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

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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 114: 3255–3267, 2015. First published September 30, 2015; doi:10.1152/jn.00302.2015.—Motor learning during reaching not only recalibrates sensorimotor estimates of leg speed 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 recalibration 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., backward or forward). 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). Furthermore, the motor and sensory consequences of locomotor adaptation may be linked, suggesting overlapping mechanisms driving changes in the motor and sensory domains.

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; Mattar et al. 2013; Ostry et al. 2010), a visuomotor rotation (Cressman and Henriques 2009; Salomonczyk et al. 2011, 2012), and after experiencing discrepancies in visual and proprioceptive estimates of the hand (Cressman and Henriques 2010; 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 (Izawa et al. 2012; Synofzik et al. 2008). This suggests that changes in the perception of hand position are a result of an error-based adaptation in the motor domain.

However, 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 (2010) showed that subjects had aftereffects in both motor and perceptual domains after they were exposed to a sensory mismatch in the absence of movement-related error signals. Another example is the well-known “rubber hand illusion” in which proprioceptive sense of the arm can be biased after synchronous tactile stimuli 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 (Choi et al. 2009; Choi and Bastian 2007; Malone et al. 2012; Malone and Bastian 2010; Morton and Bastian 2006; Reisman et al. 2005; Vasudevan et al. 2011) 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.

MATERIALS AND METHODS

Subjects

Ninety right hand- and right leg-dominant volunteers (37 men, 53 women; age: 23 ± 3.3 yr) 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 with a custom-built treadmill (Woodway, Waukesha, WI) that 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 (The MathWorks, Natick, MA) program or a custom Python program that allowed for simultaneous control of the logical/motor dysfunction. The protocol was approved by the Johns Hopkins Institutional Review Board, and all participants provided written informed consent before testing.

Experimental Protocols

General split-belt walking adaptation. In all experiments, the split-belt walking paradigm consisted of four main walking periods (Fig. 1A), as follows: Baseline: all subjects walked with tied belts (0.5 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 s) exposure to tied belt (0.5 m/s) walking before resuming split-belt walking; Postadaptation: all subjects walked with tied belts (0.5 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 with a custom Python program that allowed for simultaneous control of the

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Fig. 1. Paradigm and setup diagram for speed-matching and active position-matching tasks. A: paradigm for experiment 1 and experiment 2B. White blocks indicate tied-belt walking (0.5 m/s for both legs), gray blocks indicate split-belt walking (either both legs 1.5 m/s for Control group [experiment 1 only] or 0.5 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 0.5 m/s and right leg adjusted by subject). Initially, subjects performed baseline walking and speed-matching task blocks, each consisting of 1-min tied-belt walking and a 30-s speed task (see MATERIALS AND METHODS for task details). Next, during the adaptation block subjects experienced either a split-belt condition (Split group) or a fast-tied condition (Control group) for 15 min. Two-thirds of the way through this adaptation block a “catch trial” was introduced in which both belts were returned to baseline speeds (0.5 m/s) for 10 s, to assess the amount of motor learning. After adaptation, both groups performed 6 speed matching tasks separated by 5 tied-belt “postadaptation” 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. Subjects 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 the feet. Infrared markers on the side of the body were used for motion capture. A physical divider separated the 2 belts to avoid tripping. Subjects also wore a safety harness in case of falling, which 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.

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treadmill, real-time visual feedback, and collection of subject data. The experimental setup is shown in Fig. 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 canceled 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 introduction of a declarative memory component to the task of remembering the reference leg speed. Subjects were given 30 s 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 0.05, 0.055, or 0.065 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, 0.005 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 Fig. 1A. Subjects performed three periods of baseline (tied-belt walking) each followed by the speed-matching task. Next, they walked for 15 min in either the split-belt or the tied-belt (both belts 1.5 m/s) condition, with a 10-s catch trial occurring after the first 10 min to measure the magnitude of motor learning up to that point. Finally, all subjects walked for 12.5 min with tied belts in the postadaptation period. Walking was briefly interrupted at six time points throughout postadaptation 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 backward walking and backward speed-matching tasks. Specifically, after each pair of forward baseline and forward tasks, we added a pair of tied backward walking (0.5 m/s) and backward speed-matching tasks. The backward walking task had the same target goal of 0.5 m/s as the original speed matching task but occurred in the backward direction. To measure the generalization to backward walking in the motor domain, we also added a backward catch trial directly before the forward catch trial and a backward 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, in which 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; 2010; Mattar et al. 2013; Ostry et al. 2010; Salomonczyk et al. 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 Fig. 2B). Subjects lightly held onto the handrail in front of them.

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**Fig. 2.** Paradigm and experimental setup diagram for position perception task. **A:** experiment 2 paradigm. White and gray 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 min. 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) groups 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. Postadaptation was the same as in experiment 1 except that the divider was not used to extra proprioceptive cues. B: the subject’s left foot remained at rest, and the right leg was moved at every trial by the treadmill to a pretarget 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 of” or “behind” their left foot.
The subject’s right leg was initially moved to one of three “pretarget” locations in front of the left foot and then moved to one of nine target locations uniformly distributed in front or behind the left foot (see Fig. 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 9 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 that movement duration was fixed at 1.5 s.

The foot position perception task was performed immediately before and after 15 min of split-belt treadmill adaptation or tied-belt walking (Fig. 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 pretarget 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 (C) group 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). Finally, 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, subjects only experience the treadmill moving their feet from forward to backward; thus we tested the RFBU group to investigate whether 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 (Fig. 1A), in which subjects were given 30 s 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 20 numbered targets, which ranged from 0 to 20 (as shown in Fig. 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 the previous left foot position at heel strike. Subjects performed this task three times at baseline and at specific intervals throughout postadaptation. Prior to the beginning of the experiment all subjects were given a 2-min “warm-up” block in which they received visual feedback for both feet at heel strike and were asked to express what size steps were in front of or behind the left foot.

**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 (SLf) refers to the step length measured at fast-leg heel strike, and vice versa for slow step length (SLs)). A step symmetry value of 0 indicates symmetrical walking, and a positive value means that the fast step is larger than the slow step.

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\text{step symmetry} = \frac{\text{SLf} - \text{SLs}}{\text{SLf} + \text{SLs}} \tag{1}
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**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-s 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 that 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 five 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 \( \Delta \text{Force}_{\text{ref} - \text{test}} \) for both pre- and postadaptation, 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, \( \Delta \text{Force}_{\text{post} - \text{pre}} \).

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 postadaptation (first 5 strides of postadaptation), and late postadaptation (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 with 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 with 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 postadaptation time points when the speed-matching task was performed. Baseline task averages were compared with \( t \)-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 postadaptation time points. In experiment 2A, pre- and postadaptation values for PSE and curve slopes (uncertainty) were compared with a repeated-measures ANOVA. In experiment 2B, postadaptation data were baseline-subtracted, and we performed one-sample \( t \)-tests at each of the six postadaptation time points to measure significant changes compared with zero. Finally, 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 with 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 are shown in Fig. 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, postadaptation) are shown in Fig. 4B for all groups (note that Reverse group results 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 postadaptation, late postadaptation), 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 \(F(5,45) = 0.583, P = 0.713\). 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 postadaptation \(P < 0.001\), and late postadaptation \(P = 0.025\). 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 Fig. 5A. While both Split and Control subjects were able to match the speed of the right leg (shown in Fig. 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 postadaptation speed perception task.

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**Fig. 4.** Experiment 1 motor results for all groups. **A**: single-subject data for the step symmetry parameter is shown for both a typical Control group subject (top) and a Split group subject (bottom) for a full experiment. Orange dashed lines represent where 30-s speed matching tasks took place. Black dashed zero line represents baseline symmetry. **B**: group step symmetry results for Control group, Split group, Reverse group forward walking, and Reverse group backward walking. Curves are smoothed with a running average of 3 strides. Shaded regions represent SE. 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 indicate where the backward walking speed-matching tasks took place (Reverse group only).
Figure 5B shows group speed perception data at each of the six time points the task was performed after adaptation (data shown as \( \Delta \text{Speed} \), the size of the “overshoot” in the task response). Before the group averages shown in Fig. 5B were computed, 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 postadaptation task performance, our ANOVA showed a main effect of GROUP \( [F(1, 9) = 47.916, P < 0.001] \) and TIME \( [F(5, 45) = 11.156, P < 0.001] \) and an interaction of GROUP \( \times \) TIME \( [F(5, 45) = 13.468, P < 0.001] \). These results indicate that during postadaptation 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 motor and sensory changes decayed on a similar timescale (Fig. 4B, Fig. 5B). Like the motor aftereffects, it appears that changes in leg speed perception took ~15–16 min to return to baseline values. However, comparing motor and sensory changes in this manner presents a problem: step symmetry is a unitless parameter, yet \( \Delta \text{Speed} \) is measured in meters per second. 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 ~52% of the initial motor aftereffect. It also shows that the time courses of motor vs. sensory perceptual aftereffects decay on different timescales. To analyze this further, we performed two-way repeated-measures ANOVA (6 postadaptation time points; first 5 strides of motor postadaptation blocks and last 5 strides of each speed task) to compare the motor and perceptual decays. The ANOVA showed a main effect of MODALITY \( [F(1, 18) = 9.556, P = 0.006] \) and TIME \( [F(5, 90) = 28.907, P < 0.001] \) and an interaction of MODALITY \( \times \) 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.

**Backward walking.** Next, we asked whether forward split-belt adaptation led to a general perceptual aftereffect by testing whether it transferred to the backward direction via a Reverse group. We first confirmed that baseline backward walking performance was similar to forward walking (paired \( t \)-test, \( P = 0.590 \)). We found, however, that the baseline backward 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 postadaptation changes, making this difference less important. We also confirmed that the Split and Reverse groups adapted the same amount by showing no difference in forward walking catch trial magnitude (compare Reverse group forward walking and Split group in Fig. 4; paired \( t \)-test, \( P = 0.811 \)).

We then analyzed the transfer from forward to backward walking in the Reverse group. In the motor domain, we found small effects in the backward catch trial step symmetry, as shown in Fig. 4B (\( P = 0.038 \)). Likewise, we found a very small change in the backward speed-perception task response, as shown in Fig. 5B (\( P = 0.028 \)). The magnitudes of the backward effects were, however, closer to baseline performance than the forward walking effects.

We noted that the small motor effect in backward walking was the opposite of what we saw in the forward direction. Figure 7A illustrates this: during the catch trial for forward walking the fast leg takes a longer step while the slow leg takes a shorter step, which is a typical aftereffect. The backward walking averages 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 \( [F(1,18) = 0.207, P < 0.001] \) and also an interaction of GROUP \( \times \) TIME \( [F(1,18) = 28.358, P < 0.001] \). This suggests that forward walking showed significant changes in step lengths (from baseline to the catch trial) not present in backward walking. This is not consistent with what would be expected for true transfer of the learned pattern to backward walking.

We also looked carefully at the perceptual effect in backward walking as shown in Fig. 7B. Subjects generally improved their ability to match the leg speeds over the three baseline trials in both backward and forward walking. In the initial postadaptation 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 aftereffect from forward to backward 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 Fig. 8A. We should note that in these examples 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 \( [F(1,27) = 0.041, P = 0.960] \) or TIME \( [F(1,27) = 0.490, P = 0.490] \) or GROUP \( \times \) 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 PSE pre- and postadaptation are shown in Fig. 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 \( \times \) TIME interaction \( [F(1,27) = 2.557, P = 0.116] \).
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 Fig. 8C. Repeated-measures ANOVA showed main effects of GROUP \([F(2,27) = 7.768, P = 0.002]\) and TIME \([F(5,135) = 63.102, P < 0.001]\) and a GROUP \(\times\) 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 \((P = 0.837)\). Taken 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 that 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 Fig. 9A. Figure 9B shows group performance of the active foot position-matching task during postadaptation compared with baseline. One-sample t-tests showed no significant differences for any postadaptation tasks compared with zero (Post 1: \(P = 0.629\); Post 2: \(P = 0.790\); Post 3: \(P = 0.641\); Post 4: \(P = 0.989\); Post 5: \(P = 0.625\); Post 6: \(P = 0.990\)). 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 before and after adaptation. Typical group peak force measurements and single-subject stepping force curves for a 60% target trial are shown in Fig. 10, A and B, 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-/postadaptation changes in our main force perception parameter, \(\Delta\text{Force}_{\text{post}} - \text{Pre}\). Our ANOVA did not show significant main effects of GROUP \([F(1,72) = 0.985, P = 0.324]\) or TARGET \([F(3,72) = 0.999, P = 0.399]\) or GROUP \(\times\) TARGET interaction \([F(3,72) = 0.056, P = 0.983]\). Motor adaptation results, shown in Fig. 10D, were consistent with findings of experiments 1 and 2. In summary, our results indicate that split-belt adaptation did not produce significant changes in stepping force perception compared with tied-belt walking.

DISCUSSION

Here we show that split-belt adaptation leads to kinesthetic changes in perception of leg speed during walking but not of 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 ro-
bust, 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 deadapted 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 that 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 aftereffects 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 is 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 (Houldin et al. 2012; Noel et al. 2009) 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 min on a similar timescale (albeit at a different rate) of motor aftereffects. Furthermore, by expressing it in terms of a known motor parameter (step symmetry; see Fig. 6), we demonstrate that the sensory aftereffect does not fully account for the motor aftereffect. In fact, the initial sensory aftereffect represents only ~50% of the magnitude of the motor aftereffect and converges with the motor aftereffect after ~6–8 min 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 present 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 aftereffect during walking is in the opposite direction that was trained, which suggests that 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° visuomotor rotation resulted in a 7.3° 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-to-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 0.216 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 changes as a result of adaptation, is shown for all targets. B: representative single-trial stepping force (as % body wt) trajectory data for a Split group subject (left) and a 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). Gray curves are preadaptation and black curves postadaptation data. C: ΔForce, %, 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 and the Split group. As expected, the Split group show typical adaptation and retention of the walking pattern while the Control group do not show any changes.

Fig. 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 and test leg for both preadaptation (left) and postadaptation (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 % body wt) trajectory data for a Split group subject (left) and a 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). Gray curves are preadaptation and black curves postadaptation data. C: ΔForce, %, 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 and the Split group. As expected, the Split group show typical adaptation and retention of the walking pattern while the Control group do not show any changes.
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 (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, cerebellum-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 cerebellum 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 (Jayaram et al. 2011, 2012; Morton and Bastian 2006) 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. Furthermore, 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


