Split-belt walking adaptation recalibrates sensorimotor estimates of leg speed, but not position or force.

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Running head: Perceptual Sensory Correlates of Split-Belt Walking Adaptation.

Word count: Abstract = 237 \quad Manuscript = 6,991

Figures: 10

Conflict of interest: The authors declare no competing financial interests.

Keywords: adaptation, perception, split-belt treadmill, gait, motor learning

Acknowledgements: This work was supported by NIH HD040289.

Abstract
Motor learning during reaching not only recalibrates movement, but can also lead to small, but consistent changes in the sense of arm position. Studies have suggested that this sensory effect may be the result of recalibrating of a forward model that associates motor commands with their sensory consequences. Here we investigated whether similar perceptual changes occur in the lower limbs after learning a new walking pattern on a split-belt treadmill- a task that critically involves proprioception. Specifically, we studied how this motor learning task affects perception of leg speed during walking, perception of leg position during standing or walking, and perception of contact force during stepping. Our results show that split-belt adaptation leads to robust motor aftereffects and alters the perception of leg speed during walking. This is specific to the direction of walking that was trained during adaptation (i.e. backwards or forwards). The change in leg speed perception accounts for roughly half of the observed motor aftereffect. In contrast, split-belt adaptation does not alter the perception of leg position during standing or walking, and does not change the perception of stepping force. Our results demonstrate that there is a recalibration of a sensory percept specific to the domain of the perturbation that was applied during walking (i.e. speed, but not position or force). Further, the motor and sensory consequences of locomotor adaptation may be linked, suggesting overlapping mechanisms driving changes in the motor and sensory domains.

Introduction
Recent work has shown that reaching adaptation not only recalibrates the motor system, but can also result in changes in kinesthesia (the sense of limb position and movement). Studies in healthy adults have shown that perceived hand position can change after adapting to a force field perturbation (Haith et al. 2008; Ostry et al. 2010; Mattar et al. 2013), a visuomotor rotation (Cressman and Henriques 2009; Salomonczyk et al. 2011; Salomonczyk et al. 2012) and after experiencing discrepancies in visual and proprioceptive estimates of the hand (Cressman and Henriques 2010a; Salomonczyk et al. 2013). One idea is that changes in kinesthesia are a result of recalibration of a forward model that predicts the sensory consequences of movement (Izawa et al. 2012). For example, Cressman and Henriques (2009) showed that a visuomotor perturbation to reaching movements resulted in a roughly 20% change in perceived hand position relative to the magnitude of both a translation perturbation and a rotation perturbation. This motor and sensory recalibration appears to rely on intact cerebellar function (Synofzik et al. 2008; Izawa et al. 2012). This suggests that changes in the perception of hand position are a result of an error-based adaptation in the motor domain.

Yet, other studies suggest that these types of perceptual changes can represent a process that is independent from adaptation and forward model recalibration. One recent example from Cressman and Henriques (2010a) showed that people have aftereffects in both motor and perceptual domains after subjects were exposed to a sensory mismatch in the absence of movement related error signals. Another is the well known “rubber hand illusion” in which proprioceptive sense of the arm can be biased following synchronous tactile stimulus of a subject’s unseen hand and a displaced rubber hand that the subject can see (Botvinick and Cohen 1998). Finally, we have shown that patients with cerebellar ataxia can change their proprioceptive hand estimates to match a visual estimate, independent of motor adaptation.
(Block and Bastian 2012). These results suggest that although motor and sensory recalibration processes often take place simultaneously, motor adaptation is not necessary for sensory realignment to occur.

To date, most work has focused on adaptation of movements of the arm. It is well known that similar motor adaptation processes occur during walking. We have previously shown that split-belt treadmill walking adaptation leads to adaptation and storage of several kinematic measures including step length and timing (Reisman et al. 2005; Morton and Bastian 2006; Choi and Bastian 2007; Choi et al. 2009; Vasudevan et al. 2011; Malone and Bastian 2010; Malone et al. 2012) and kinetic parameters such as ground reaction forces and the center of pressure (Mawase et al. 2013). It is unclear whether perceptual changes will also occur in any of these domains. Walking and reaching require different kinds of control, the former using rhythmic motor networks to produce the stepping pattern whereas the latter relies more on visuomotor control to direct the hand (Pearson 2000). However, both involve the cerebellum, and might show similar effects from recalibration of a forward model.

Little is known about changes in the perceptual-kinesthetic domain during walking. We are only aware of one study that investigated changes in speed perception after split-belt walking. Jensen and colleagues (1998) found that after split-belt walking, subjects experienced a perceptual aftereffect such that the leg that experienced a fast speed felt slower afterward and vice versa. In that study, kinematic data were not recorded, so investigators could not examine the extent of motor learning or the relationship between motor and sensory aftereffects of learning. Furthermore, changes in other perceptual parameters such as position and force have not been investigated in the context of split-belt adaptation. Here we asked which perceptual sensory changes, if any, are associated with split-belt adaptation and how they relate to changes
in the motor domain. The study was divided into separate experiments to independently measure perception of leg speed, foot position, and stepping force. We hypothesized that split-belt adaptation could lead to perceptual changes in all three parameters.

**Material and Methods**

**Subjects**

Ninety right hand and right leg dominant volunteers (37 M, 53 F; Age: 23 yrs ± 3.3) participated in this study. All subjects were prescreened for self-reported handedness, leg dominance and neurological/motor dysfunction. The protocol was approved by the Johns Hopkins Institutional Review Board and all participants provided written informed consent before testing.

**General Experimental Setup**

*Split-belt treadmill.* Split-belt walking adaptation was studied using a custom-built treadmill (Woodway, Waukesha, WI) which had two separate belts driven by independent motors. Speed commands for each belt were sent to the treadmill through either a custom MATLAB (The MathWorks, Natick, MA) program or a custom Python program in the Vizard (WorldViz, California USA) development environment, depending on the task performed by the subject. Vertical forces exerted on each belt were recorded at 1000 Hz. Subjects wore a safety harness which did not support their body weight and were positioned in the middle of the treadmill with one leg on each belt.

*Optotrak motion analysis.* Kinematic data were collected at 100 Hz using Optotrak (Northern Digital, Waterloo, ON, Canada). Bilateral infrared-emitting markers were placed over the toe (fifth metatarsal head), ankle (lateral malleolus), knee (lateral femoral epicondyle), hip (greater trochanter), pelvis (iliac crest), and shoulder (acromion process).
Experimental Protocols

General split-belt walking adaptation

In all experiments, the split-belt walking paradigm consisted of four main walking periods (Figure 1A), as follows: Baseline: all subjects walked with tied belts (.5 m/s). Adaptation: subjects experienced either a 3:1 belt-speed perturbation (“Split”) or tied belts (“Control”) condition (both belts: 1.5 m/s). Catch trial: To probe the magnitude of learning during adaptation, subjects were given a brief (10 second) exposure to tied belt (.5 m/s) walking before resuming split-belt walking. Post-adaptation: all subjects walked with tied-belts (.5 m/s) to analyze motor aftereffects (i.e. how subjects unlearn the new walking pattern).

Experiment 1A: Walking Speed Perception

To investigate changes in leg speed perception due to split-belt walking, we designed a speed-matching task using the psychophysical method of adjustment, similar to previous work (Jensen et al. 1998). This was done using custom a Python program which allowed for simultaneous control of the treadmill, real-time visual feedback, and collection of subject data. The experimental setup is shown in Figure 1B. Subjects were positioned on the treadmill and instructed to place their left hand on a handrail in front of the treadmill and their right hand on a small keypad. Vision of the legs was obstructed via an opaque drape, and auditory cues of speed from the treadmill motors were cancelled via headphones playing white noise. Initially, the left leg was driven to walk at a constant speed of 0.5 m/s, while the right leg was not moving. Subjects were instructed to press up or down arrows on the keypad in front of them to adjust the speed of the right leg until they perceived it to match the speed of the left leg (reference leg). Reference leg speed was always 0.5 m/s to avoid introducing a declarative memory component to the task of remembering the reference leg speed. Subjects were given 30 seconds to complete
the task, and were given feedback on the amount of time remaining via a television monitor in front of the treadmill. When the right leg was within the range 0.0 - 0.45 m/s, key presses resulted in speed increments of .05, .055, or .065 m/s (these increments were varied with each iteration of the task so subjects were unable to simply count the number of key presses needed to reach the target speed). Once the speed passed 0.45 m/s, key presses resulted in a smaller change in speed, .005 m/s, to allow for fine control of speed as the right leg approached the target speed.

For Experiment 1A, subjects were randomly assigned into one of two groups: Split (n=10) and Control (n=10). The experimental paradigm is shown in Figure 1A. Subjects performed three periods of baseline (tied-belt walking) each followed by the speed-matching task. Next, they walked for 15 minutes in either split-belt or tied-belt (both belts 1.5 m/s) conditions, with a 10 second catch trial occurring after the first 10 minutes to measure the magnitude of motor learning up to that point. Lastly, all subjects walked for 12.5 minutes with tied belts in the post-adaptation period. Walking was briefly interrupted at six time-points throughout post-adaptation so subjects could perform the speed-matching task to assess decay of sensory aftereffects over time.

**Experiment 1B: Generalization of Walking Speed Perception**

To determine whether perceptual speed changes after split-belt adaptation were general changes in speed perception or specific to the split-belt walking task, we modified the walking speed perception paradigm to investigate whether forward-direction split-belt walking induced perceptual speed changes in the backward walking direction (Reverse group; n=10). The paradigm was similar to that of the original walking speed perception experiment, but in addition to all of the forward walking and forward speed matching tasks, subjects also performed backwards walking and backwards speed matching tasks. Specifically, after each pair of forward
baseline and forwards tasks, we added a pair of tied backwards walking (.5 m/s) and backwards speed matching tasks. The backwards walking task had the same target goal of 0.5 m/s as the original speed matching task, but occurred in the backwards direction. To measure the generalization to backwards walking in the motor domain, we also added a backwards catch trial directly before the forward catch trial and a backwards speed matching task directly after adaptation to measure generalization in the perceptual domain.

**Experiment 2A – Passive Foot Position Perception**

To investigate changes in passive foot position perception, we designed a position task using the psychophysical method of constant stimuli, where subjects were repeatedly asked to judge the location of their right foot relative to their left foot at various locations. This method was used to mirror analogous reaching adaptation studies that investigated changes in perceived hand position (Cressman and Henriques 2009, 2010a; Mattar et al. 2013; Ostry et al. 2010; Salomonczyk 2011). Subjects were oriented on the treadmill with one leg on each belt, and were instructed to keep their left foot fixed under their trunk (as shown in Figure 2B). Subjects lightly held on to the handrail in front of them. The subject’s right leg was initially moved to one of three “pre-target” locations in front of the left foot, then moved to one of nine target locations uniformly distributed in front or behind the left foot (see Figure 2C). Once the target location was reached, subjects were instructed to verbally express whether they felt their right foot was “in front” of or “behind” their left foot. The task was repeated in a pseudorandom fashion such that each of the nine targets was visited 12 times, resulting in 108 total trials. As in Experiment 1, vision of the legs was obstructed for the duration of the task, and to prevent subjects from using auditory cues to detect how far the right belt was moved to reach the target they wore headphones, which played white noise for the duration of the experiment. Right belt velocity was
variable to reach each target (e.g. faster movements for farther targets) to ensure movement
duration was fixed at 1.5 seconds.

The foot position perception task was performed immediately before and after 15 minutes
of split-belt treadmill adaptation or tied-belt walking (Figure 2A). Subjects were randomly
assigned to one of three groups, which performed slightly different variations of the task in order
to investigate leg-specific and movement direction-specific changes. Figure 2C illustrates the
experimental groups and their pre-target locations. The Right-Fast Top-Down (RFTD) group
performed the foot position perception task such that the right foot was moved to an initial
position in front of the left foot, and split-belt adaptation was performed with the right leg as the
“fast” leg. The Control group (C) performed the same perceptual task, but walked with tied belts
at a speed of 1.5 m/s instead of split-belt walking (i.e. did not learn a new walking pattern).
Lastly, the Right-Fast Bottom-Up (RFBU) group performed split-belt walking with the right leg
as the “fast” leg (as the RFTD group did), but performed the foot position perception task with
the right foot initially moved to a position behind the left foot before proceeding to the final
target. During forward walking, the subject only experiences the treadmill moving their feet from
forward to backward, thus we tested the RFBU group to investigate if any effects were direction-
specific.

Experiment 2B – Active Foot Position Perception

To determine whether any perceptual position changes after split-belt adaptation are
specific to the active walking context, we had a separate group of participants (Active Position
group; n=10) perform a foot position-matching task while walking. The paradigm mirrored that
of Experiment 1A (Figure 1A), where subjects were given 30 seconds to match their right foot
ankle position at heel strike to the previous left foot ankle position at heel strike while walking
with tied belts at a speed of 0.5 m/s. Subjects were given visual feedback of the position of their left (i.e. reference) step on a television monitor. Visual feedback was presented on a television monitor via a grid of twenty numbered targets, which ranged from 0 to 20 (as shown in Figure 1C). Each rectangular target represented 2 cm in physical treadmill space. At each left heel strike, subjects received end-point feedback in the form of a red sphere at the appropriate target, which represented the anterior-posterior distance between their left ankle and the average of their left/right hip positions. The mapping between step distance and visual feedback on the display was linear. No feedback was given for the right step, and subjects were asked to use their sense of foot position to match their right foot position to that of the previous left foot position at heel strike. Subjects performed this task three times at baseline and at specific intervals throughout post-adaptation. Prior to the beginning of the experiment all subjects were given a 2 minute “warm-up” block where they received visual feedback for both feet at heel strike and were asked to explore different size steps in order to gain an understanding of the visual feedback mapping. Similar to Experiment 1A, subjects performed the task with a divider on the treadmill that separated the legs and wore a drape that obstructed visual feedback of the legs. Auditory feedback was not removed, as it did not provide any relevant cues.

Experiment 3 – Stepping Force Perception

To determine whether stepping force perception changes during split-belt adaptation, we developed a stepping force perception task employing a form of the method of adjustment (see Figure 3B for experimental setup). Subjects were asked to adjust the amount of force when stepping on the belt with one foot and then recreate the force with the other foot. This force-matching task was performed immediately before and after 15 minutes of split-belt treadmill adaptation (Split group; n=10) or tied-belt walking (Control group; n=10) (Figure 3A). During
all walking, visual feedback of the legs was obstructed as in the previous experiments. Before any baseline walking, subjects were first instructed to stand on the treadmill so body weight could be recorded via force plates in the treadmill and to complete a training period to become familiar with the task. To perform the task, subjects were presented with one of four visual targets (a white box displayed on a screen in front of the treadmill) with varying height, representing 40%, 50%, 60%, and 70% (all ± 5%) of their body weight. For instance, when the 50% body weight target was displayed, the box represented 45-55% of the subject’s body weight. The following describes a typical trial made up of a “reference” step and a “test” step. In the first half of each trial, subjects were asked to perform a “reference” step in order to assess how accurately they could produce a given force with visual feedback. For these trials, the target appeared, and subjects were asked to take a step forward with their left leg, exerting force on the left treadmill belt. As force was applied to the belt, a green bar on the visual display increased in height to demonstrate the amount of force applied. Subjects were instructed to exert a force such that the height of the green bar was as close to the center of the white box as possible. In the second half of the trial, subjects performed a “test” step in order to assess how well they could remember and replicate the force exerted by the left foot during the reference trial. Unlike the reference trial, subjects did not receive visual feedback of the force applied, but were shown the same target. The entire trial (reference + test step) was repeated a total of 40 times, with each reference and test force pair executed 10 times. In order to control for position of stepping, elastic bands were placed in front and behind the subject to give tactile cues for where to start and end a step (approximately 16 inches apart).

Data Analysis

Motor Adaptation
In all three experiments, our primary measure of adaptation in the motor domain was step symmetry – a parameter previously shown to adapt robustly during split-belt treadmill walking (Reisman et al. 2005), calculated as the difference in fast and slow step lengths, normalized to their sum to allow for comparisons across subjects who might take different-sized steps and have different leg lengths (Eq. 1) (Malone and Bastian 2010). Step length was defined as the anterior-posterior distance between the ankle marker of each leg at heel strike of the leading leg (i.e. fast step length ($SL_f$) refers to the step length measured at fast-leg heel strike, and vice versa for slow step length ($SL_s$)). A step symmetry value of 0 indicates symmetric walking, and a positive value means that the fast step is larger than the slow step.

$$Step\ Symmetry = \frac{SL_f - SL_s}{SL_f + SL_s} \quad (Eq. \ 1)$$

Walking Speed Perception

The walking speed perception task was designed to measure the ability of subjects to match the speed of their right leg to that of the left (set at a constant speed of 0.5 m/s). To assess performance, we recorded changes in right leg speed as the task was performed and quantified each subject’s response to the task as the final speed of the right leg at the end of each 30-second trial.

Passive Foot Position Perception

Passive foot position was measured by fitting a standard logistic function (using psignifit, see http://bootstrap-software.org/psignifit/) to each subject’s responses in the position task before and after split-belt adaptation. For each foot position target, we calculated the percentage of subject responses indicating the right foot was perceived to be in front of the left. This information was used to determine the point of subjective equality (PSE: the point at which each subject’s response accuracy was 50%), indicating the subject’s ability to detect changes in a
stimulus (in this case, changes in foot position).

Active Foot Position Perception

Active foot position was measured by calculating the difference between the left and right ankle positions at heel strike for two consecutive steps. Specifically, we subtracted the left ankle position at heel strike from the subsequent right ankle position at heel strike (i.e. positive values indicate the right foot stepped in front of the left). For each task, we calculated this value for the last 5 strides and then averaged them for a final response.

Stepping Force Perception

Differences in applied stepping force between the reference force and the test force were calculated as $\Delta Force_{Test-Ref}$ for both pre and post-adaptation, where the reference leg was the right leg and the test leg was the left leg. To determine changes in force perception before and after split-belt adaptation, we calculated our main outcome parameter, $\Delta Force_{Post-Pre}$.

Statistical Analysis

Motor Assessments:

Step symmetry was calculated at specific time-points throughout each experiment: Baseline (last 10 strides of baseline walking), Early adaptation (first 5 strides of adaptation), Catch trial (first 3 strides of catch trial), Late adaptation (last 10 strides), Early post-adaptation (first 5 strides of post-adaptation), and Late post-adaptation (last 10 strides). One-way ANOVAs or t-tests were used to compare baseline-walking averages. One-way repeated-measures ANOVAs were used to compare these six time-points with factor TIME to assess within-group changes in step symmetry during split-belt walking. We then used two-way repeated-measures ANOVAs to compare data between groups with factors GROUP and TIME. Post-hoc analysis
was performed using Fisher’s least significant difference (LSD) test. The Greenhouse-Geisser correction was used as needed to correct for violations of Mauchly’s test of sphericity.

**Sensory Assessments:**

Performance on sensory tasks was compared between groups using two-way repeated-measures ANOVAs with factors GROUP and TIME (Experiments 1 and 2) or GROUP and TARGET (Experiment 3). For Experiment 1, six time-points were used: the post-adaptation time-points when the speed-matching task was performed. Baseline task averages were compared using t-tests. To compare the decay of motor and sensory aftereffects in Experiment 1, we additionally used two-way repeated measures ANOVA with factors MODALITY (i.e. step symmetry during either motor or sensory tasks) and TIME across the six post-adaptation time-points. In Experiment 2A, pre and post-adaptation values for PSE and curve slopes (uncertainty) were compared using a repeated measures ANOVA. In Experiment 2B, post-adaptation data was baseline-subtracted, and we performed one sample t-tests at each of the six post-adaptation time-points to measure significant changes compared to zero. Lastly, in Experiment 3, we compared changes in force perception at the 40%, 50%, 60%, and 70% body-weight force targets. In all cases, post-hoc analysis was performed using Fisher’s LSD test. The Greenhouse-Geisser correction was used as needed to correct for violations of Mauchly’s test of sphericity.

**Results**

**Experiment 1:**

*Motor learning is necessary for change in leg speed perception*

We first confirmed whether subjects from the Split group learned and retained a new walking pattern and that the Control group did not. Subjects in both Split and Control groups
were able to complete the walking task without difficulty. Typical single subject data is shown in Figure 4A. As expected, split-belt walking resulted in robust adaptation of step symmetry, while tied-belt walking resulted in no change. Group data, truncated to the lowest number of strides across groups for each walking period (baseline, adaptation, post-adaptation) are shown in Figure 4B for all groups (note: Reverse Group results (green) are discussed in the following section). Baseline walking step symmetry, measured by the mean step symmetry of the last 10 strides of baseline walking, was not significantly different between Split and Control groups (p = 0.896). Analyzing changes in step symmetry across walking periods (baseline, early adaptation, catch trial, late adaptation, early post-adaptation, late post-adaptation), our one-way ANOVA demonstrated that the Split group significantly altered their step symmetry (F(5,45) = 86.165, p < 0.001), but the Control group did not (F(5,45) = .583, p = 0.713). Post-hoc comparisons in the Split group showed significant changes between baseline step symmetry and early adaptation (p < 0.001), catch trial (p < .001), early post-adaptation (p < 0.001), and late post-adaptation (p = 0.025). These results were as expected, as we have previously shown that step symmetry adapts in this manner as a result of split-belt treadmill walking (Reisman et al. 2005).

To parallel the motor adaptation result, we saw similar changes in leg speed perception as a result of split-belt walking. Specifically, while the Split group demonstrated altered performance in the speed-matching task after split-belt adaptation, no change was seen in the Control group. Typical single subject responses to the speed matching task are shown in Figure 5A. While both Split and Control subjects were able to match the speed of the right leg (shown in Figure 5A) to that of the left leg (held constant at 0.5 m/s) before adaptation, only Split Group subjects exhibited changes in their response after the adaptation period. The overshoot response in the Split group subject indicates a change in leg speed perception after adaptation: the “fast” leg
during adaptation (right leg) was perceived to be moving slower after adaptation. As such, Split group subjects overshot the target speed of 0.5 m/s during the post-adaptation speed perception task.

Figure 5B shows group speed perception data at each of the six time points the task was performed after adaptation (data shown as $\Delta$Speed, the size of the “overshoot” in the task response). Before computing group averages shown in Figure 5B, each subject’s baseline performance was subtracted from subsequent data for the purpose of normalization. No significant differences were found between Split and Control group baseline task performance ($p = 0.308$). Comparing post-adaptation task performance, our ANOVA showed a main effect of GROUP ($F(1,9)=47.916$, $p < 0.001$), TIME ($F(5,45)=11.156$, $p < 0.001$) and an interaction of GROUP x TIME ($F(5,45)=13.468$, $p < 0.001$). These results indicate that during post-adaptation, the Split group demonstrated changes in leg speed perception compared with the Control group that eventually decayed.

One goal of the present study was to investigate how changes in sensory perception as a result of walking adaptation might relate to changes in the motor domain. Our data suggest that both motor and sensory changes decayed on a similar time-scale (Figures 4B, 5B). Like the motor aftereffects, it appears that changes in leg speed perception took approximately 15-16 minutes to return to baseline values. However, comparing motor and sensory changes in this manner presents a problem: step symmetry is a unitless parameter, yet $\Delta$Speed is measured in m/s. As a resolution, we carried out a subsequent analysis to determine the step symmetry values for each corresponding time-point during the speed-matching task. Figure 6 shows that the initial aftereffect in the speed-matching task is approximately 52% of the initial motor aftereffect. It also shows that the time-course of motor versus sensory perceptual after-effects decay on
different timescales. To analyze this further, we performed two-way repeated measures ANOVA (six post-adaptation times points; first 5 strides of motor post-adaptation blocks and last 5 strides of each speed task) to compare the motor and perceptual decays. The ANOVA showed a main effect of MODALITY \( F(1,18)= 9.556, \ p = 0.006 \), TIME \( F(5,90)= 28.907, \ p < 0.001 \) and an interaction of MODALITY x TIME \( F(5,90)= 4.189, \ p = 0.014 \). Post-hoc comparisons showed that time points 1-4 were significantly different between groups (\( p < 0.05 \)) but time point 5 (\( p = 0.103 \)) and time point 6 (\( p = 0.124 \)) were not significantly different, suggesting different decay rates between motor and perceptual aftereffects.

**Backwards walking**

Next, we asked whether forward split-belt adaptation led to a general perceptual aftereffect by testing if it transferred to the backward direction via a Reverse group. We first confirmed that baseline backwards walking performance was similar to forward walking (paired t-test, \( p = 0.590 \)). We however found that the baseline backwards perceptual speed task was biased lower than the forward walking baseline task (paired t-test, \( p = 0.001 \)). Our main interest however, was in observing pre to post-adaptation changes, making this difference less important. We also confirmed that both the Split and Reverse groups adapted the same amount by showing no difference in forward walking catch trial magnitude (compare light green and blue on Figure 4, paired t-test \( p=0.811 \)).

We then analyzed the transfer from forward to backwards walking in the Reverse Group. In the motor domain, we found small effects in the backwards catch trial step symmetry, as shown in Figure 4B (dark green circle, \( p = 0.038 \)). Likewise, we found a very small change in the backwards speed-perception task response, as shown in Figure 5B (dark green symbol, \( p = \).
The magnitude of the backwards effects were however, closer to baseline performance
than the forward walking effects.

We noted that the small motor effect in backwards walking was the opposite of what we
saw in the forward direction. Figure 7A illustrates this: during the catch trial for forward walking
(closed symbols) the fast leg takes a longer step while the slow leg takes a shorter step, which is
a typical aftereffect. The backwards-walking averages (open symbols) show that subjects take
smaller steps and exhibit a small but opposite trend in the catch trial, with the slow leg taking the
longer step. When comparing the two groups with two-way repeated measures ANOVA we saw
that there was a main effect of TIME (F(1,18=.207, p < 0.001) and also an interaction of GROUP
x TIME (F(1,18)=28.358, p < 0.001). This suggests that the forward walking showed significant
changes in steps lengths (from baseline to the catch trial) not present in backwards walking. This
is not consistent with what would be expected for true transfer of the learned pattern to
backwards walking.

We also looked carefully at the perceptual effect in backwards walking as shown in
Figure 7B. Subjects generally improve their ability to match the leg speeds over the 3 baseline
trials in both backwards and forwards walking. In the initial post-adaptation task response there
is a robust perceptual aftereffect in the forward task while the backward task is not significantly
different from the target speed (p = 0.712). This supplementary analysis seems to suggest
minimal or no transfer of the perceptual after-effect from forward to backwards walking.

Experiment 2:

No change in perceived passive foot position after adaptation
In contrast to the significant change in leg speed perception found in Experiment 1, we found no significant difference in perceived foot position in the passive context after split-belt adaptation. Typical single subject responses and logistic fits for the passive foot position perception task are shown in Figure 8A. We should note that in these examples, that there is a change in uncertainty (slope of the curves). However, when comparing these slopes (between 25% and 75% positions) between groups we found no significant effects of GROUP (F(1,27) = 0.041, p=0.960), TIME (F(1,27) = 0.490, p = 0.490) or GROUP x TIME interaction (F(2,27) = 0.719, p=0.496). Logistic fits for each task for all of the subjects had significant goodness of fit (as measured by deviance values in psigniFit). Group changes in point of subject equality (PSE) pre and post-adaptation are shown in Figure 8B. In general, data showed that subjects who performed the task in the top-down direction (RFTD and C) had a positive PSE bias (i.e. they perceived the right leg to be positioned more posteriorly than it actually was), and the bottom-up group (RFBU) demonstrated a negative bias. However, our repeated measures ANOVA showed no main effect of GROUP (F(2,27)=1.394, p = 0.265) or TIME (F(1,27)= 0.880, p = 0.356), but revealed a significant GROUP x TIME interaction (F(2,27)=6.887, p= 0.004). Post-hoc analysis did not show any significant differences between individual groups.

Motor behavior for all three groups is shown in Figure 8C. Repeated measures ANOVA showed main effects of GROUP (F(2,27)=7.768, p =.002), TIME (F(5,135) = 63.102, p < 0.001), and a GROUP x TIME interaction (F(10,135) = 15.632, p < 0.001) for step symmetry. As expected, post-hoc tests revealed that the Control group was significantly different from the groups that experienced split-belt adaptation (RFTD: p = 0.003; RFBU: p = 0.012), but no significant difference was found between the RFTD and RFBU groups (p = 0.837).
together, these results demonstrate that split-belt adaptation did not produce significant changes in passive foot position perception.

No change in perceived active foot position after adaptation

Like our results from Experiment 2A, we found no changes in perceived foot position after split-belt adaptation in the active walking context. We first ensured the amount of motor learning was equivalent to the Split group in Experiment 1A using an independent-samples t-test for the catch trial, which showed no significant differences in average step symmetry values between these groups (p = 0.407). The average group motor learning curve for Experiment 2B is shown in Figure 9A. Figure 9B shows group performance of the active foot position-matching task during post-adaptation compared to baseline. One-sample t-tests showed no significant differences for any post-adaptation tasks compared to zero (Post 1: p = 0.629; Post 2: p = 0.790; Post 3: p = 0.641; Post 4: 0.989; Post 5: 0.625; Post 6: 0.990). Together, the results from Experiments 2A and 2B demonstrate no perceptual changes in foot position due to split-belt adaptation in either passive or active walking contexts.

Experiment 3:

No change in perceived foot force production after adaptation

Similar to the results of foot position perception, we found no differences in stepping force perception after split-belt adaptation. Specifically, we investigated changes in stepping force perception between the two legs pre and post-adaptation. Typical group peak force measurements and single subject stepping force curves for a 60% target trial are shown in Figures 10A and 10B, respectively. For 40%, 50% and 60% targets, subjects in both groups tended to overshoot force on the reference leg, but this overshoot was much more pronounced in
the test leg. Figure 10C shows group data for pre/post-adaptation changes in our main force perception parameter, \( \Delta Force_{post-pre} \). Our ANOVA did not show significant main effects of GROUP (\( F(1,72) = .985, p = 0.324 \)), TARGET (\( F(3,72) = 0.999, p = 0.399 \)), or GROUP x TARGET (\( F(3,72) = 0.056, p = 0.983 \)) interaction. Motor adaptation results, shown in Figure 10D, were consistent with findings of Experiment 1 and 2. In summary, our results indicate that split-belt adaptation did not produce significant changes in stepping force perception compared to tied-belt walking.

**Discussion**

Here we show that split-belt adaptation leads to kinesthetic changes in leg speed perception during walking, but not stepping force or foot position in standing or walking. Specifically, the leg that moved faster during adaptation is perceived to move slower afterwards. This perceptual aftereffect is robust, decays with unlearning of the motor behavior, and is specific to the learned direction of walking.

We were surprised to find that sensory changes resulting from split-belt adaptation were specific to leg speed perception and did not occur for perceived passive or active foot position. While split-belt treadmill walking mainly causes a perturbation in leg speed, it also perturbs the position of the feet at heel strike and toe off. Our previous work (Malone and Bastian 2010) shows that like step symmetry, the angle about which the legs oscillate (an indicator of foot position) is initially perturbed, adapts, and shows robust aftereffects with split-belt walking. In related work, we showed that the landing position of each foot relative to one another is a motor output that is stored and actively de-adapted after split-belt walking (Malone et al. 2012). As such, we expected that this kinematic change would occur alongside a comparable change in
perceived foot position. However, this was not the case. When testing for perceived changes in passive foot position (treadmill initiated movements) we did not observe any significant changes in PSE or uncertainty. Based on previous work which showed that the cerebellum is vital for proprioception of active, self-driven movements, but not passive movements (Bhanpuri et al. 2013), one might expect that split-belt walking could lead to perceptual changes when probed in the active, rather than passive, context. However, results from the active foot position-matching task (Experiment 2B) paralleled those from the passive task, demonstrating no perceptual change in foot position regardless of the active or passive context.

It has been shown that split-belt walking also leads to after-effects in ground reaction forces and the motion of the center of pressure (Mawase et al. 2013). Because of this, we tested for perceptual changes in stepping force after split-belt adaptation but found no difference. We reasoned that stepping from one foot to the other would be similar enough to walking to see any perceptual effects, though we acknowledge that this might not be the case. We also cannot claim to have ruled out a change in passive force perception in the absence of movement (e.g. subjects could be asked to lie in a supine position and judge the force exerted on the bottom of their foot isometrically). That being said, we think it’s likely that other adaptation paradigms that involve specific force perturbations to the leg would result in recalibration of perceived force. For example, motor adaptation paradigms using force fields to perturb the leg during walking (Noel et al. 2009; Houldin et al. 2012) or elastic bands to assist or resist leg motions (Fortin et al. 2009; Savin et al. 2010) might recalibrate force perception.
The present study expands on previous work demonstrating that leg speed perception is recalibrated during split-belt treadmill walking. In particular, Jensen et al. (1998) showed that split-belt adaptation results in a fairly immediate change in the perception of leg speed such that the “fast” leg during adaptation feels slower after adaptation. Here we additionally show that rather than a transient change, this sensory aftereffect gradually decays over a period of 5-15 minutes on a similar timescale (albeit at a different rate) of motor aftereffects. Further, by expressing it in terms of a known motor parameter (step symmetry; see Figure 6), we demonstrate that the sensory aftereffect does not fully account for the motor aftereffect. In fact, the initial sensory aftereffect represents only approximately 50% of the magnitude of the motor aftereffect and converges with the motor aftereffect after approximately 6-8 minutes of washout. Other mechanisms, such as use-dependent plasticity and conscious control of walking, may explain the residual motor aftereffects not accounted for by the sensory recalibration.

Our results also show that both the motor and sensory consequences of split-belt adaptation are unique to the direction of adaptation. In other words, forward-direction adaptation has minimal to no aftereffects in the backward direction. This result builds upon previous findings that the motor aftereffects of split-belt walking are direction-specific (Choi and Bastian 2007). It should be noted that our current work shows very small transfer in the motor and perceptual domains, but our additional analysis suggests that these effects may be due to other factors. The small motor after-effect during walking is in the opposite direction that was trained, which suggests another mechanism might be at play. The perceptual effect could be explained by subjects’ initial baseline bias (underestimate) that improved with practice. After forward adaptation they showed no perceptual effect in backward walking.
While we have shown that locomotor adaptation only affects perception of leg speed, studies of the sensory consequences of reaching adaptation have primarily focused on changes in felt hand position. For instance, Salomonczyk and colleagues (2011) showed that adaptation to an abrupt, 30 degree visuomotor rotation resulted in a 7.3 degree shift in perceived hand position—a 24.3% change relative to the size of the perturbation. Our subjects, on the other hand, exhibit a change in perceived foot position of only 7 mm. It has been recently suggested that a split-belt treadmill perturbation with a 3:1 belt speed ratio, like the one used in this study, results in a spatial perturbation of 200 mm (Finley et al. 2015). As such, this 7 mm change in position perception can be quantified as a negligible 3.4% of the size of the perturbation. Leg speed perception, however, appears to be a much more salient percept for split-belt walking. Subjects in the Split group of Experiment 1 exhibited a .216 m/s change in perceived leg speed compared with baseline performance. Given the speed perturbation size of 1 m/s (the difference in the belt speeds during adaptation), this change in perception can be quantified as 21.6% - much closer to that of hand position perception found in the aforementioned reaching study. Considering that force field reaching adaptation studies frequently use perturbations that are velocity dependent (Haith et al. 2008; Ostry et al. 2010; Mattar et al. 2013), we were surprised to find that the effect of reaching adaptation on hand velocity perception has yet to be investigated. We speculate that determining this relationship would help inform us on the difference in control systems between reaching and walking adaptation.

The underlying mechanisms driving the change in leg speed perception following split-belt walking have yet to be determined. Anstis et al. (1995) showed that simply jogging on a regular treadmill can produce changes in perceived movement speed, suggesting a possible connection between sensory recalibration and use-dependent processes. Given that our split-belt
subjects exhibited perceptual aftereffects but control (fast, tied-belt walking) subjects did not, we interpret the sensory recalibration we observed to be closely tied to the error-driven, cerebellar dependent motor adaptation that occurs during split-belt walking. Along these lines, Izawa et al. (2012) and Synofzik et al. (2008) have argued that in reaching adaptation, recalibration of perceptual estimates are cerebellar-dependent. On the other hand, Henriques et al. (2014) suggested the above studies may have seen cerebellar patient deficits that are not purely due to a failure in predicting sensory consequences, as this is hard to measure. They state that these deficits might also be due to changes in felt hand position (pure proprioceptive recalibration) rather than exclusively efferent-based predictions. That explanation seems unlikely -- if a general proprioceptive recalibration occurred we might expect to see changes in the perceived speed of backward walking, which we did not. It is well known that the cerebellum is necessary for updating a forward model and driving locomotor adaptation (Morton and Bastian 2006; Jayaram et al. 2011; Jayaram et al. 2012), and plays a critical role in sensory perception of active hand movements (Bhanpuri et al. 2013). Furthermore, given that the cerebellum receives vast amounts of sensory information relevant to walking adaptation such as foot contact (Apps and Lidierth 1989) and limb angle (Bosco and Poppele 2001), it is likely to play an important role in changes in kinesthesia. Given this, as well as the fact that the sensory recalibration we observed was dependent on concurrent motor adaptation, we favor the possibility that the cerebellum plays an important role in the recalibration of leg speed perception we demonstrate in the present study.

We have shown that split-belt treadmill adaptation leads to changes in active leg speed perception, but not perceived foot position or stepping force. Further, we have demonstrated that the sensory changes resulting from split-belt adaptation are specific to the direction of learning. We speculate that the cerebellum plays a critical role in the effects we observed, and suggest that
testing these concepts on patients with cerebellar lesions may help elucidate the mechanisms underlying the sensory consequences of locomotor adaptation.

References


Figure captions

Figure 1. Paradigm and experimental setup diagram for speed-matching and active position-matching tasks. A: Paradigm for Experiment 1 and Experiment 2B. White blocks indicate tied belt walking (.5 m/s for both legs), grey blocks indicate split-belt walking (either both 1.5 m/s for Control Group (Experiment 1 only) or .5 m/s for left leg and 1.5 m/s for right leg for Split Group), and orange blocks indicate speed matching tasks (left leg .5 m/s and right leg adjusted by subject). Initially, subjects performed 3 baseline walking and speed matching task blocks, each consisting of 1 minute tied belt walking and a 30 second speed task (see Methods for task details). Next, during the adaptation block subjects either experienced a split-belt condition (Split Group) or a fast-tied condition (Control Group) for 15 minutes. Two-thirds of the way through this adaptation block a “catch trial” was introduced where both belts were returned to baseline speeds (.5 m/s) for 10 seconds, to assess amount of motor learning. After adaptation, both groups performed 6 speed matching tasks separated by 5 tied-belt “post-adaptation” blocks of increasing length (note: figure is not to scale). B: Experiment 1 speed matching task setup where subjects actively walked on the treadmill and pressed the keypad to change the speed of the right belt to match the constant left belt speed. Subject wore headphones that played white noise to cancel auditory treadmill cues and a flexible cloth drape in front of them to eliminate visual cues of feet. Infrared markers on the side of the body were used for motion capture. Physical divider separated two belts to avoid tripping. Subject also wore a safety harness in case of falling but did not support body weight. C: Setup and feedback seen by subjects in Experiment 2B (Active Position group). The experimental setup was similar to that of Experiment 1 except that no headphones were worn since the treadmill was not changing speed. Subjects received visual feedback at heel strike for the length of their step (anterior-posterior difference of left
ankle position minus hip marker position) in the form of a red sphere. No feedback was given for the right foot. Subjects were instructed to match their right foot position at heel strike to their previous left foot position at heel strike.

**Figure 2.** Paradigm and experimental setup diagram for position perception task. A: Experiment 2 paradigm. White and grey blocks represent baseline and split-belt walking with the same speeds described in Experiment 1. Orange blocks represent where the position task took place (roughly 10 min in length). Baseline walking was reduced to 4 minutes. The length of adaptation was the same as in Experiment 1. During adaptation, the Right Fast Top Down (RFTD, dark blue) and Right Fast Bottom Up (RFBU, light blue) experienced a 3:1 split perturbation with their right leg as the “fast leg”. Finally, the Control group (red) walked with fast tied belts as in Experiment 1. Post-adaptation was the same as in Experiment 1. B: Experiment 2 position task setup was the same as in Experiment 1 except the divider was not used to eliminate extra proprioceptive cues. The subject’s left foot remained at rest and the right leg was moved at every trial by the treadmill to a pre-target and then to a final target around the left foot. Subjects then proceeded to give a verbal response of whether they felt their right foot was either “in front” or “behind” their left foot.

**Figure 3.** Paradigm and experimental setup diagram for stepping force perception task. A: Paradigm for Experiment 3. All walking portions (white and grey boxes) were the same as Experiment 2 except baseline walking was reduced to 2 minutes. Orange blocks indicate where the force task (roughly 5 minutes in length) took place. Experiment 3 only had two groups: Split Group that experienced a 3:1 perturbation with right leg as “fast leg” and a Control Group that
walked with fast tied belts during adaptation, as was done in Experiment 1. B: Experiment 3 stepping force perception task setup. Subject stood on the treadmill in front of a television monitor where they were prompted to “step left” first and then “step right” at every trial. For the reference stepping force of each trial (done with left leg) subjects saw a target (white dashed rectangle) and a green bar increased in height depending on their stepping force. They were instructed to fluidly execute a step such that their maximum force hit the middle of the target rectangle. For the “test” stepping force (done with right leg) they were instructed to recreate the same force they exerted during the reference step but with no visual force feedback. Flexible elastic bands (shown in green) served as cues to indicate where subjects should step.

Figure 4. Experiment 1 motor results for all groups. A: Single subject data for the step symmetry parameter is shown for both a typical Control (top) and a Split Group subject (bottom) for a full experiment. Orange dashed lines represent where 30-second speed matching tasks took place. Black dashed zero line represents baseline symmetry. B: Group step symmetry results for the Control (red), Split (blue), Reverse Group forward walking (light green) and Reverse Group backwards walking (dark green). Curves are smoothed with a running average of 3 strides. Shaded regions represent standard error of the mean (SEM). Closed circles represent the tied belt catch trial. Light orange dashed lines indicate where the forward walking speed-matching tasks took place (all groups) and dark orange dashed lines indicates where the backwards walking speed matching tasks took place (only Reverse Group).

Figure 5. Speed matching task results for all groups (Experiment 1). A: Typical speed matching task responses for a Control Group subject (top) and Split Group (bottom) are shown. Subject
speed adjustment responses (keypad presses) are plotted for the third baseline task (grey), initial
post-adaptation tasks (black), as well as the target speed (.5 m/s) in the black dashed line. The
speed at the end of each 30-second task block is the final response for that task and is used to
calculate group averages. From this figure we see that while both subjects are accurate in
achieving the target speed during baseline, only the Split Group subject shows an increase in
their response after adaptation, indicating a change in leg speed perception. B: Average group
speed matching task aftereffects for Experiment 1A: Control (red) and Split (blue) and
Experiment 1B: Reverse Group forward walking task (lime green) and Reverse Group backward
walking task (dark green) are shown. Baseline averages (mean of 3 baselines task responses) are
subtracted from the post-adaptation values. Error bars represent SEM.

**Figure 6.** Motor and speed task motor behavior after-effect decay for Experiment 1A. Plot with
group averages for the Split Group (blue) and Control Group (red) are shown for motor
aftereffects (solid lines) and corresponding step symmetry at the end of each task for each group
(dashed lines). Baseline averages subtracted for each. Solid lines indicate step symmetry
averages (5 strides) at the beginning of all post-adaptation walking blocks and also at the end of
the last block. Dashed lines and open circles indicate step symmetry averages (5 strides) at the
end of each post-adaptation speed-matching task. The control group showed no change. Time
points 1-4 were significantly different between the motor after-effect and the speed matching
effect in the Split belt group (p < 0.05), indicated by the asterisk.

**Figure 7.** Reverse Group forward and backwards walking step length averages and perceptual
speed task results (Experiment 1B). A: Step length averages for baseline and catch trial. Open
symbols and dashed lines represent backwards walking and solid symbols and lines are forward walking. Fast leg data during adaptation (right leg) are shown as triangles and slow leg as circles. While baseline step lengths for backwards walking are shorter than forward walking, they are both symmetric. However, the forward group shows a typical aftereffect in the catch trial with a longer fast leg step and shorter slow leg step (results in a large positive step symmetry value). The backwards walking shows the opposite trend, though much smaller changes (small negative step symmetry). This suggests this is not true transfer from forward to backwards walking direction. B: Three baseline and initial post-adaptation averages for perceptual speed task for Reverse Group. These data show that in the backwards speed matching task, subjects tended to have a bias further away from the target speed. Importantly, the post-adaptation backwards speed task was not significantly different from the target speed (p=.712), suggesting this is not a true aftereffect.

Figure 8. Position perception task results and corresponding motor results (Experiment 2). A: Representative Split Group subject (left) and Control subject (right) psychometric fits for position task for pre (grey) and post-adaptation (black). The x-axis represents the position of the right foot relative to the left foot. Each tick (9 total) is an individual final target location where subjects were asked whether their right foot was either ‘in front’ or ‘behind’ the left. The y-axis is the percentage of times the subject answered right in front of left. Logistic curves are fit to these points. The .5 mark is the point of subjective equality (PSE) and where 50% of the time they answered right in front of left. The PSE was our measure of where they perceived their foot to be located. B: Group pre (grey) and post-adaptation (black) PSE averages. Error bars represent SEM. C: Step symmetry values for all groups.
Figure 9. Group motor and perceptual results for active position task (Experiment 2B). A: Group motor learning curve (step symmetry) for all walking blocks averaged across subjects (shaded regions indicate SEM). Foot-position tasks occurred at the orange dashed lines. Comparison of amount of learning (i.e. catch trial magnitude) were not significantly different from the Split group in Experiment 1A (p = 0.407). B: Baseline-subtracted group averages for right-left ankle positions at heel strike for each post-adaptation task, as a function of time. Error bars represent SEM. One sample t-tests showed no significant differences from zero for any of the six post-adaptation tasks.

Figure 10. Force matching perception task results and corresponding motor results (Experiment 3). A: Group peak force averages for all 4 stepping force targets for reference leg (filled circles) and test leg (open circles) for both pre (left) and post-adaptation (right). Reference leg forces are closer to desired targets than the test leg but both showed overshooting, especially on the lower percentage targets. B: Representative single trial stepping force (as percentage of body weight) trajectory data for a Split Group subject (left) and Control Group subject (right). Circles show example peak forces that are extracted to use as final response for each trial. Solid curves represent the reference force trajectories (with visual feedback) and dashed curves represent opposite test leg force trajectories (without visual feedback). Grey curves are pre-adaptation and black curves are post-adaptation data. C: $\Delta$Force$_{Post-Pre}$, the main parameter used to quantify how force perception changes as a result of adaptation, is shown for all targets. D: Group step symmetry averages for the Control Group (red) and Split Group (blue). As expected, the split group shows typical adaptation and retention of the walking pattern while the control does not show any changes.
Experiment 1 and 2B

Baseline

1 min 30 s x 3

Adaptation

10 min 10 s 5 min

Post-Adaptation

30 s 30 s 1.5 min 3.5 min 7.5 min

Catch

- tied belt (slow)
- split-belt (3:1) or tied-belt (fast)
- walking speed matching task

B

Subject Controlled Speed

Left Leg Right Leg

C

Constant 0.5 m/s Subject Controlled Speed

L Ankle Pos Hip Pos
Experiment 2A

Baseline
- 4 min
- 108 Trials
- ~10 min

Adaptation
- 10 min
- 10 s
- 5 min
- Split-belt (3:1) or tied-belt (fast)
- Catch

Post-Adaptation
- 108 Trials
- ~10 min
- 5 min

A

B

C

Left Foot (Fixed)
Right Foot (Moved)

160
140
120

80
60
40
20
0
-20
-40
-60
-80
-120
-140
-160

Control (C)
Right Fast Top Down (RFTD)

Right Fast Bottom Up (RFBU)

[Position Relative to Left Foot in mm]
Experiment 3

Baseline

2 min

40 Trials
~5 min

Adaptation

10 min

10 s

5 min

Post-Adaptation

40 Trials
~5 min

5 min

A

B

A

B

Step Left

1

force matching task

split-belt (3:1) or
tied-belt (fast)

tied belt (slow)

A

Control Group Subject

Step Symmetry

Number of Strides

Baseline
Adaptation
Catch Trial
Post-adaptation

B

Split Group Subject

Step Symmetry

Number of Strides

Baseline
Adaptation
Catch Trial
Post-adaptation

Control Group
Split Group
Rev Group (Fwd Walking)
Rev Group (Bkwd Walking)
Baseline
Fwd Speed Task
Bkwd Speed Task

Exp. 1A
Exp. 1B
A

Baseline Catch Trial

Step Length [m]

-△- Fast Leg (Fwd Walking)
-●- Slow Leg (Fwd Walking)
-Δ- Fast Leg (Bkwd Walking)
-○- Slow Leg (Bkwd Walking)

Baseline Catch Trial

B

Baseline 1 Baseline 2 Baseline 3 Post-Adaptation

Fwd Speed Task
Bkwd Speed Task

Target Speed

Speed [m/s] 0.75 0.7 0.65 0.6 0.55 0.5 0.45

TARGET SPEED
A

Split Group Subject

Control Group Subject

Right Foot Position Relative to Left [mm]

% of Responses Right in Front of Left

- Pre Adaptation
- Post Adaptation
- Point of Subjective Equality (PSE)

A PSE (e.g. negative)

B

PSE [mm]

RF
TD
C
RF
BU

Pre Adaptation
Post Adaptation

C

Step Symmetry

Number of Strides

Control Group
RFBU Group
RFTD Group
Baseline
Position Task
A

Pre Adaptation

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B

Split Group Subject

- Pre Ref
- Pre Test
- Post Ref
- Post Test
- Target

C

\[ \Delta \text{Force}_{pre} \]

\[ \Delta \text{Force}_{post} \]

D

Control Group
Split Group
Baseline
Task

\[ \text{Step Symmetry} \]

Number of Strides