Mapping the Influence of Spatiotemporal Asymmetries on Energetic Cost and Reactive Balance during Walking

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Introduction

The hypothesis that the nervous system optimizes energetic cost during walking has long been supported by computational models and numerous behavioral studies [1]–[3]. However, there remains some disagreement about whether this process naturally occurs when people perform short-term adaptations to walking in novel environments. Recently, a number of groups have sought to better understand the factors driving adaptation by exploring how people adjust to walking on a split-belt treadmill. In this paradigm, participants walk on a treadmill with two separate belts which can be independently controlled to move at different speeds. When exposed to this asymmetry in belt speeds, participants initially walk with longer steps on the slow belt and shorter steps on the fast belt. However, over the course of multiple minutes, this asymmetry is reduced until the difference between step lengths converges toward zero. Although the acquisition of a symmetric walking pattern occurs simultaneously with a reduction in metabolic cost and muscle activity [4], it remains to be seen if symmetry is truly the energetically optimal strategy for split-belt walking. An alternative hypothesis that has yet to be explored is that the acquisition of a symmetric walking pattern may be driven by a desire to enhance stability.

Methods

Here, we present a set of behavioral experiments aimed at characterizing how energetics and stability are influenced by spatiotemporal asymmetries during walking. First, we asked whether walking with equal step lengths is the energetically optimal strategy for walking on a split-belt treadmill. To address this question, we used a biofeedback approach to map the landscape relating step length asymmetry to metabolic cost while participants walked on a split-belt treadmill with a belt speed ratio of 3:1. Second, we tested the feasibility of characterizing how step length asymmetry influences the reactive control of balance during normal walking. In each experiment, participants were instructed to walk while matching their step lengths to visual targets (Figure 1). Target levels of step length asymmetry equal to 0%, +/- 5%, +/- 10%, and +/-15%, were used to span the range of feasible behaviors on the treadmill. Positive asymmetries correspond to longer steps on the fast belt. During the first experiment, energetic cost was assessed through measures of oxygen consumption

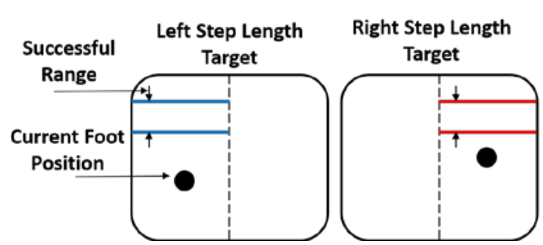

Figure 1: Schematic of visual feedback of actual and desired foot position for a left and right step.

and carbon dioxide production. For the second experiment, reactive control of balance was assessed by analyzing the effects of treadmill perturbations on the time course of changes in step length asymmetry and whole-body angular momentum. Perturbations were applied to each belt independently and were triggered to occur at foot-strike.

Experimental Results

For the first experiment, we expected that the step length asymmetry associated with the minimum metabolic cost would be normally distributed around zero, consistent with symmetry being the energetically optimal solution for walking on a split-belt treadmill. However, we rejected the null hypothesis that the distribution's median was equal to zero (p=0.016). Instead, we found that the distribution of step length asymmetries associated with the minimum metabolic cost was biased towards positive values with a median of approximately 5%. This suggests that moderately positive asymmetries, which are not typically observed during locomotor adaptation are frequently the most economical strategy.

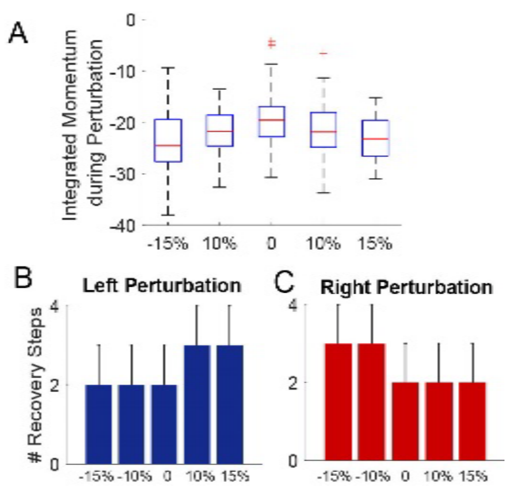

Figure 2: Step length asymmetries impair reactive balance control.

In the second experiment, we found that perturbation recovery strategies were systematically influenced by the level of step length asymmetry. As the magnitude of asymmetry increased, there was a systematic increase in whole body rotation (Figure 2A) indicating that spatiotemporal asymmetries increase the susceptibility to a loss of balance. Analysis of the multistep recovery strategies revealed that large positive and negative asymmetries also increased the number of recovery steps for left and right perturbations, respectively (Figure 2B & C).

Overall, these results refute the hypothesis that adaptation to walking on a split-belt treadmill is solely driven by energetic optimization. Symmetry may, instead, be selected during adaptation as a strategy to maximize stability. Our preliminary results suggest that asymmetry is detrimental to balance control during locomotion on a standard treadmill, but it remains to be seen how reactive balance control is regulated in the context of split-belt walking.

References

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