2011)*.*

1. 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 thank the reviewer for this comment and have now provided a plot within the body of this response which we are calling supplementary figure 1 to address this and previous reviewer comments (R1 comments #7). First, we believe the variability in the simulations figure (Figure 3) likely represents the variation of targets performed on each iteration of the simulation. On each iteration of the simulation, there is a new set of random targets drawn from the distributions for each their respective conditions. That set of targets is used to simulate both models for that iteration. We believe this is why the variability in the simulation plot increase from the Consistent to the High Variability conditions. To ensure this is the case we provide supplementary figure 1, as the reviewer suggested, which includes stride by stride data of the pilot subjects who completed both conditions along with separate model fits for better visualization (especially in the High Variability condition). Here we can see that the models follow the data quite well and the there is greater variability in the model during the High Variability condition when compared with the Consistent Condition.*

*Supplementary figure 1:*

