Published in final edited form as:

J Biomech. 2017 February 28; 53: 136–143. doi:10.1016/j.jbiomech.2017.01.012.

Two biomechanical strategies for locomotor adaptation to split-belt treadmill walking in subjects with and without transtibial amputation

Brian P. Selgrade, Megan E. Toney, and Young-Hui Chang*

Comparative Neuromechanics Laboratory School of Applied Physiology, Georgia Institute of Technology, Atlanta, GA, USA

Abstract

Locomotor adaptation is commonly studied using split-belt treadmill walking, in which each foot is placed on a belt moving at a different speed. As subjects adapt to split-belt walking, they reduce metabolic power, but the biomechanical mechanism behind this improved efficiency is unknown. Analyzing mechanical work performed by the legs and joints during split-belt adaptation could reveal this mechanism. Because ankle work in the step-to-step transition is more efficient than hip work, we hypothesized that control subjects would reduce hip work on the fast belt and increase ankle work during the step-to-step transition as they adapted. We further hypothesized that subjects with unilateral, trans-tibial amputation would instead increase propulsive work from their intact leg on the slow belt. Control subjects reduced hip work and shifted more ankle work to the step-to-step transition, supporting our hypothesis. Contrary to our second hypothesis, intact leg work, ankle work and hip work in amputees were unchanged during adaptation. Furthermore, all subjects increased collisional energy loss on the fast belt, but did not increase propulsive work. This was possible because subjects moved further backward during fast leg single support in late adaptation than in early adaptation, compensating by reducing backward movement in slow leg single support. In summary, subjects used two strategies to improve mechanical efficiency in split-belt walking adaptation: a CoM displacement strategy that allows for less forward propulsion on the fast belt; and, an ankle timing strategy that allows efficient ankle work in the step-to-step transition to increase while reducing inefficient hip work.

Keywords

Adaptation; split-belt; walking; amputee; efficiency; biomechanics

*Corresponding author. Tel.: +1 404 894 9993. yh.chang@ap.gatech.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Introduction

When walking under novel conditions, the nervous system gradually modifies locomotor control in response to sensory feedback. Adaptation is characterized biomechanically by a movement parameter changing gradually in response to an altered environment (Martin et al. 1996) and by aftereffects, which linger when the environmental perturbation is removed. Because aftereffects do not immediately dissipate when the perturbation is removed, they indicate predictive control of movement (Ogawa et al., 2014; Kagerer, et al., 1997).

Locomotor adaptation can be studied during split-belt treadmill walking, in which each belt moves at a different speed (Prokop et al. 1995). Over several minutes of split-belt walking, interlimb parameters such as step length symmetry and double support time adapt (Reisman et al., 2005). Step length symmetry adaptation is a robust finding replicated in stroke survivors (Reisman et al. 2007; Reisman et al. 2013), Parkinson's disease patients (Roemmich et al. 2014a; Roemmich et al. 2014b), and many conditions in healthy subjects (Malone, Bastian, 2010; Torres-Oviedo, Bastian, 2012; Torres-Oviedo, Bastian, 2010; Finley et al., 2014). During split-belt walking, ground reaction forces (GRF) exhibit predictive changes at initial contact, although vertical GRF in single support and propulsive GRF changes immediately, indicating reactive control (Mawase et al., 2013; Ogawa et al., 2014). Over the course of split-belt adaptation, subjects reduce muscle activity and metabolic power (Finley et al., 2013).

Metabolic power decreases during split-belt adaptation, but changes in joint mechanical work that may cause this improved efficiency are unknown. During steady walking, metabolic cost is determined largely by trailing leg work in the step-to-step transition (STS), which increases with metabolic rate (Donelan, et al. 2002a). Trailing leg work in STS is more efficient than single support work (Kuo, 2002) and comes predominantly from the ankle while single support work comes more from the hip (Farris, Sawicki, 2012; Zelik et al., 2015). This result explains increased metabolic cost in trans-tibial amputees (Houdijk et al., 2009; Adamczyk, Kuo, 2015) and healthy subjects with immobilized ankles (Wutzke, et al., 2012). However, changes in joint work during split-belt adaptation are largely unknown. Only ankle work in late stance and hip work in swing have been quantified in split-belt adaptation (Roemmich et al. 2014a, Hinkel-Lipsker, Hahn, 2016). Furthermore, split-belt walking has not been tested on trans-tibial amputees. Because trans-tibial amputees have limited propulsion from their prosthesis (Silverman et al. 2008; Fey, et al., 2011), split-belt walking with the prosthesis on the fast belt is a useful model of compensation during locomotor adaptation.

The purposes of this study were to: (1) determine how joint work changes as subjects adapt to split-belt walking; and, (2) explore biomechanical compensation mechanisms trans-tibial amputees use during split-belt walking. Our primary hypothesis is that controls would reduce hip work and increase trailing leg STS ankle work on the fast belt over adaptation. We propose this switch from hip work to trailing ankle work as a joint-level biomechanical mechanism for reducing metabolic power during split-belt adaptation. Our primary focus was work from the fast leg joints, which have much higher work than slow leg joints and should thus contribute more to metabolic power. Given that amputees lack a biological ankle

on the fast belt, have less adaptability on the amputated side (Houdijk et al. 2012), and do more work with the intact than the amputated leg (Houdijk et al. 2009; Adamczyk, Kuo, 2015), we further hypothesized that amputees would be unable to increase fast (prosthetic) leg ankle work and would instead increase slow (intact) leg work as they adapted. Lastly, based on decreasing slow leg braking force during able-bodied split-belt adaptation (Ogawa et al. 2014), we hypothesize that, for both amputees and controls, slow leg collisional energy loss would decrease as subjects adapted.

Methods

Subjects

Eight trans-tibial amputees (6 male, 1 congenital, 7 traumatic, BW:80.4±16.9kg, intact leg length:92.0±6.4cm) and eight matched controls (6 male, BW:81.5±14.1kg, leg length: 91.8±4.7cm) gave informed consent prior to participating in this study approved by the Georgia Tech Institutional Review Board. Amputees wore their own prostheses with energy storage and return feet, passive elastic feet that provide more propulsion than a solid-ankle cushioned heel foot but less than a powered ankle (Wezenberg et al. 2014; Herr, Grabowski, 2012). All amputees had their prostheses for over 6 months before testing.

Experimental Protocol

We first determined preferred walking speed (PWS) on the treadmill for each subject. Belt speeds started at 1.3m/s and were varied by 0.1m/s increments. Subjects indicated if each speed was “too fast,” “too slow” or “just right.” We implemented our protocol relative to each subject’s PWS, because amputees and controls have similar metabolic power at PWS rather than fixed walking speeds (Houdijk et al. 2009). Since amputees had slower average PWS (1.17 versus 1.29m/s, $p=0.049$), controls walked slightly faster on average.

Presentation of walking conditions was similar to previous studies (Fig. 1, Reisman, et al., 2005; Ogawa, et al. 2014). Subjects completed three baseline trials with belts at the same speed (tied-belt at 75%, 150%, and 75%PWS), then walked 15 minutes in a split-belt condition, with one belt at 150%PWS and one at 75%PWS. Amputees walked with the intact leg on the slow belt, because, in pilot tests, some amputees had difficulty balancing with the prosthesis on the slow belt. For all trials, the leg moving at 150% PWS during adaptation will be called the “fast leg”, and the contralateral leg will be called the “slow leg”. Lastly, subjects completed a 10-minute, post-adaptation trial with tied belts at 75% PWS. Subjects wore a safety harness throughout and held an anterior handrail for the first 30 seconds of each trial to prevent falls. Subjects were instructed that, if necessary, they should view their feet in a mirror in front of them rather than looking down.

Data Collection and Analysis

We collected data in 2-minute intervals during continuous walking for all experimental conditions. Gaps of 10–20 seconds between intervals allowed set-up of the next interval on the computer, but we collected the first 2 minutes and last minute of all trials. We collected kinematic data using a six-camera system (120Hz, VICON Motion Systems, Oxford, UK) and markers placed bilaterally on the anterior and posterior superior iliac spines, greater

trochanter, heel, second metatarsophalangeal joint and lateral thigh, knee, shank, and malleolus. Markers were placed on the prostheses at the same locations as on the intact leg (Silverman, et al., 2008; Morgenroth, et al., 2011). Thigh and shank markers were placed in line with their proximal and distal joints. Force plates (1080Hz, AMTI, Watertown, MA, USA) beneath each treadmill measured GRF from each leg. We low-pass filtered force and marker position using a 4th order Butterworth filter with 10-Hz cutoff frequency.

We calculated positive external work (W^+ , Eq 1) and collisional energy loss (W^- , Eq 2) of each leg on the CoM by integrating the dot product of GRF and CoM velocity (v_{com}), integrating CoM acceleration derived from GRF to find v_{com} (Eq 3a,b; Donelan, et al., 2002b). We determine integration constants using the belt speed of the leg of interest (van Ingen Schenau, 1980), requiring average vertical velocity over a stride to equal zero and average anterior-posterior velocity to equal belt speed in order to calculate integration constants. Using different integration constants for each leg better represented what the legs experienced physiologically (see supplement).

$$W^+ = \int^+ GRF \cdot v_{com} dt \quad (1)$$

$$W^- = \int^- GRF \cdot v_{com} dt \quad (2)$$

$$v_{com,ap} = \int [(GRF_{slowleg,ap} + GRF_{fastleg,ap})/m] dt \quad (3a)$$

$$v_{com,vert} = \int [(GRF_{slowleg,vert} + GRF_{fastleg,vert})/m] dt \quad (3b)$$

Subscripts denote the leg and gait phase for which work was calculated. Positive and negative integrals were calculated in Matlab (MathWorks, Natick, MA) using the trapz function. We calculated work during pendular phase, fast-leading STS and slow-leading STS. Pendular phase began with maximum vertical v_{com} , which occurred just after toe off, and ended with minimum vertical v_{com} , approximating single support. STS was slightly longer than double support. Rather than single and double support determined by GRF, we used pendular phase and STS, because CoM redirection occurs over a longer period than double support and is better represented with minimum and maximum v_{com} (Adamczyk and Kuo, 2009; Donelan et al. 2002a). To remove effects of body size, we normalized work by leg length and body weight.

We calculated positive work at each joint by integrating the dot product of the angular velocity (ω_{joint}) and moment (M_{joint}).

$$W_{\text{joint}} = \int^+ M_{\text{joint}} \cdot \omega_{\text{joint}} dt \quad (4)$$

We calculated joint moments with custom inverse dynamics Matlab code (Toney, Chang, 2013; Toney, Chang, 2016), using included joint angles for the ankle and knee and the thigh segment angle for the hip. We calculated joint work over STS, pendular phase, and full stance phase.

Comparison of changes in collisional energy loss and positive work during adaptation suggested abnormal CoM movement, so we conducted a post hoc analysis of CoM displacement. To find CoM position in a fixed (laboratory) reference frame, we averaged anterior-posterior pelvic marker position. CoM displacement in single support was the difference in CoM position from the beginning (contralateral toe-off, GRF<32N) to the end of single support (contralateral heel strike). We calculated step length symmetry (SLS), defining step length (SL) as the distance between heel markers at heel strike (Reisman et al., 2005).

$$SLS = (SL_{\text{fast leading}} - SL_{\text{slow leading}}) / (SL_{\text{fast leading}} + SL_{\text{slow leading}}) \quad (5)$$

Statistical Analysis

We performed statistical analyses (IBM SPSS, Armonk, NY, USA), defining early and late adaptation as the averages of the first 5 steps after subjects released the handrail and the last 5 steps of adaptation, respectively. We defined early and late post-adaptation the same way and compared these data to the last 5 steps of each baseline trial. Because holding the handrail may have affected GRF, we excluded all data when subjects held the handrail. For all variables, we found effect size (ES; Eq 6) between early and late adaptation or between early and late post-adaptation.

$$ES = (\text{late average} - \text{early average}) / (\text{late average deviation}) \quad (6)$$

For step length symmetry and CoM displacement, we compared all trials using repeated measures ANOVA (rmANOVA). We performed three rmANOVAs per work variable. One rmANOVA compared the fast leg in trials when it moved at 150% PWS (fast baseline, early and late adaptation). Another compared the fast leg when it moved at 75%PWS (slow baseline, early and late post-adaptation). The third compared slow leg work in all trials except fast baseline. When we found significant differences, we used Bonferroni tests for pairwise comparisons to minimize experiment-wise type I error. Multiple rmANOVAs were conducted to avoid comparing work in trials when the leg moved at different speeds, because belt speed affected work calculations. Because controls walked faster than amputees, we did not compare amputees with controls.

Results

All subjects displayed stereotypical responses in step kinematics. Compared to baseline, both controls and amputees exhibited negative step length asymmetry in early adaptation (controls: ES=2.74; $p=0.034$; amputees: ES=1.51; $p=0.013$) and positive asymmetry in early post-adaptation (controls: $p=0.031$; amputees: $p=0.031$). Although they appear to overshoot zero asymmetry as they adapt, neither group significantly differed from baseline step length symmetry in late adaptation (controls: ES=1.17; $p=0.97$; amputees: ES=0.11; $p=1.00$) or late post-adaptation (Fig. 2; controls: ES=0.39; $p=1.00$; amputees: ES=0.69; $p=1.00$). Step length symmetry decreased significantly from early to late post-adaptation for controls (ES=3.39; $p=0.044$) and approached significance for amputees (ES=2.06; $p=0.097$).

Controls decreased both fast hip (ES=0.65; $p=0.036$) and fast ankle work (ES=1.47; $p=0.015$) between early and late adaptation (Fig. 3). In early adaptation, controls performed greater fast ankle work during stance compared to fast baseline ($p=0.010$). In early post-adaptation, controls performed less fast ankle work during stance versus slow baseline ($p=0.010$). Controls returned to baseline ankle work in late adaptation and late post-adaptation.

Controls changed fast ankle work timing, shifting the majority of work from pendular phase to STS ($p=0.006$; Fig. 4A,C). In contrast, amputees did not change fast (prosthetic) ankle work (Fig. 3B,D) or ankle work timing (Fig. 4B,D). While amputees did not alter hip work during adaptation, they used less hip work in stance during adaptation than fast baseline ($p=0.001$). Hip work timing and knee work were unchanged for both groups.

Fast collisional energy loss in STS increased over adaptation and decreased over post-adaptation for both groups (Fig. 5). Controls' collisional energy loss increased during adaptation (ES=1.86; $p=0.001$) and decreased during post-adaptation (ES=2.00; $p=0.014$). Similarly, amputees' collisional energy loss increased during adaptation (ES=1.29; $p=0.006$) and decreased during post-adaptation (ES=0.97; $p=0.043$). Fast pendular phase work significantly decreased for controls during adaptation ($p=0.004$); otherwise, leg work did not significantly change during adaptation (see supplement). Slow leg work had no significant changes between early and late adaptation, but both groups had significantly higher slow leg pendular work throughout adaptation than in slow baseline (see supplement).

While adapting to split-belt walking, all subjects adopted asymmetric CoM movement in the fixed (laboratory) reference frame. In baseline, subjects moved backward during single support and forward during double support. CoM displacement in double support remained unchanged during adaptation. Both controls and amputees increased backward displacement in fast single support between early and late adaptation (Fig. 6). Subjects compensated by reducing backward displacement during slow single support in late adaptation to maintain CoM position (Fig. 7). By late adaptation, backward CoM displacement during single support in all subjects became asymmetric, with greater posterior displacement on the fast belt (controls: ES=1.24; $p=0.033$; amputees: ES=1.02, $p=0.013$) and less posterior displacement on the slow belt versus baseline (controls: ES=1.96, $p=0.007$; amputees: ES=1.26, $p=0.021$). This change was quicker for amputees than controls.

Discussion

Step length symmetry has typical adaptation pattern in both controls and amputees

Changes in step length symmetry were consistent with previous studies (Reisman et al. 2005; Malone, Bastian, 2010; Vazquez et al., 2015). Both controls and amputees initially responded to split-belt walking by taking longer steps with the slow leg leading, but returned to baseline step length symmetry by late adaptation. Both groups had the opposite aftereffect in early post-adaptation, indicating predictive control. Therefore, the lack of sensory feedback in the amputees' distal limb did not impede the ability to adapt step length symmetry.

Controls switch to trailing ankle work during adaptation

The data support the hypothesis that, for controls, fast hip work would decrease and trailing ankle work during STS would increase during split-belt adaptation. A previous study indicates ankle work is largely based on belt speed (Hinkel-Lipsker, Hahn, 2016). The fast ankle always performs much more work than the slow ankle, and, across all joints, work depended on belt speed. Bilateral comparison in late adaptation should be avoided when drawing conclusions about adaptation, however, because belt speed differences can obscure single leg changes. Here, fast ankle work decreased from early to late adaptation although belt speed was unchanged. In contrast with prior work (Hinkel-Lipsker, Hahn, 2016), this result suggests that the ankle is a site of adaptation. This finding agrees with prior biomechanical (Roemmich et al. 2014a) and electromyographic (Finley et al. 2013) evidence of adaptation at the ankle.

More importantly, control subjects adjust ankle work timing to later in stance; ankle work shifts from pendular phase to STS. Trailing leg ankle work during STS is more efficient than hip work during pendular phase (Kuo, 2002; Yeom, Park, 2011; Donelan et al., 2002a). Also, the ankle's contribution to forward progression increases with trailing leg angle (Hsiao et al. 2015), so ankle work during pendular phase – when the leg is upright – is inefficient. Thus, switching from hip and ankle work in pendular phase to trailing ankle work in STS likely contributes to metabolic power reduction (Finley, et al. 2013) during split-belt adaptation.

Amputees changed neither fast (prosthetic) ankle nor fast hip work over adaptation. The unchanged ankle work indicates any energy stored in the prosthesis as collisional work increased did not increase ankle work at toe off. Although amputees did not change joint work or timing, they still adapted step length symmetry the same way controls did, indicating that the ankle timing strategy used by controls is not necessary to alter step length symmetry. We suspected amputees to compensate with slow (intact leg) work, but this did not change during adaptation. Slow leg work was much lower than fast leg work, so changes in slow leg work may have been obscured by stride-to-stride variations in work. CoM displacement appears to be a more sensitive measure of slow leg adaptation.

Although fast trailing leg work increased as controls adapted, this change was not significant ($p=0.268$). Smaller belt speed ratios result in smaller adaptive changes (Reisman, et al., 2005), so the 2:1 ratio may have been too small to reach significance. Additionally, we

excluded data from the first 30 seconds of adaptation and post-adaptation, when holding the handrail may have affected GRF. The handrail was necessary for subject safety and is often used with clinical populations (e.g. Reisman et al., 2007; Roemmich et al., 2014a), but changes occurs most rapidly in adaptation and post-adaptation. This is likely why we found fewer significant differences within post-adaptation, when changes are quicker than in adaptation (Malone, Bastian, 2010; Selgrade, Chang 2015). Given that we excluded the first 30 seconds of each trial, subjects must have adapted ankle work timing and pendular phase work gradually and robustly for significant differences to still be detectable.

Collisional energy loss and CoM displacement

In amputees and controls, collisional energy loss exhibited a typical pattern, increasing in adaptation and showing an aftereffect indicative of predictive control. This is consistent with feedforward control of braking GRF (Mawase et al., 2013; Ogawa et al., 2014). Typically, braking and propulsive forces increase with walking speed (Park, Park, 2013; Nilsson, Thorstensson, 1989), so no net work is performed on the CoM. In split-belt adaptation, however, energy loss in braking increased without concomitant propulsive work increases. How can subjects maintain anterior-posterior position on a split-belt treadmill if net work decreases?

After further analysis, we discovered a second adaptation strategy related to anterior-posterior CoM position control that is unique to split-belt walking and may explain the observed changes in mechanical and metabolic power. This is the first observation that subjects use a CoM displacement strategy that exploits a characteristic unique to split-belt walking and may contribute to decreased energetic costs. Subjects move further backwards in a fixed reference frame when only on the fast belt, remained stationary on the slow belt, and regained forward COM position during STS. The benefit of asymmetric CoM displacement is that it is energetically less expensive to propel oneself forward (relative to the belt) at lower velocity than at higher velocity. This allows subjects to maintain overall position without producing positive work equivalent to collisional energy loss.

Slow leg work

Our hypotheses regarding slow leg work were unsupported. We hypothesized that amputees would increasingly rely on the slow (intact) leg as they adapted to split-belt walking. Amputees did have higher slow leg pendular work than baseline, but so did controls, and it was maintained throughout adaptation. Interestingly, slow leg pendular work resembled pendular work in fast baseline, not slow baseline, suggesting split-belt walking is not simply a hybrid of fast and slow walking by each leg, but rather a newly adapted form of walking. Both groups also used the CoM displacement strategy; however, amputees adopted this strategy more quickly than controls. Amputees were unable to increase fast (prosthetic) trailing ankle work, so they quickly used their slow (intact) leg to maintain treadmill position. Amputees generally rely on their intact leg as a compensation strategy (Houdijk et al. 2009; Adamczyk, Kuo 2015), which may explain why they adopted this strategy earlier than controls.

Furthermore, slow leg collisional energy loss did not change significantly for either subject group. Like slow leg braking GRF (Ogawa et al. 2014), slow collisional energy loss decreased, but this was not significant for either group ($p>0.25$). Reducing collisional energy loss would improve efficiency (Ruina et al. 2005), but, since slow leg work was relatively low, there may have been insufficient energetic benefit to spur adaptation of slow leg work.

This study had additional limitations. In order to walk comfortably, subjects were allowed to view their foot placement in a mirror, which can alter adaptation. Despite this, step length symmetry adaptation was similar to prior studies (e.g. Reisman et al. 2005). Additionally, determining walking speeds from PWS meant amputees walked more slowly than controls, preventing us from comparing them statistically. Future work with identical belt speeds for amputees and their matched controls could better assess differences between these populations. Lastly, future work should investigate amputees' metabolic changes during split-belt adaptation. While we expect amputees to reduce metabolic power from allowing more backwards CoM movement in fast single support, the reduction may be smaller than in controls, because amputees cannot alter fast ankle work timing.

Conclusion

Control subjects adapt to split-belt walking using two strategies: they change ankle work timing, increasing fast ankle work during STS while reducing inefficient hip work, and they allow their CoM to move farther backward during fast single support while limiting backward motion on the slow belt. Because amputees had their prostheses on the fast belt, they quickly relied on the CoM displacement strategy throughout adaptation, but they still adapted step length symmetry without using the ankle work timing strategy. Both the ankle timing and CoM displacement strategies may contribute to reduced metabolic power during split-belt adaptation.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This research was funded through NIH Grants NICHD 5T32-HD-055180 and NINDS 5R01NS069655.

The authors have no conflicts of interest to disclose.

References

- Adamczyk PG, Kuo AD. Mechanisms of gait asymmetry due to push-off deficiency in unilateral amputees. *IEEE Trans Neur Syst Rehab Engr*. 2015; 23(5):776–785.
- Adamczyk PG, Kuo AD. Redirection of center-of-mass velocity during the step-to-step transition of human walking. *J Exp Biol*. 2009; 212:2668–2678. [PubMed: 19648412]
- Donelan JM, Kram R, Kuo AD. Mechanical and metabolic determinants of the preferred step width in human walking. *Proc Roy Soc Biol Sci*. 2001; 268:1985–1992.
- Donelan JM, Kram R, Kuo AD. Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J Exp Biol*. 2002a; 205(23):3717–3127. [PubMed: 12409498]

- Donelan JM, Kram R, Kuo AD. Simultaneous positive and negative external mechanical work in human walking. *J Biomech.* 2002b; 35:117–124. [PubMed: 11747890]
- Farris DJ, Sawicki GS. The mechanics and energetics of human walking and running: a joint level perspective. *J R Soc Interface.* 2012; 9:110–118. [PubMed: 21613286]
- Fey NP, Klute GK, Neptune RR. The influence of energy storage and return foot stiffness on walking mechanics and muscle activity in below-knee amputees. *Clin Biomech.* 2011; 26(10):1025–1032.
- Finley JM, Bastian AJ, Gottschall JS. Learning to be economical: the energy cost of walking tracks motor adaptation. *J Physiol.* 2013; 591(4):1081–1095. [PubMed: 23247109]
- Finley JM, Statton MA, Bastian AJ. A novel optic flow pattern speeds split-belt locomotor adaptation. *J Neurophysiol.* 2014; 111:969–976. [PubMed: 24335220]
- Herr HM, Grabowski AM. Bionic ankle-foot prosthesis normalizes walking gait for persons with leg amputation. *Proc Roy Soc B.* 2012; 279:457–464.
- Hinkel-Lipsker JW, Hahn ME. Novel kinetic strategies adopted in asymmetric split-belt treadmill walking. *J Mot Behav.* 48(3):209–217. 201.
- Houdijk H, Pollmann E, Groenewold M, Wiggerts HO, Polonski W. The energy cost for the step-to-step transition in amputee walking. *Gait Post.* 2009; 30:35–40.
- Houdijk H, van Ooijen MW, Kraal JJ, Wiggerts HO, Polonski W, Janssen TWJ, Roerdink M. Assessing gait adaptability in people with a unilateral amputation on an instrumented treadmill with projected visual context. *Phys Ther.* 2009; 92(11):1452–1460.
- Hsiao H, Knarr BA, Higginson JL, Binder-Macleod SA. The relative contribution of ankle moment and trailing limb angle to propulsive force during gait. *Hum Mov Sci.* 2015; 39:212–221. [PubMed: 25498289]
- van Ingen Schenau GJ. Some fundamental aspects of the biomechanics of overground versus treadmill locomotion. *Med Sci Sports Exer.* 1980; 12(4):257–261.
- Kagerer FA, Contreras-Vidal JL, Stelmach GE. Adaptation to gradual as compared with sudden visuomotor distortions. *Exp Brain Res.* 2007; 115:557–561.
- Kuo AD. Energetics of actively powered locomotion using the simplest walking model. *J Biomech Engr.* 2002; 124:113–120.
- Malone LA, Bastian AJ. Thinking about walking: effects of conscious correction versus distraction on locomotor adaptation. *J Neurophysiol.* 2010; 103:1954–1962. [PubMed: 20147417]
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT. Throwing while looking through prisms II. Specificity and storage of multiple gaze-throw calibrations. *Brain.* 1996; 119:1199–1211. [PubMed: 8813283]
- Mawase F, Haizler T, Bar-Haim S, Karniel A. Kinetic adaptation during locomotion on a split-belt treadmill. *J Neurophysiol.* 2013; 109(8):2216–2227. [PubMed: 23365187]
- Morgenroth DC, Segal AD, Zelik KE, et al. The effect of prosthetic foot push-off on mechanical loading associated with knee osteoarthritis in lower extremity amputees. *Gait Post.* 2011; 34:502–507.
- Nilsson J, Thorstensson A. Ground reaction forces at different speed of human walking and running. *Acta Physiol Scand.* 1989; 136:217–227. [PubMed: 2782094]
- Ogawa T, Kawashima N, Ogata T, Nakazawa K. Predictive control of ankle stiffness at heel contact is a key element of locomotor adaptation during split-belt treadmill walking in humans. *J Neurophysiol.* 2014; 111(4):722–732. [PubMed: 24225544]
- Park H, Park S. Increase of push-off propulsion to compensate heel strike loss during step-to-step transition is limited at faster gait speeds. *Int J Precision Engr Manufact.* 2013; 14(5):825–829.
- Prokop T, Berger W, Zijlstra W, Dietz V. Adaptational and learning processes during human split-belt locomotion: interaction between central mechanisms and afferent input. *Exp Brain Res.* 1995; 106(3):449–56. [PubMed: 8983988]
- Reisman DS, Block HJ, Bastian AJ. Interlimb coordination during locomotion: what can be adapted and stored? *J Neurophysiol.* 2005; 94:2403–15. [PubMed: 15958603]
- Reisman DS, Wityk R, Silver K, Bastian AJ. Locomotor adaptation on a split-belt treadmill can improve walking symmetry post-stroke. *Brain.* 2007; 130:1861–1872. [PubMed: 17405765]

- Reisman DS, McLean H, Keller J, Danks KA, Bastian AJ. Repeated split-belt treadmill training improves poststroke step length asymmetry. *Neurorehab Neur Rep*. 2013; 27(5):460–468.
- Roemmich RT, Hack N, Akbar U, Hass CJ. Effects of dopaminergic therapy on locomotor adaptation and adaptive learning in persons with Parkinson's disease. *Behav Brain Res*. 2014a; 268:31–39. [PubMed: 24698798]
- Roemmich RT, Nocera JR, Stegemoller EL, Hassan A, Okun MS, Hass CJ. Locomotor adaptation and locomotor adaptive learning in Parkinson's disease and normal aging. *Clin Neurophysiol*. 2014b; 125:313–319. [PubMed: 23916406]
- Ruina A, Bertram JEA, Srinivasan M. A collisional model of the energetic cost of support qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J Theor Biol*. 2005; 237:170–192. [PubMed: 15961114]
- Selgrade BP, Chang Y. Locomotor control of limb force switches from minimal intervention principle in early adaptation to noise reduction in late adaptation. *J Neurophysiol*. 2015; 113:1451–61. [PubMed: 25475343]
- Silverman AK, Fey NP, Portillo A, et al. Compensatory mechanisms in below-knee amputee gait in response to increasing steady-state walking speeds. *Gait Post*. 2008; 28:602–609.
- Toney ME, Chang Y. Humans robustly adhere to dynamic walking principles by harnessing motor abundance to control forces. *Exp Brain Res*. 2013; 231:433–443. [PubMed: 24081680]
- Toney ME, Chang Y. The motor and the brake of the trailing leg in human walking: leg force control through ankle modulation and knee covariance. *Exp Brain Res*. 2016; 234:3011–3023. [PubMed: 27334888]
- Torres-Oviedo G, Bastian AJ. Seeing is believing: effects of visual context clues on learning and transfer of locomotor adaptation. *J Neurosci*. 2010; 30(50):17015–17022. [PubMed: 21159971]
- Torres-Oviedo G, Bastian AJ. Natural error patterns enable transfer of motor learning to novel contexts. *J Neurophysiol*. 2012; 107(1):346–356. [PubMed: 21957223]
- Vazquez A, Statton MA, Busgang SA, Bastian AJ. Split-belt walking adaptation recalibrates sensorimotor estimates of leg speed, but not position or force. *J Neurophysiol*. 2015; 114:3255–2567. [PubMed: 26424576]
- Wezenberg D, Cutti A, Bruno A, Houdijk HJ. Differentiation between solid-ankle cushioned heel and energy storage and return prosthetic foot based on step-to-step transition cost. *J Rehabil Res Dev*. 2014; 51(10):1579–1590. [PubMed: 25860285]
- Wutzke CJ, Sawicki GS, Lewek MD. The influence of a unilateral fixed ankle on metabolic and mechanical demands during walking in unimpaired young adults. *J Biomech*. 2012; 45:2405–2410. [PubMed: 22840758]
- Yeom J, Park S. A gravitational impulse model predicts collision impulse and mechanical work during a step-to-step transition. *J Biomech*. 2011; 44:59–67. [PubMed: 20971468]
- Zelik KE, Takahashi KZ, Sawicki GS. Six degree-of-freedom analysis of hip, knee, ankle and foot provides updated understanding of biomechanical work during human walking. *J Exp Biol*. 2015; 218:876–886. [PubMed: 25788726]

	slow baseline	fast baseline	slow baseline	adaptation split-belt condition	post-adaptation
fast (amputated) leg	75% PWS	150% PWS	75% PWS	150%PWS	75%PWS
slow (intact) leg	75% PWS	150% PWS	75% PWS	75%PWS	75%PWS
	2 min	2 min	2 min	15 min	10 min

Figure 1.
Experimental protocol (PWS - preferred walking speed)

Figure 2.

Step length symmetry for able-bodied control subjects (A & C) and trans-tibial amputees (B & D). C and D display averages of the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA) and post-adaptation (EP, LP). * indicates significant difference ($p < 0.05$) from early adaptation and † indicates significant difference ($p < 0.05$) from early post-adaptation. Vertical bars indicate standard error across subjects.

Figure 3.

“Fast” leg ankle work (blue circles) and hip work (red circles) during stance for controls (A, C and E) and trans-tibial amputees (B, D and F). C and D display averages of ankle work in the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA) and post-adaptation (EP, LP). E and F display hip work averaged over the same strides * indicates significant difference ($p < 0.05$) from early adaptation and † indicates significant difference ($p < 0.05$) from early post-adaptation. Vertical bars indicate standard error across subjects.

Figure 4.

Percentage of “fast” ankle work done during pendular phase (x) or step-to-step transition (o) for controls (A, C and E) and amputees (B, D and F). C and D display averages of trailing ankle work in STS over the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA) and post-adaptation (EP, LP). E and F display ankle work during pendular phase averaged over the same strides. * indicates significant difference ($p<0.05$) from early adaptation. Vertical bars indicate standard error across subjects.

Figure 5.

Collisional energy loss at the “fast” leading leg during STS for able-bodied control subjects (A and C) and trans-tibial amputees (B and D). C and D display averages of the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA) and post-adaptation (EP, LP). * indicates significant difference ($p<0.05$) from early adaptation and † indicates significant difference ($p<0.05$) from early post-adaptation. Vertical bars indicate standard error across subjects.

Figure 6.

Center of mass (CoM) displacement in a fixed reference frame during fast leg single support for controls (panels A and C) and amputees (x, panels B and D). C and D display averages of the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA). * indicates significant difference ($p < 0.05$) from early adaptation. Vertical bars indicate standard error across subjects.

Figure 7.

Center of mass (CoM) displacement in a fixed reference frame during slow leg single support for controls (panels A and C) and amputees (panels B and D). C and D display averages of the last 5 steps of each baseline trial (BS, BF) and the first and last 5 steps of adaptation (EA, LA). * indicates significant difference ($p < 0.05$) from early adaptation. Vertical bars indicate standard error across subjects.