Video Article

Using a Split-belt Treadmill to Evaluate Generalization of Human Locomotor Adaptation

Erin V.L. Vasudevan[1,2], Rami J. Hamzey[1,2], Eileen M. Kirk[2]

[1]Physical Therapy, School of Health Technology and Management, Stony Brook University

[2]Motor Learning Lab, Moss Rehabilitation Research Institute, Einstein Healthcare Network

Correspondence to: Erin V.L. Vasudevan at erin.vasudevan@stonybrook.edu

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Abstract

Understanding the mechanisms underlying locomotor learning helps researchers and clinicians optimize gait retraining as part of motor rehabilitation. However, studying human locomotor learning can be challenging. During infancy and childhood, the neuromuscular system is quite immature, and it is unlikely that locomotor learning during early stages of development is governed by the same mechanisms as in adulthood. By the time humans reach maturity, they are so proficient at walking that it is difficult to come up with a sufficiently novel task to study *de novo* locomotor learning. The split-belt treadmill, which has two belts that can drive each leg at a different speed, enables the study of both short- (*i.e.*, immediate) and long-term (*i.e.*, over minutes-days; a form of motor learning) gait modifications in response to a novel change in the walking environment. Individuals can easily be screened for previous exposure to the split-belt treadmill, thus ensuring that all experimental participants have no (or equivalent) prior experience. This paper describes a typical split-belt treadmill adaptation protocol that incorporates testing methods to quantify locomotor learning and generalization of this learning to other walking contexts. A discussion of important considerations for designing split-belt treadmill experiments follows, including factors like treadmill belt speeds, rest breaks, and distractors. Additionally, potential but understudied confounding variables (*e.g.*, arm movements, prior experience) are considered in the discussion.

Video Link

The video component of this article can be found at https://www.jove.com/video/55424/

Introduction

A split-belt treadmill has two belts that can drive each leg at a different speed or in a different direction. This device was first used over 45 years ago as a tool to study coordination between the legs (*i.e.*, interlimb coordination) during walking[1]. This, and other early studies primarily used cats as an experimental model[1,2,3], but insects were also studied[4]. The first investigations of split-belt locomotion in human infants and adults were published in 1987 and 1994, respectively[5,6]. These initial studies in both human and non-human animals mostly investigated short-term (*i.e.*, immediate) adjustments in interlimb coordination to preserve stability and forward progression when the legs are driven at different speeds. A 1995 study noted that longer periods (several minutes) of split-belt walking impaired the ability of human adults to accurately perceive treadmill belt speed and make adjustments to equalize speeds on each side. This suggests that the sensorimotor mapping of walking had been recalibrated[7]. However, it was not until 2005 that the first detailed kinematic report of human motor adaptation over 10 minutes of split-belt treadmill walking was published[8].

Motor adaptation refers to an error-driven process during which sensorimotor mappings of well-learned movements are adjusted in response to a new, predictable demand[9]. It is a form of motor learning that occurs over an extended practice period (minutes to hours) and results in after-effects, which are changes in the movement pattern when the demand is removed and/or conditions return to normal. For example, walking on split-belts initially causes people to walk with asymmetric interlimb coordination, resembling a limp. Over several minutes of split-belt walking, people adapt their walking coordination so that their gait becomes more symmetric. When the two belts subsequently return to the same speed (*i.e.* tied-belts), thus restoring normal walking conditions, people demonstrate after-effects by walking with asymmetric coordination. These after-effects must be actively de-adapted or unlearned over several minutes of tied-belt walking before normal walking coordination is restored[8].

Following the 2005 Reisman *et al.*[8] kinematic analysis of split belt walking in humans, use of the split-belt treadmill in published research has increased approximately ten-fold compared to the previous decade. Why is the split-belt treadmill becoming more popular as an experimental tool? Split-belt ambulation is clearly a laboratory task – the closest real-world analog is turning or walking in a tight circle, but the split-belt treadmill induces a much more extreme version of turning, with one leg being driven two- to four-times faster than the other. The fact that the split-belt treadmill is a highly unusual walking task offers several advantages for studying locomotor learning. First, it is novel for most people regardless of age and independent of walking experience; it is easy to screen experimental participants for novelty of split-belt walking. Second, the split-belt treadmill induces sizeable changes in interlimb coordination that are not quickly resolved. The relatively slow rates of adaptation and de-adaptation permit us to study how different training interventions can alter these rates without approaching a ceiling. Third, the kinematic[8,10],

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kinetic[11,12,13,14], electromyographic[6,15,16], and perceptual[7,17,18,19] modifications that occur with split-belt treadmill adaptation have been well-studied, as has the neural control of this task[20,21,22]. In other words, adaptations to the split-belt treadmill have been documented and replicated by several different groups, making this a well-characterized locomotor learning task.

Over the past ten years, several studies have demonstrated the task- and context-specific nature of split-belt adaptation. After-effects following split-belt adaptation are significantly reduced in amplitude if they are tested under different conditions from the training condition. For example, after-effects are smaller if the person is moved to a different environment (*e.g.*, over ground walking[23]), performs a different locomotor task (*e.g.*, backward walking or running[13,24]), or even walks at a speed that differs from the speed of the slower belt during adaptation[25]. Efforts to establish parameters governing the generalization of locomotor adaptation are ongoing.

The objective of this paper is to describe a protocol for using the split-belt treadmill to investigate human locomotor adaptation and generalization of the adapted pattern to other walking contexts (*i.e.*, different walking speeds and environments). While the protocol described here is most directly derived from that used in Hamzey *et al.*[25] (**Figure 1a**), it should be noted that this protocol was informed by a number of studies that preceded it[8,23,24,26,27,28]. The method was originally developed to test the hypothesis that maintaining constancy in walking speed between the treadmill and over ground environments would improve generalization of split-belt walking across these different environments[25]. In the protocol section below, we give instructions on how to replicate this version of the split-belt treadmill method, with notes that indicate how certain protocol steps may be modified to for different method purposes.

Protocol

All procedures have been approved by the Institutional Review Board at Stony Brook University.

1. Experimental Set-up

Note: Refer to **Supplementary File 1-Definitions** for definitions of common terms used in split-belt treadmill experiments.

1. Screen all participants for prior experience with the split-belt treadmill.
   NOTE: People have been shown to readapt faster to the split-belt treadmill following a prior exposure to it[29,30]. The timescale over which people "forget" the split-belt treadmill is not presently known; thus, prior experience with the split-belt treadmill may be a confounding variable if it is not controlled.
2. Conduct all testing in a quiet environment, and minimize activity in the testing room.
3. Set up a motion tracking system (according to system instructions) to record movement on a split-belt treadmill and on an over ground walkway.
   NOTE: For example, the current protocol used a motion tracking system with active LED markers. Four tripod-mounted sensor units detected the three-dimensional position of the active markers, with two units placed on either side (right and left) of the treadmill and two on either side of a 7 m over ground walkway.
4. Outfit the participant with motion tracking markers, electromyography, *etc*.
5. Consider including a partition between the two belts of the split-belt treadmill to prevent the legs from crossing over to the contralateral belt. This partition is not strictly necessary for neurologically-intact adults but may be helpful for testing children or clinical populations. Note that the presence of a partition likely increases step width; however, the extent to which this affects split-belt adaptation is unknown.
6. Set up a safety harness over the treadmill to protect the participant from falling during treadmill walking.
   NOTE: The harness should not support body weight, unless this is part of the research question. Although falling during treadmill walking is exceedingly rare, many research ethics boards require safety harness use.
7. Maintain consistency in arm movement across the experimental paradigm and across participants. When deciding on the type of arm movement (*e.g.*, holding handrails, swinging arms naturally), consider what will be comfortable for the subject group and whether typical arm swing will obscure the visibility of critical markers used for motion capture (*e.g.*, for markers placed on the hips).
   1. Regardless of arm movement, instruct all participants to hold handrails while starting and stopping the treadmill for safety.
8. Maintain consistency in incline across the experimental paradigm.
   NOTE: To our knowledge, all published split-belt treadmill protocols, including the current one, have used zero incline for treadmill and over ground walking.

2. Baseline Period

Note: The purpose of the baseline period is to establish what normal walking coordination is for each person. Baseline coordination should be tested in all the conditions in which after-effects are tested. For example, in the current protocol, after-effects were tested during treadmill and over ground walking at different speeds (0.7 and 1.4 m/s). Therefore, baseline over ground and treadmill trials at 0.7 and 1.4 m/s were included. This allows a direct comparison of after-effects to baseline walking coordination at the same speed and context. Over ground walking baseline trials can be eliminated when the experimental objectives do not include generalization to over ground walking.

1. For over ground baseline trials, instruct the participant to walk over the ground on a walkway where motion capture data can be collected. Collect a minimum of 10 stride cycles to establish the baseline over ground walking.
   1. If the motion capture system only allows for motion capture within a limited space, have the participant perform several passes (*e.g.*, trials) through the motion capture space. At the end of each trial, instruct the participant to stop, turn in place, and prepare for the researcher's cue to begin the next trial.
   2. For each trial, ensure that at least two stride cycles are performed within the motion capture space, not including the first and last stride cycles.

NOTE: These initial and final stride cycles will be discarded from analysis as they are acceleration/deceleration strides, not steady-state walking.

3. Have the participants perform several (typically 10) over ground walking trials.
    1. If a specific speed is desired, have the participant walk at that speed on the treadmill (on tied-belts) to familiarize him/her with the task. Then, move back to the walkway, instruct the participant to walk at the same speed as he/she did on the treadmill, and time the participant during each trial of over ground walking. Give verbal feedback in between each trial to speed up or slow down, if needed[25].

2. For treadmill baseline trials, instruct the participant to walk on tied-belts for 1 - 5 min.
NOTE: This constitutes a single baseline trial. If the participant is unfamiliar with treadmill walking, this period may be lengthened to allow the person to become comfortable with the task.
    1. Match the speed(s) of baseline trials to the speed(s) at which the after-effects will be tested, to allow for comparison of pre- and post-adaptation gait coordination at equivalent speeds.
    NOTE: Multiple baseline trials (*i.e.*, 1 - 5 min blocks) at different tied-belt speeds may be required; for example, in the current protocol, baseline trials at tied-belt speeds of 0.7 m/s and 1.4 m/s were collected because those were the speeds used to evaluate after-effects.

3. Adaptation Period

Note: Participants do not need to be instructed that they are about to walk on split-belts. In many experiments, including the current one, participants are not told whether belts will be tied- or split-; they are simply told when the treadmill will be starting or stopping. This allows the experimenter to measure the effects of an unanticipated change in the walking environment.

1. While the participant is standing on the stationary treadmill belts, start the split-belt treadmill with one belt running faster than the other and allow the participant to walk for at least 7 min (10 - 15 min is more common).
    1. Instruct the participant to look straight ahead, not down at their feet.
    2. Set one belt speed faster than the other (*e.g.*,2 - 3 fold differences between belt speeds).
    NOTE: Higher speed ratios have been used in the past[8,31]. The current protocol uses 0.7:1.4 m/s for a 2:1 ratio.
        1. Either randomize which leg is driven by the slower belt or consistently choose one leg (either dominant or non-dominant) as the leg that is driven by the slower belt.
        2. The belt speed differential may be introduced gradually (fast belt speed is incrementally increased and/or slow belt speed incrementally decreased over several min) or abruptly (from stopped position, belts accelerate to target speed within seconds).
        NOTE: The way that split-belts are introduced can affect how individuals adapt, how well they transfer the adapted pattern to different walking environments, and how well they re-adapt to split-belts 24 h later[27,32]. Presently, most split-belt walking protocols (including the current one) introduce the split-belts abruptly.
        3. If it is anticipated that breaks will be needed (*e.g.*, for young children, older adults, or individuals with limited mobility), add predetermined rest breaks to the protocol for all participants. Ensure that the length of these breaks is consistent; unanticipated breaks should be recorded and timed, as this may be a factor to consider in analysis[33].

4. Catch Trial

Note: Catch trials are performed on the treadmill (tied-belts) and are used to briefly test the participant's after-effects thus far in the protocol, indicating how much they have adapted. A catch trial is a short (usually < 20 s) period of tied-belt walking to quickly evaluate the development of after-effects during the split-belt adaptation period.

1. Once the participant has fully adapted to split-belts (minimum of 7 min split-belt walking), briefly stop the belts and restart the treadmill with both belts running at the same speed. Perform the catch trial by starting the treadmill at the same speed as the slower belt during split-belt adaptation[28] as after-effects will be largest here.
    1. To maximize after-effect amplitude following split-belt adaptation at 0.7:1.4 m/s, perform the catch trial at 0.7 m/s.

2. To mitigate de-adaptation, end the catch trial (*i.e.*, stop the treadmill) once the participant has taken about five strides at the desired catch trial speed (~ 10-15 s).
3. To evaluate after-effects in catch trials performed at multiple different walking speeds (or other changes in walking contexts, *e.g.*, forwards and backwards walking[24]), re-adapt the participant for at least 2 min on split-belts between each catch trial.
NOTE: The order of catch trials should be randomized[25] and/or the first catch trial should be re-tested near the end of the adaptation period to determine if there was a systematic decrease in after-effect size with repeated switching between tied-belts (catch trials) and split-belts (re-adaptation)[28].
4. Following the last catch trial, stop the treadmill and restart it with split-belts (same configuration as adaptation - see step 3.1.2) for 2-5 min to allow the participant to re-adapt.

5. Post-adaptation - Testing After-effects During Over Ground Walking

Note: This step is optional and depends on the objectives of the experiment. In the present protocol, the objectives included assessment of generalization to over ground walking, thus a post-adaptation over ground testing period was included.

1. Stop the treadmill and transfer the participant to the over ground walkway using a wheelchair, to prevent participants from taking unrecorded steps prior to reaching the recording area.
2. Instruct the participant to walk along the over-ground walkway, as in step 2.1.
    1. If a specific walking speed is desired, instruct individuals to replicate the baseline walking speed[25].
    2. To completely wash-out over ground walking after-effects so that people return to their baseline coordination, have the participants perform 10-15 walking passes on a 6 m over ground walkway
    NOTE: This has been shown to be sufficient[26,27] and amounts to roughly 30 strides[27]. If over ground walking is not continuously recorded (*e.g.*, several passes are taken through the recording area), there will be several steps that are not analyzed in between each over ground walking trial, as the participant slows down, turns in place, and starts walking in the other direction. The rate of de-adaptation in over ground post-adaptation (OG PA) trials should be cautiously interpreted unless the experimental set-up allows for continuous recording of over ground walking.

6. Post-adaptation - Testing After-effects During Treadmill Walking

NOTE: As in step 5, this step is optional and depends upon the study objectives. If an OG PA period was included, the subsequent treadmill post-adaptation period tests for the presence of treadmill after-effects after over ground after-effects have been washed-out[23,26,27]. If there was no OG PA period, the treadmill post-adaptation period can be used to evaluate treadmill after-effects (first 1 - 5 strides of post-adaptation) and/or treadmill de-adaptation rates[22,29,34].

1. If there was no OG PA, at the end of the adaptation period, stop the treadmill briefly and re-start with tied-belts. If there was an over ground walking period, use the wheelchair to transport the participant back to the stationary treadmill and re-start with tied-belts; the wheelchair is important to minimize the number of steps that are not recorded.
    1. To simply measure after-effect size, record tied-belt walking for a short period (*e.g.*, 30 s). In order to assess rates of de-adaptation, record continuous tied-belt walking for a minimum of 10 min to ensure complete wash-out of after-effects.
    2. Set the speed of tied-belts during the post-adaptation period as per the hypotheses posed, as the largest treadmill after-effects occur when the tied-belt speed matches that of the slower belt during split-belt adaptation[25,28]. If adaptation is performed at split-belt speeds of 0.7 and 1.4 m/s, set the tied belt speed at 0.7 m/s to observe the largest after-effects.

Representative Results

Walking on a split-belt treadmill initially causes large asymmetries in interlimb coordination. Over a period of 10 - 15 min, symmetry in many of these measures is gradually restored. Detailed descriptions of how kinematic walking parameters change over the course of split-belt treadmill adaptation have been published elsewhere[8,10]. This paper focuses on two measures of interlimb coordination: step length and double support duration. Step length is calculated as the anterior-posterior distance between the two feet (*i.e.*, the distance between motion tracking markers placed on the lateral malleoli) at initial contact (*i.e.*, heel strike). Slow step length is calculated when the leg on the slower belt touches down; fast step length is calculated at fast leg heel strike. Step length is primarily considered a spatial measure of interlimb coordination, although it can also be influenced by changes in the timing of gait[10]. Double support duration is a temporal measure of interlimb coordination, defined as the duration of the period when both feet are in contact with the ground; slow double support occurs at the end of slow leg stance, and fast double support is at fast leg terminal stance. Double support duration is reported as a percentage of the stride cycle duration. For both step length and double support duration, the differences between values obtained from each leg give a measure of walking symmetry (symmetric gait: difference = 0; asymmetric gait: difference ≠ 0). The absolute values of these two metrics during post-adaptation walking are collectively referred to as "after-effect amplitudes".

Figure 1 shows representative results from two participants in a split-belt treadmill experiment[25]. The participants were young adults (< 40 years of age) with no neurological or orthopedic injuries or illnesses. The purpose of this experiment was to test how walking speed influences the expression of split-belt treadmill after-effects in different environments (*i.e.*, walking on the treadmill and walking over the ground). The experiment started with baseline walking periods on the treadmill and over the ground at the different speeds of walking (0.7 and 1.4 m/s); these same walking speeds were used to test after-effects later in the experiment. Both participants walked with near-symmetric spatial (step length difference) and temporal (double support difference) interlimb coordination during these baseline trials.

Next, participants walked on split-belts with their dominant leg on the fast belt (slow belt speed: 0.7 m/s; fast belt speed: 1.4 m/s). The split-belts initially induced asymmetries in interlimb coordination but, over several strides, both participants adapted to restore baseline symmetry. Following 10 min of split-belt walking, the belts were stopped and re-started with both belts running the same speed to determine after-effect size (*i.e.*, catch trials). These catch trials tested treadmill after-effects at 0.7 m/s and 1.4 m/s (order randomized), with a 2 min re-adaptation period in between. In catch trials, both participants demonstrated after-effects that were expressed as asymmetries opposite from the direction of the asymmetry induced by the split-belt treadmill at the beginning of the adaptation period. After-effects tested at the slow speed (0.7 m/s) were larger than those tested at the fast speed (1.4 m/s), a result that was confirmed in group analyses[25,28].

Following the final catch trial, participants re-adapted to split-belts and then were transported by wheelchair to the walkway for OG PA trials. Depending on group assignment, they were asked to walk at either the slow (0.7 m/s) or fast (1.4 m/s) speed. While both participants demonstrated after-effects (gait asymmetries compared to baseline) in OG PA trials, these after-effects were not as large as the ones tested on the treadmill, nor did they appear to be affected as much by walking speed. After-effects in Participant 1 who walked over ground at the slower speed were approximately the same size as after-effects in Participant 2 who walked over ground at the faster speed; this too was reflected in group analyses. In this particular experiment, treadmill post-adaptation trials were not conducted because the treadmill after-effects tested during catch trials were sufficient to test the hypotheses. However, many experiments that test over ground after-effects subsequently return to the treadmill to test treadmill after-effects[23,26].

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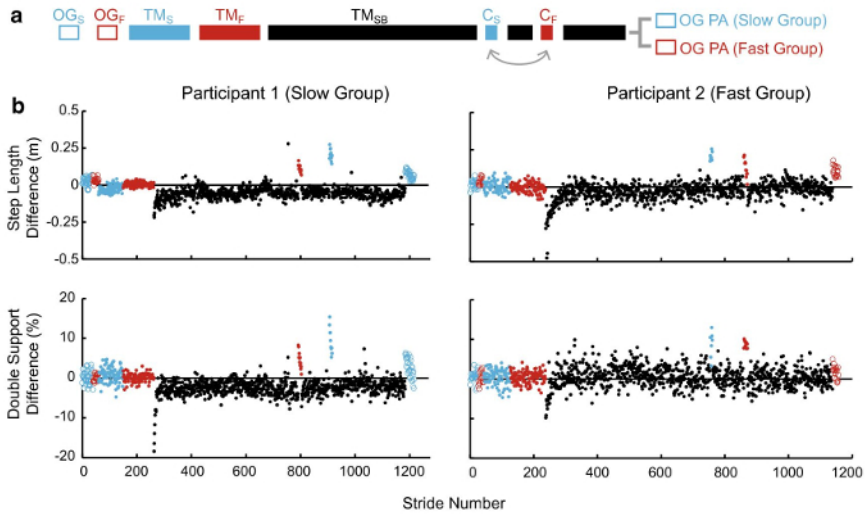

Figure 1: Experimental Paradigm (a) and Step-by-Step Plots of Split-belt Adaptation (b). (a) In the experimental paradigm, filled blocks indicate treadmill (TM) walking, while open blocks indicate over-ground (OG) walking. Breaks between treadmill blocks indicate that the treadmill was briefly stopped and restarted to reconfigure belt speeds. Slow trials, denoted by subscript "S", were conducted at 0.7 m/s; fast trials ("F") were at 1.4 m/s. The speeds of the slow and fast belts during split-belt trials (SB) were 0.7 and 1.4 m/s, respectively. 10 s tied-belt catch trials at slow (C_S) and fast (C_F) speeds were randomly ordered near the end of adaptation. All participants experienced an identical paradigm until reaching the post-adaptation phase of the experiment, at which point they were randomly assigned to a slow or fast over-ground walking group. **(b)** Single participant stride-by-stride plots of changes in step length difference (top) and double support difference (bottom). For reference, perfect symmetry is shown by the horizontal axis at 0. Color coding corresponds to that in (a). From Hamzey *et al.*[25] with permission from Springer. Please click here to view a larger version of this figure.

Discussion

Numerous studies have now shown that people adapt gait coordination on a split-belt treadmill in order to restore symmetry in interlimb coordination parameters like step length and double support duration. When natural walking conditions are restored following split-belt walking, participants continue using the adapted gait pattern, leading to after-effects that have to be unlearned in order to return to normal walking coordination. Researchers primarily use adaptation rate and after-effect amplitude to quantify the ability to learn this new walking pattern and to generalize this learning to other walking environments and tasks. Correctly interpreting these changes in adaptation rates and after-effect amplitude requires careful adherence to key steps in the experimental design and consideration of other factors that may influence these measures. In the following sections, we highlight these considerations, discuss scaling treadmill speed for participants of different heights, and discuss how this technique fits into the broader motor learning field.

Critical steps within the protocol

The work described in representative results[25,28] emphasizes the importance of considering the walking speed when developing a split-belt adaptation protocol in neurologically intact individuals. As shown in **Figure 1**, treadmill after-effects are largest when they are tested on tied-belts matched to the speed of the slower belt during adaptation[25,28]. Therefore, we recommend that split-belt protocols be designed such that treadmill baseline coordination and after-effects can be tested at the same speed as the slower belt during adaptation. We also recommend that investigators begin after-effect analysis only after the belts reach 80% of their final speed since very small speed differences (0.2 m/s) can influence treadmill after-effect size[28]. Interestingly, after-effects tested during over ground walking are not as sensitive to walking speed as treadmill after-effects[25]. Therefore, it is more important to precisely select and control walking speed during treadmill after-effect trials than it is during over ground after-effect trials in young, neurologically-intact adults.

In addition to controlling walking speed, it is important to minimize distractors and other activity in the testing room during split-belt adaptation experiments. This recommendation is based on research showing that watching a television program during split-belt walking slowed adaptation rates compared to non-distracting conditions in both healthy younger (< 30 years)[34] and older (> 50 years)[33] adults. Incorporating rest breaks into the protocol can also affect adaptation - recent work has shown that adults over 50 years old "forget" the adapted pattern during seated 5 min rest breaks in between split-belt walking trials, whereas adults younger than 30 years old do not[33]. If breaks occur during a split-belt treadmill protocol, the time and duration of each break should be documented and possibly considered as a factor in analysis, particularly when the study sample includes individuals other than healthy young adults. If it is anticipated that participants will need breaks (*e.g.*, young children or populations susceptible to fatigue), standardized breaks should be integrated into the study protocol for all participants[35].

Modifications and troubleshooting

There exists a great range of walking speeds that could be considered as part of a split-belt treadmill protocol. While many researchers opt for whole-number ratios for split-belt speed (*e.g.*, 2:1, 3:1, 4:1 differences), there is no reason why other ratios could not be used (*e.g.*, as in Yang *et al.*[31]). In addition, while the current protocol uses the same treadmill speeds for everyone (all adults; randomly assigned to different groups), it may be necessary to adjust the treadmill speeds to the size of the person being tested. For example, in Vasudevan *et al.*[35], split-belt adaptation was compared across people ranging in age from 3 - 40 years; clearly there were large differences in leg length across this sample. To account for this, treadmill speeds were scaled according to the leg length. If the leg length was 1.0 m, split-belt treadmill speeds were set to 1.0:2.0 m/

s. If the leg length was 0.35 m, split-belt treadmill speeds were set to 0.35:0.7 m/s. This approach led to split-belt speeds that were manageable for all of the participants, and the initial asymmetry induced by split-belts was comparable across age groups. Since this paper was published, our group has also used the Froude number[36] to normalize treadmill speed across participants of different heights[37]. The Froude number is a dimensionless parameter used to normalize the pendulum-like movement of walking in people of different leg lengths and under different loading conditions. This relationship stipulates that walking velocity is proportionate to the square root of leg length. Therefore, a better approach in the future may be to scale velocity with the square root of leg length, and not absolute leg length. While the absolute treadmill speeds may be varied in split-belt treadmill protocols, we recommend maintaining a consistent split-belt speed ratio across participants.

Thus far in this discussion three factors were highlighted as primary considerations in designing split-belt experiments: walking speed, distraction, and breaks. However, this is not an exhaustive list. There are numerous possible protocol modifications, some of which have already been shown to affect adaptation and/or after-effects, including the addition or deprivation of sensory stimuli[26,38,39,40], the rate of acceleration of treadmill belts at the beginning of split-belt trials[27], the practice structure[29], and providing feedback during adaptation[34,41]. After-effects following split-belt walking are very robust and have been replicated in numerous studies (*e.g.* [8,24,25,26,27,28,29,35]). If this protocol does not result in robust after-effects, possible causes include cerebellar damage or immaturity[21,35,42], inadequate adaptation speed ratios, or improper selection of tied-belt speeds to test after-effects (see discussion section (a) and [25,28]).

Limitations of this technique

It is important to acknowledge that the split-belt treadmill evaluates the ability to perform one type of locomotor learning. Specifically, it evaluates locomotor adaptation, defined using the terminology of Martin *et al.*[9] as the gradual, trial-and-error process of modifying a well-learned movement (*e.g.*, walking) in response to a novel perturbing context or environment (*e.g.*, split-belt treadmill). In other words, locomotor adaptation can be considered as one component of motor skill learning, but there are also many other mechanisms for learning a new movement.

Similarly, there are several ways to quantify locomotor adaptation including assessment of gait kinematics[8,10], kinetics[11,12,13,14], electromyography[6,15,16], and perception of gait asymmetry[7,17,18,19]. The above protocol is limited to discussion of step length and double support time, as these measures most specifically addressed our research question in Hamzey *et al.*[25] regarding the spatial and temporal generalization of locomotor adaptation on a step-by-step basis. While a comprehensive discussion of each measure of locomotor adaptation is beyond the scope of this paper, a wide range of alternate split-belt treadmill protocols and outcome measures exist, each of which can be used to evaluate unique hypotheses.

Another limitation of the split-belt treadmill is that many commonly used measures of gait adaptation (*e.g.*, step length) are captured at discrete time points (*e.g.*, heel strike). However, walking is a continuous movement and adaptation is an ongoing process that occurs while walking. Many methods of quantifying adaptation thus reduce a continuous process down to discrete time points. This may be a concern in computational modelling, where the time course of adaptation is a key variable (see discussion section (e) for more detail about computational modeling of adaptation data).

Significance of the technique with respect to existing/alternative methods

While this is not the only method by which to study locomotor adaptation and learning (*e.g.*, also see [43,44,45,46,47,48,49,50]), the split-belt treadmill paradigm has many strengths. First, the split-belt treadmill is novel for most people and it is easy to screen people for past split-belt treadmill experience. This enables the study of adaptation to a truly novel perturbation, unlike weighting the leg, tripping, or stepping over obstacles, which most mature, terrestrial, legged animals have experienced before. Second, it requires no instruction, so very young children[31,35,42] and people with limited voluntary motor control (*e.g.*, after stroke or brain injury)[23,51,52] can still perform this task. In fact, people with asymmetric gait following stroke may even experience long-term benefits in walking coordination following repeated split-belt treadmill training[53]. In summary, the split-belt treadmill offers a powerful technique to study locomotor adaptation across many diverse populations with different locomotor experiences, and even offers the possibility of a therapeutic benefit to some.

Future applications or direction after mastering this technique

There are many questions that remain unresolved about factors that affect split-belt treadmill adaptation, including some points that arose in the protocol section. For example, the effects of the type of arm movement (*e.g.*, holding onto bars versus swing arms naturally) and the effects of leg dominance on locomotor adaptation have not yet been thoroughly investigated (although see [54]). Furthermore, while a growing body of computational work has started to model the processes of locomotor adaptation[10,55,56,57], this area of inquiry is still underdeveloped in comparison to computational modelling of upper limb or eye movement (*i.e.*, saccade) adaptations. This disparity is partly due to walking being a more complicated movement than reaching or eye saccades, because it involves two limbs, multiple joints, and engages other systems related to postural control and stability. The increased difficulty of modeling walking data is also due to the fact that walking is a continuous movement, whereas reaching and saccades are discrete movements. The first reach or eye movement in the adaptation block is indicative of the participant's initial reaction to the changed sensorimotor parameters of the task. In contrast, the first data point for walking adaptation is obtained only once the treadmill has reached 80% of its target speed. While the treadmill gets up to speed, the legs are gathering information about the relative speeds of the belt even before data collection is initiated. Thus, by the time the first data point is recorded in walking adaptation, the person has already obtained information about the adaptation task. Depending on how quickly people can adjust gait coordination to this information, adaptation processes may be occurring prior to the first analyzable steps. This causes the first reaction to split-belts to change with repeated exposures[29] and in different participant groups[52], adding difficulty to the modeling process because the starting point is not always the same. Nonetheless, some very interesting computational work has started to emerge[10,55,56,57], that will likely enrich the field and generate predictions about how people will respond to different variations of the split-belt treadmill protocol in the future.

Disclosures

The authors have nothing to disclose.

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