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Large Propulsion Demands Increase Locomotor Adaptation at the Expense of Step Length Symmetry

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There is an interest to identify factors facilitating locomotor adaptation induced by split-belt walking (i.e., legs moving at different speeds) because of its clinical potential. We hypothesized that augmenting braking forces, rather than propulsion forces, experienced at the feet would increase locomotor adaptation during and after split-belt walking. To test this, forces were modulated during split-belt walking with distinct slopes: incline (larger propulsion than braking), decline (larger braking than propulsion), and flat (similar propulsion and braking). Step length asymmetry was compared between groups because it is a clinically relevant measure robustly adapted on split-belt treadmills. Unexpectedly, the group with larger propulsion demands (i.e., the incline group) changed their gait the most during adaptation, reached their final adapted state more quickly, and had larger after-effects when the split-belt perturbation was removed. We also found that subjects who experienced larger disruptions of propulsion forces in early adaptation exhibited greater after-effects, which further highlights the catalytic role of propulsion forces on locomotor adaptation. The relevance of mechanical demands on shaping our movements was also indicated by the steady state split-belt behavior, during which each group recovered their baseline leg orientation to meet leg-specific force demands at the expense of step length symmetry. Notably, the flat group was nearly symmetric, whereas the incline and decline group overshot and undershot step length symmetry, respectively. Taken together, our results indicate that forces propelling the body facilitate gait changes during and after split-belt walking. Therefore, the particular propulsion demands to walk on a split-belt treadmill might explain the gait symmetry improvements in hemiparetic gait following split-belt training.

Keywords: human, split-belt locomotion, motor adaptation, kinetics, kinematic, gait, walking

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INTRODUCTION

There is an interest in increasing the extent of locomotor adaptation induced by split-belt walking because repeated exposure to this task can lead to gait improvements post-stroke. Notably, promising studies have shown that walking with the legs moving at different speeds (i.e., split-belt walking) results in long-lasting reduction of step length asymmetry post-stroke when walking overground (Reisman et al., 2013; Betschart et al., 2018; Lewek et al., 2018). This is important for gait rehabilitation post-stroke because step length asymmetry can lead to other comorbidities such as musculoskeletal injuries (Jørgensen et al., 2000) and joint pain (Patterson et al., 2012).

While split-belt walking could be beneficial, it is not effective in all stroke individuals (Reisman et al., 2013; Lewek et al., 2014) and it is still unclear why some stroke survivors re-learn to walk symmetrically but others do not. Thus, it is fundamental to identify factors contributing to split-belt adaptation so that we can manipulate them to facilitate motor corrections in all individuals.

The increased mechanical work (Selgrade et al., 2017), step length asymmetry (Reisman et al., 2005), and hence metabolic effort (Finley et al., 2013), upon introducing the split-belt environment are thought to drive locomotor adaptation. Notably, these three factors are large during the initial steps of split-belt walking and are minimized as subjects learn to walk in the split-belt context (Finley et al., 2013; Selgrade et al., 2017). Thus, modulating anterior–posterior forces applied at the feet during split-belt walking could facilitate locomotor adaptation given their direct impact on mechanical work and step lengths in regular gait (Donelan et al., 2002). In particular, we hypothesized that altering braking forces could modulate the adaptation of gait based on prior studies showing that braking forces are tightly regulated during split-belt walking (Ogawa et al., 2014). Notably, braking forces are suddenly disrupted when the split-belt perturbation is introduced and this perturbation is reduced as subjects adapt their gait. Thus, we proposed that braking forces could facilitate subject-specific locomotor adaptation and therefore, increasing these forces would augment the extent of gait changes during and after this task (i.e., after-effects).

To test this hypothesis, we assessed subjects' gait before, during, and after split-belt walking at different inclinations, which naturally and distinctively modulated the braking and propulsion forces experienced at the feet (Lay et al., 2006, 2007). We found that inclination increased locomotor adaptation and after-effects as hypothesized, but not through the proposed mechanism. While the braking and propulsion forces were adapted and exhibited after-effects, it was the propulsion forces that augmented the gait changes during and after split-belt walking. Specifically, decline walking, which accentuated braking forces, did not lead to as much adaptation of step length asymmetry as incline walking, which augmented propulsion forces. In addition, propulsion forces during baseline and early adaptation were highly predictive of step length after-effects at an individual level. Interestingly, each inclination group recovered their baseline leg orientation to meet force demands at the expense of step length symmetry, which was surprising given the consistent human tendency to self-select symmetric step lengths in the split-belt environment (Yokoyama et al., 2018). Taken together, our findings suggest that propulsion demands, rather than braking ones, facilitate locomotor adaptation and after-effects induced by split-belt walking.

MATERIALS AND METHODS

We investigated the effect of modulating anterior–posterior forces applied at the feet on gait adaptation during and after split-belt walking under distinct slopes (i.e., flat, decline, and incline), which naturally altered braking and propulsion forces (Lay et al., 2006, 2007). To this end, we evaluated the kinetic and kinematic adaptation and after-effects of 24 young healthy subjects (12 men and 12 women, 24 ± 4.9 years of age) randomly assigned to one of three groups experiencing the split-belt adaptation protocol in a flat, incline, or decline configuration ($n = 8$ each). Written and informed consent was obtained from all participants prior to participation. The University of Pittsburgh Institutional Review Board approved the experimental protocol, which conformed to the standards set by the Declaration of Helsinki, except for registration in a database.

General Paradigm

All subjects experienced the same split-belt paradigm illustrated in Figure 1A. Only the inclination at which subjects walked was altered across groups to determine the role of anterior–posterior ground reaction forces on the adaptation and after-effects of kinetic and kinematic gait features. We specifically tested subjects at three inclinations: flat (0°), incline (8.5°), or decline (−8.5°). These slopes were selected based on previous studies investigating walking on inclined surfaces (e.g., Lay et al., 2006) and because greater inclinations were too strenuous for split-belt walking, as assessed in pilot studies. Subjects from each group walked at the specified inclination throughout the experiment, including baseline and post-adaptation. Baseline: Subjects first experienced a baseline epoch to characterize their gait at the specific inclination at which they were going to walk throughout the study. During the baseline epoch, subjects walked with the belts moving at the same speeds (i.e., tied condition). Belts moved either at a slow (0.5 m/s), fast (1.5 m/s), and medium (1 m/s) speeds for at least 50 strides. Strides were counted in real-time using raw kinetic data. A stride was defined as the period between two consecutive heel strikes (i.e., foot landing) of the same leg. Adaptation: The adaptation epoch was used to assess subjects' ability to adjust their locomotor pattern in response to a split-belt perturbation. During this period, one leg moved three times faster than the other (0.5 and 1.5 m/s) for 600 strides (~10 min), except for one subject in the decline group who experienced the adaptation condition for 907 strides (due to technical difficulties in heel strike detection). This subject was not excluded from the analysis given that this participant's behavior did not differ from that of other subjects and its inclusion or exclusion did not alter our conclusions. The leg walking fast was the dominant leg, which was determined as the self-reported leg used to kick a ball. Post-adaptation: This epoch was used to assess the after-effects when the split-belt condition was removed. Subjects experienced tied walking at the medium speed (1 m/s) for 600 strides at their group-specific slope. The speeds for the adaptation and post-adaptation periods were chosen based on other studies in young subjects (e.g., Reisman et al., 2005) so that the fast speed in the 3:1 belt ratio was not at the walk-to-run speed transition for any participant. The duration of the adaptation and post-adaptation period was comparable to studies in healthy and clinical populations (e.g., Reisman et al., 2009) to ensure that all individuals had enough exposure to the split condition and could complete the entire protocol at all inclinations. In addition, subjects in all groups where given resting breaks every

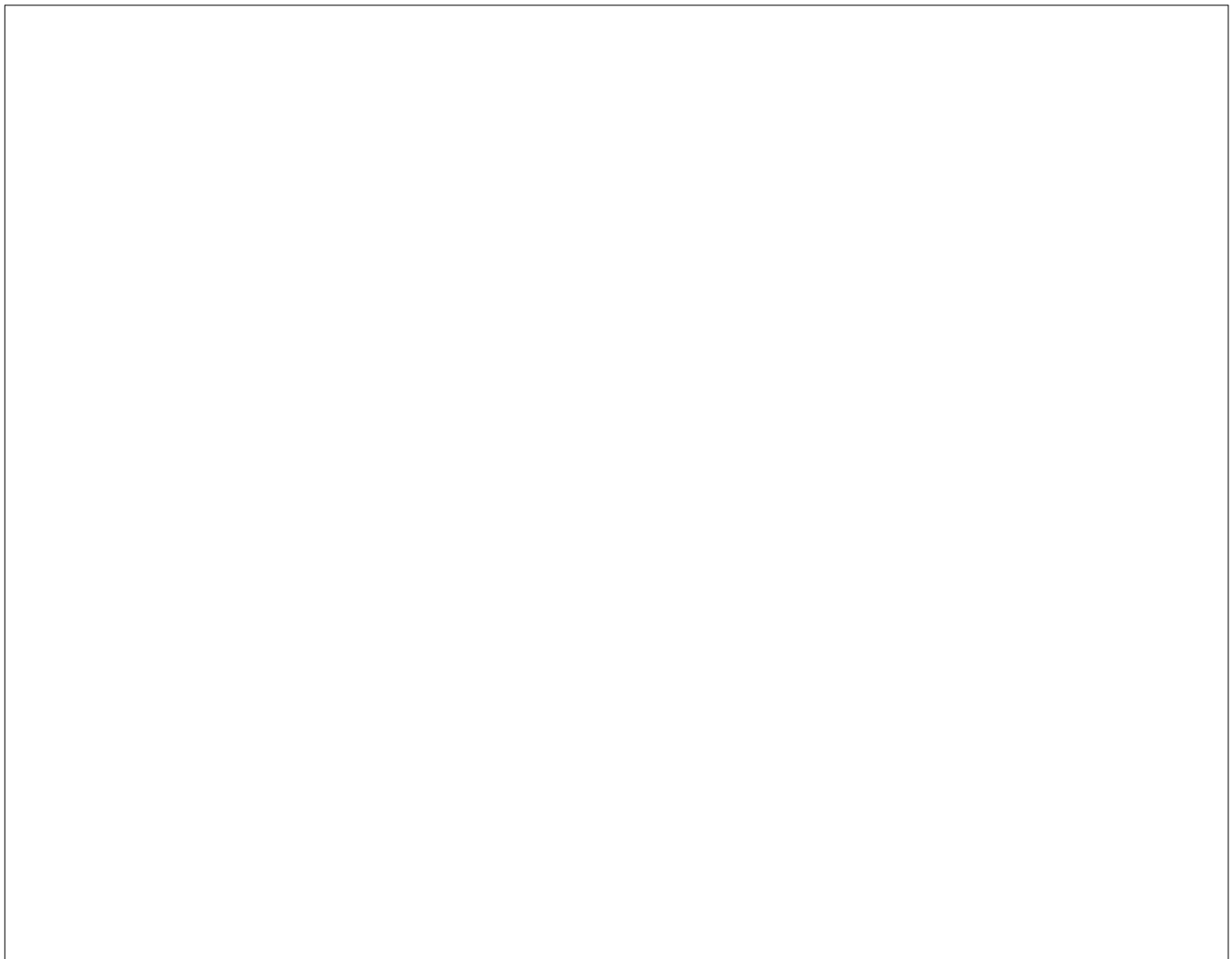

FIGURE 1 | Experimental Paradigm and Kinetic and Kinematic Analysis. (A) Paradigm used for all sloped conditions to assess locomotor adaptation during and after split-belt walking. Subjects from each group walked either incline (8.5), at, or decline (–8.5) throughout the experiment, including baseline and post-adaptation. All groups experienced the same number of strides per epoch (baseline: between 50 and 150, adaptation: 600, post-adaptation: 600). Dashed lines indicate when the resting breaks occurred.(B) The decomposition of step length into leading ( ) and trailing ( ) leg positions with respect to the body is illustrated for each sloped condition. This decomposition was done because it is known that inclination affects these aspects of step length differently (Leroux et al., 2002; Dewolf et al., 2017, 2018). Also note that when taking a step, the step length will depend on the position of the leading and trailing leg, which are generating a braking and propulsion force, respectively.(C) We used the peak braking and peak propulsion force for each step to compute outcome measures of interest, such as the Adapt measure. This measure was computed to quantify increments or reductions in magnitude within the adaptation epoch of each speci c parameter. Note that increases in magnitude were de ned as positive changes, whereas decreases in magnitude were de ned as negative changes.

200 strides during the adaptation and post-adaptation epochs to prevent fatigue.

Data Collection

Kinematic and kinetic data were used to characterize subjects' ability to adapt their gait during adaptation, and maintain the learned motor pattern during post-adaptation. Kinematic Data: Kinematic data were collected with a passive motion analysis system at 100 Hz (Vicon Motion Systems, Oxford, United Kingdom). Subjects' behavior was characterized with passive re ective markers placed symmetrically on the ankles (i.e., lateral malleolus) and hips (i.e., greater trochanter) and asymmetrically on shanks and thighs (to di erentiate the legs). The origin of the kinematic data was rotated with the treadmill in the incline and decline conditions such that the axis (`vertical' in the at condition) was always orthogonal to the surface of the treadmill (Figure 1B). Gaps in raw kinematic data were lled with a quintic spline interpolation (Woltring; Vicon Nexus Software, Oxford, United Kingdom). Kinetic Data: Kinetic data were collected with an instrumented split-belt treadmill at 1,000 Hz (Bertec, Columbus, OH, United States). Force plates were zeroed prior to each testing session so that each force plate's weight did not a ect the kinetic measurements. In addition, the reference frame was rotated at the inclination of each speci c experiment such that the anterior–posterior forces were aligned with the surface on which the subject walked. A heel strike was identi ed