In search of a common mechanism for motor savings: Experience-dependent changes in learning parameters during locomotor adaptation

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Faster relearning of the same perturbation when introduced again (i.e. savings) reflects the formation of a new motor memory. Initial attempts to model adaptation for an external perturbation were based on state space models composed of a fast and one or multiple slow processes[1,2]. However, these linear multiple-rate state space models could not explain savings that occur after a prolonged period of washout[3,4], and across days[5,6]. Instead, a recently non-linear state space model[4] and context-dependent models[2,7] were suggested to better explain a variety of phenomena reported in the motor adaptation literature, including savings. While evidence of savings has been accumulated from different systems and across paradigms, adaptation and savings was mainly modeled based on reaching adaptation results, and to the best of our knowledge, was never modeled for locomotor adaptation. The generalization of adaptation models which were constructed based on reaching experiments to locomotor adaptation is questionable, as the two behaviors differ greatly with respect to their neuronal substrates, the nature of the behavior, and the role of visual feedback. While locomotion is rhythmic and depends on central pattern generators located mainly in the spinal cord, reaching movements are discrete, guided by visual input and depend in cortical substrates. Commonalities between the computational components leading to adaptation and savings of reaching and locomotor adaptation may shed light on the neuronal and mechanistic basis of motor savings.

We investigate the computational basis of locomotor adaptation in two experiments; in the first, subjects adapted to speed perturbations during walking on a split-belt treadmill (Fig. 1A), briefly *deadapted* and then readapted (Fig 1C). In a second experiment, subjects readapted after a prolonged period of *washout* of initial adaptation (Fig. 1C). We compared the performance of a linear dual-rate state space model with state space models with changing parameters (Eq. 1), under the hypothesis that locomotor adaptation leads to changes in learning parameters that would last beyond the decay of the hidden state of the system. Furthermore, we explored the relationship between the initial and the readaptation phases, hypothesizing that the magnitude of savings will be proportional to the learning achieved during the initial exposure to adaptation. This was done by measuring of the inter-subject correlation of the slow and fast learning components that were fitted independently to the adaptation and readaptation phases. Our primary adaptation index was the Center of Pressure (COP) symmetry (Fig. 1B).

Firstly, we show that a linear state space model with multiple timescales is not sufficient to explain savings during locomotor adaptation. Instead, we show that locomotor adaptation leads to changes in learning parameters, so that even after a prolonged washout, learning rates are faster during readaptation (Fig. 2A-J, $p<0.05$). Still, the fact that learning parameters change through learning does not mean that they are independent; it could be that the changes in parameters are proportional to their initial values. We therefore investigated the dependency of error rates and learning parameters as seen in the inter-subject correlation patterns between adaptation and readaptation blocks. We found significant inter-subject correlation of the middle error rates- computed as the average of the COP symmetry on trials 2-30 in the adaptation and readaptation phases (Fig. 3A, $p<0.01$). We then moved to examining the correlation pattern of the estimated learning parameters and found that only the slow adaptation and fast readaptation learning parameters were significantly correlated in both experiments (Fig. 3B, $p<0.05$).

Our results suggest that savings in locomotion and reaching adaptation paradigms show similar properties, and thus may depend on common neuronal mechanisms. The fact that savings was proportional to the slow learning parameter during the adaptation period provides further evidence for the role of the slow learning process in the formation of new motor memories.

References

[1] Smith et al. PLoS Biol (2006); **[2]** Lee & Schweighofer, J Neurosci (2009); **[3]** Krakauer at al. J Neurosci (2005); **[4]** Zarahn et al. J Neurophysiology (2008); **[5]** Robinson et al. J Neurophysiology (2006); **[6]** Malone at al. J Neurosci (2011); **[7]** Ingram et al. PLoS Computational Biol (2011).

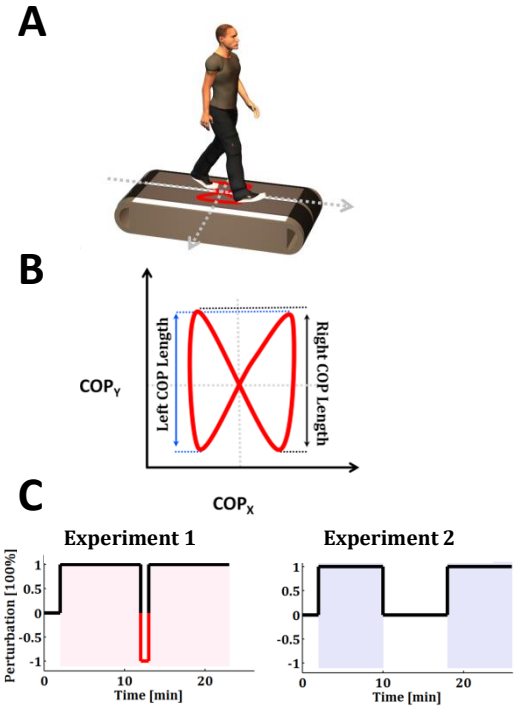

Figure 1: Experimental design and protocols. (A) Subjects walked on a split-belt treadmill with two separated belts. (B) Schematic example for one COP profile during one gait cycle. (C) Left panel: protocol of the *deadaptation* experiment: baseline (2 min), adaptation (10 min), deadaptation (30 sec) and readaptation (10 min). Right panel: protocol of the *washout* experiment 2: baseline (2 min), adaptation (8 min), washout (8 min) and readaptation (8 min).

Dual-rate varving parameter model:

Equation 1:

$$e(n) = D \cdot f(n) - y(n)$$

$$y(n) = x_f(n) + x_s(n)$$

$$x_f(n+1) = A_f(p) \cdot x_f(n) + B_f(p) \cdot e(n)$$

$$x_s(n+1) = A_s(p) \cdot x_s(n) + B_s(p) \cdot e(n)$$

$$A_f(p) < A_s(p) < 1,\ B_s(p) < B_f(p) < 1$$

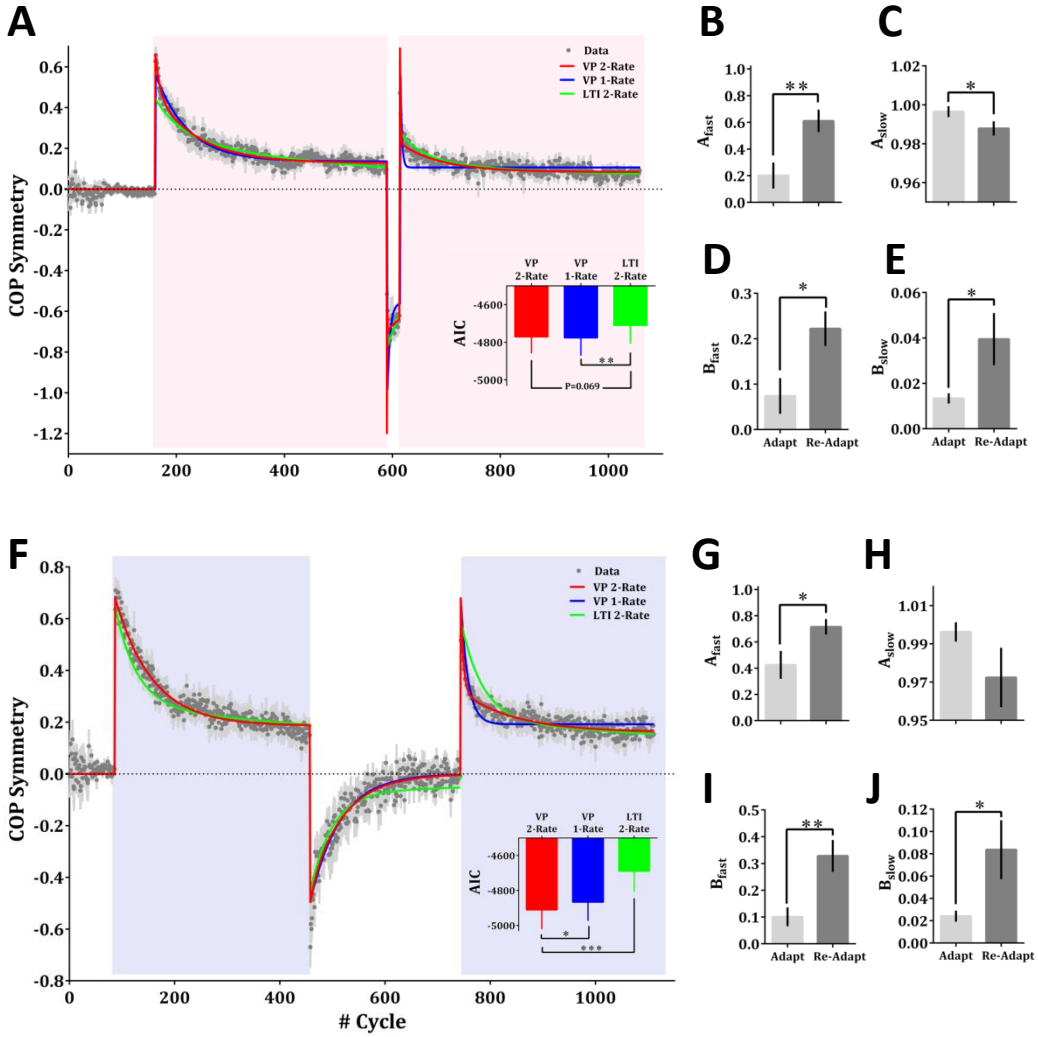

Figure 2: Group data and models predictions. (A) Across-subject averaged COP symmetry (gray points) of the *deadaptation* experiment. Color lines represent the fits of the SSM models: green line represents the prediction of the LTI dual-rate SSM, blue line represents the prediction of the varying parameters single-rate SSM and red line represents the prediction of the varying parameters dual-rate SSM. Inset shows the across-subject averaged Akaike Information Criterion (AIC) for each model. (B-E) Learning and forgetting rates averaged across subjects during adaptation (light gray bar) and readaptation (dark gray bar) of the varying parameter model the *deadaptation* experiment. (F) Across-subject averaged COP symmetry and models prediction for the *washout* experiment. Inset shows the across-subject averaged AIC for each model. (G-J) Learning and forgetting rates averaged across subjects during adaptation (light gray bar) and readaptation (dark gray bar) of the varying parameter model during *washout* experiment.

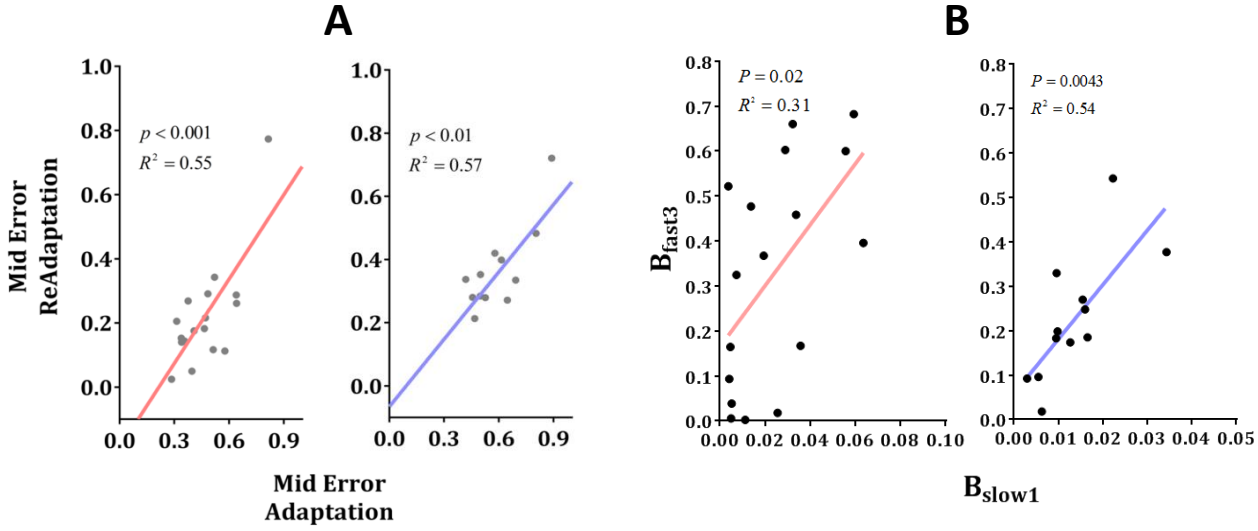

Figure 3: Inter-subject correlation. (A) Correlation of the middle error in adaptation and readaptation periods in the *deadaptation* (left) and *washout (right)* experiments. (B) Correlation of the slow learning parameter from adaptation period and the fast learning parameter from readaptation period during *deadaptation* (left) and *washout* (right) experiments.