Title: Split-Belt walking induces changes in active, but not passive, perception of step length

Authors: Dr. Carly Sombric[1], Marcela Gonzalez-Rubio[1], Dr. Gelsy Torres-Oviedo[1]
[1]Department of Bioengineering, University of Pittsburgh, Pittsburgh, PA

Corresponding Author:
Dr. Gelsy Torres-Oviedo
Department of Bioengineering
4420 Bayard Street
Suite 110, Pitt
Pittsburgh, PA 15213
Univerity of Pittsburgh
gelsyto@pitt.edu

Abstract

The estimation of limbs' position is critical for motor control. While motor adaptation changes the estimation of limb position in volitional arm movements, this has not been observed in locomotion. We hypothesized that split-belt walking with the legs moving at different speeds changes the estimation of the legs' position when taking a step. Thus, we assessed young subjects' perception of step length (i.e., inter-feet distance at foot landing) when they moved their legs (active perception) or these were moved by the experimenter (passive perception). Step length's active, but not passive perception was altered by split-belt walking; indicating that adapted efferent inputs changed the perceived limbs' position without changing information from sensory signals. These perceptual shifts were sensitive to how they were tested: they were observed in the trailing, but not the leading leg, and they were more salient when tested with short than long step lengths. Our results suggest that sensory changes following motor adaptation might arise from mismatched limb position estimates from different sensory sources (i.e., proprioception and vision), which is less prominent in walking. We also speculate that split-belt walking could improve the deficient perception of step length post-stroke, which contributes to their gait asymmetry impairing patients' mobility.

Introduction

Successful motor control requires accurate estimation of limb position, which is achieved through a combination of afferent and efferent signals. Afferent information from sensory

signals is used to estimate limb position. In addition, efferent information also contributes to the estimation of limb position through prediction of sensory consequences prior to movement execution. The integration of actual and predicted sensory information, from afferent and efferent signals (respectively), is beneficial because it results in more accurate limb's estimation in space (e.g., [1–4]). It has been shown that subjects' estimation of limb position is altered following motor adaptation to a persistent stimulus (e.g., a constant force [5]). These adjustments to the estimation of limb position can be due to either adaptation of afferent or efferent information. Shifts in sensory information after motor adaptation have been observed with passive perception tasks during which subjects use afferent information to localize their limb after it has been passively moved (e.g., [5–12]). Moreover, predicted sensory consequences (from efferent information) rely on internal models that are recalibrated during motor adaptation. Thus, the integration of adapted sensory predictions with actual sensory information leads to changes in limb estimation that are assessed through active perceptual tasks, which require subjects to localize their limb after active movements [5,10,11,13–15]. In summary, the critical ability to estimate the position of our limbs in space using afferent and efferent information is altered by motor adaptation.

Interestingly, the effects of motor adaptation on the estimation of limb position in walking remains elusive. Namely, a recent study probing the perception of one leg position with respect to the body did not find passive or active perceptual after-effects despite robust motor after-effects [16]. This might be due to how perceptual after-effects were tested given evidence that passive and active perceptual changes post-adaptation are

61 sensitive to the condition in which they are evaluated [17–19]. For example, passive
62 perceptual after-effects depend on the limb that is tested [13], raising the possibility that
63 clearer perceptual changes could be observed when probing both limbs contributing to
64 each step length. Similarly, active perceptual after-effects might be regulated by test
65 condition such as walking speed; given that this factor alters the magnitude of motor
66 after-effects [20], and hence the recalibration of internal models underlying active
67 perceptual shifts. It is important to understand the influence of sensorimotor adaptation
68 on perception of limb position because stroke survivors have difficulty perceiving that
69 their step lengths are asymmetric [21]. Thus, it is of clinical interest to determine the extent
70 to which the estimation of limb position could be shifted following sensorimotor
71 adaptation in locomotion.
72
73 In summary, we investigated the effects of sensorimotor adaptation on the estimation
74 of limb position in walking. We hypothesized that sensorimotor adaptation alters the
75 estimation of step length, which requires concurrent localization of each leg's position.
76 We further hypothesized that walking condition, such as walking speed and/or step size,
77 would regulate the shifts in active perception of limb positions since walking speed alters
78 motor after-effects [20] and walking speed also alters step size (e.g., [22,23]). To test these
79 hypotheses, we separately investigated shifts in passive and active perception of step
80 length following sensorimotor adaptation in walking. Passive perception was assessed by
81 externally moving subjects' legs, whereas active perception was evaluated by instructing
82 subjects to take steps of different lengths. Importantly, the active perception task was
83 performed under distinct walking speeds and step sizes to test our hypothesis that active

perceptual effects depend on the condition in which they are tested. We assessed both passive and active perception since it is possible that sensorimotor adaptation only induces changes in the integration of afferent and efferent information, but not in afferent information alone.

Results

Passive Perception of Step Length was Not Adapted Following Split-belt Walking

We aimed to determine the extent to which locomotor adaptation induced a change in the estimation of limb position purely based on afferent information. To this end, adaptation effects in passive step length perception (i.e., passive perceptual after-effects) and movements (i.e., motor after-effects) were assessed in a group of unimpaired young subjects (n=8, 2 females, 24.8±4.8 yrs.) following a split-belt adaptation paradigm known to induce sensorimotor recalibration (e.g., [24]). We found motor, but not perceptual after-effects. After-effects were defined as differences in step length (Figure 1a-b) or step length asymmetry (Figure 1c) before and after the Adaptation epoch. These after-effects were significantly different between the split and tied sessions in the motor domain (Figure 1b: paired t-tests: slow leg's step length: $p<0.001$; fast leg's step length: $p<0.001$; Figure 1c: step length asymmetry: $p<0.001$). In contrast, we did not observe perceptual after-effects based on sensory information alone. Subjects' passive perception of their step length was assessed with a task in which participants indicated their estimated step length after the legs were moved by the experimenter to different step length sizes

(Figure 1a: short, comfortable, long). We did not observe significant changes in subjects' perception of the slow leg's step length across testing sessions (Figure 1a: one-way repeated measures ANOVA testing the effect of session; p=0.98). While we found a significant session effect on the perception of fast leg's step length (Figure 1a: p=0.035), this constituted a very small perceptual shift (0.8 ± 1.5 cm) compared to the significant motor after-effects in the fast leg's step length (11.7 ± 5.9 cm) and the slow leg's step length (-20.1 ± 6.7 cm). Thus, we observed a significant, but marginal adaptation effect on the perception of the fast leg's step length. In sum, split-belt walking produced robust motor after-effects, but did not change subjects' estimation of step lengths based on sensory (afferent) information alone.

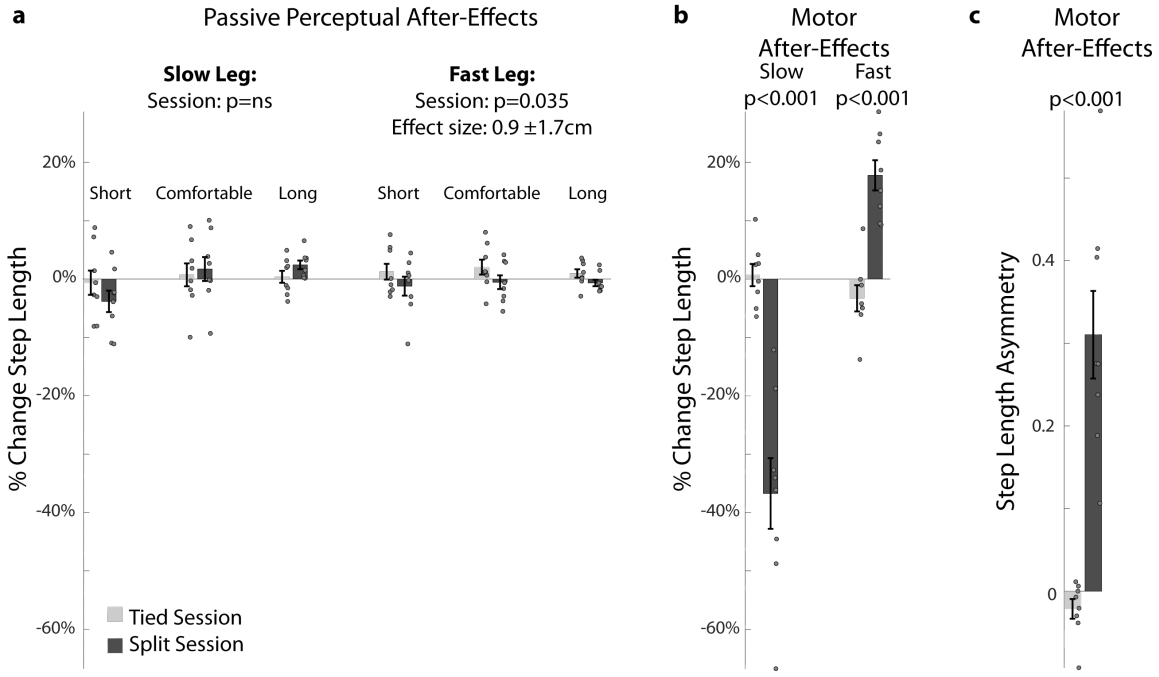

Figure 1 Split-belt walking did not induce changes in passive perception of step lengths | (a-b) In all plots, step length is defined as the distance between the ankles at heel strike (i.e., when the foot hits the ground). Change in step length was computed as the difference in step length before and after the Adaptation epoch,

which during the control session was an extended period of tied walking (light grey) and during the split session was an extended period of split walking (dark grey). These changes were expressed as a percentage of each subject's mean step length during baseline walking at 1 m/s to account for different step sizes across individuals. Negative and positive values indicate that step lengths were either perceived shorter or longer, respectively, after the Adaptation epoch compared to before. **(a) Passive Perception After-Effects**: Bars' height indicates group mean changes in perception after the Adaptation epoch relative to baseline behavior. Dots indicate values for each individual and error bars indicate standard errors. Passive perception was quantified by probing subjects' perception of three step length sizes (short, comfortable, and long) imposed by passively moving subjects' legs. Each participant's weight was equally distributed between the legs when their step length perception was probed. **(b) Motor After-Effects of individual legs:** Bars' height indicates group mean changes in step length after either the tied session or the split session. Standard errors and individual values (dots) are also displayed. **(c) Motor After-Effects of step length asymmetry**: Step length asymmetry is defined as the differences between step lengths of two consecutive steps normalized by the sum of these step lengths. Positive values indicate that steps taken with the dominant leg are longer compared to those taken with the non-dominant leg; and vice versa for negative values. Bar height indicates group mean changes in step length symmetry after the Adaptation epoch. Standard errors and individual values are also displayed.

Active Perception of Step Length was Modulated in Both Legs After Split-Belt Walking

Unlike passive perception, subjects' active perception of step length based on efferent information changed after split-belt walking compared to after tied walking. We evaluated subjects' (n=27, 16 females, 25.1±5.4 yrs.) active perception of step length by prompting step lengths of two distinct magnitudes (i.e., long or short) on a VR headset (see Methods section). We specifically assessed whether participants overshot or undershot these target step lengths after an Adaptation epoch, which consisted of an extended period of tied walking during the tied session and split-belt walking during the split session. Active perception after-effects were quantified as differences in executed

156 step lengths before and after the Adaptation epoch (i.e., %Change in Step Length).
157 Perceptual after-effects were subsequently compared between the two testing sessions to
158 determine if split-belt adaptation induced changes in the active perception of step length.
159 Importantly, perceptual and motor after-effects were tested under distinct walking speeds
160 (i.e., mid and slow) to determine if walking condition had a similar effect on active
161 perceptual after-effects, as it does on motor after-effects [20]. Thus, we had a total of three
162 groups labeled by the step length size that was prompted first in the perceptual task and
163 the speed at which it was tested (Long-MidSpeed, Short-MidSpeed, Short-SlowSpeed).
164 Figure 2a shows that following split-belt walking, all groups undershot (negative values)
165 or overshot (positive values) target step lengths with the leg that walked slow (slow leg)
166 or fast (fast leg), respectively, during the Adaptation epoch. This indicated that subjects
167 perceived their step lengths to be either longer or shorter than actual when stepping with
168 the slow or fast leg, respectively. Consistently, we found a significant effect of session on
169 the active perception of the slow ($p<0.001$) and fast step lengths ($p<0.001$) with one-way
170 repeated measures ANOVAs. These shifts in perception of individual leg's step length
171 led to significant differences in step length asymmetries during the active perceptual task
172 across sessions (Figure 2c: session effect: $p<0.001$).
173
174 *Active Perception of Step Length was Modulated by Step Size, but Not Walking Speed*
175
176 Subsequent analysis on the split session indicated that step length size, but not walking
177 speed, had an effect on active perception after-effects. Specifically, a two-way repeated
178 measures ANOVA indicated a significant interaction between leg and step length size

(leg#step length size: p =0.004) for the groups starting the perceptual task with different step lengths sizes, but the same walking speed (i.e., Short-MidSpeed vs. Long-MidSpeed). This interaction was driven by greater after-effects in the perception of the fast leg's step length when taking short (Figure 2a, red bar) compared to long (Figure 2a, blue bar) step lengths (two sample t-test: p=0.024). This might be due to greater similarities between training and testing in the short vs. long conditions. Namely, the executed step lengths during the training condition (i.e., split-belt walking, Late Adaptation in Figure 2a insert, white background) were qualitatively more similar to the target step lengths in the Short-MidSpeeds group (Figure 2a insert, red background) than in the Long-MidSpeeds group (Figure 2a insert, blue background). Conversely, we did not find an interaction between leg and walking speed (leg#speed: p =0.16) for the groups that walked at different speeds, but same step lengths in the active perceptual task (i.e., Short-MidSpeed vs. Short-SlowSpeed). This contrasted the effect of walking speed on motor after-effects (Figure 2b). Specifically, the slow step length motor after-effects were larger when tested at slow than mid walking speeds (Figure 2b: two sample t-test between pooled mid speed groups vs. a slow speed group; p=0.008), whereas they were the same for fast step lengths (p=0.83). Thus, the effect of speed on step length asymmetry (Figure 2b: p=0.001) was due to the slow step length after-effects. In summary, split-belt walking induces motor and active perceptual after-effects that are regulated by the way they are tested: motor after-effects are altered by walking speed, whereas perceptual after-effects are altered by step length size.

Active Perception of Step Length Decayed Without Fully Washing Out Motor After-Effects

We observed that the active perceptual after-effects decayed as they were tested, but their washout did not fully eliminate motor after-effects. Namely, we found that perceptual after-effects decayed exponentially as people walked in the active perceptual task (Figure 3a: $y = c + ae^{(-x/\tau)}$). This exponential decay was clearly observed in the active perception of the slow step length in all groups (Figure 3a, top panel: τ [95% CI]; Short-MidSpeed: 24.8 [31.0, 20.8], Long-MidSpeed: 17.7 [14.1, 23.6], Short-SlowSpeed: 27.1 [19.4, 45.0]), but only in the fast step length for groups tested with the short target first (Figure 3a, bottom panel: τ [95% CI]; Short-MidSpeed: 25.7 [19.4, 37.8], Long-MidSpeed: 2.4 [-0.86, 3.0], Short-SlowSpeed: 53.2 [37.2, 93.1]). These findings further support that subjects did not have perceptual shifts of the fast leg's step length when probed with long steps. Interestingly, the active perceptual task did not fully washout motor after-effects. This was tested by comparing perceptual after-effects at the end of the active perceptual task (Figure 3b: Late Perception) and the remaining motor after-effects tested immediately afterwards (Figure 3b: Early Post-Adaptation). Of note, the belts moved at the same tied speed in both instances. The only experimental difference is that in Late Perception subjects aimed at their comfortable step length (recorded during baseline walking) while wearing the VR headset, whereas in Early Post-Adaptation they walked unconstrained (i.e., without any specific instruction) and without VR headset. Thus, washout of motor after-effects by the active perceptual task is expected, as indicated by the qualitatively smaller motor after-effects during Early Post-Adaptation

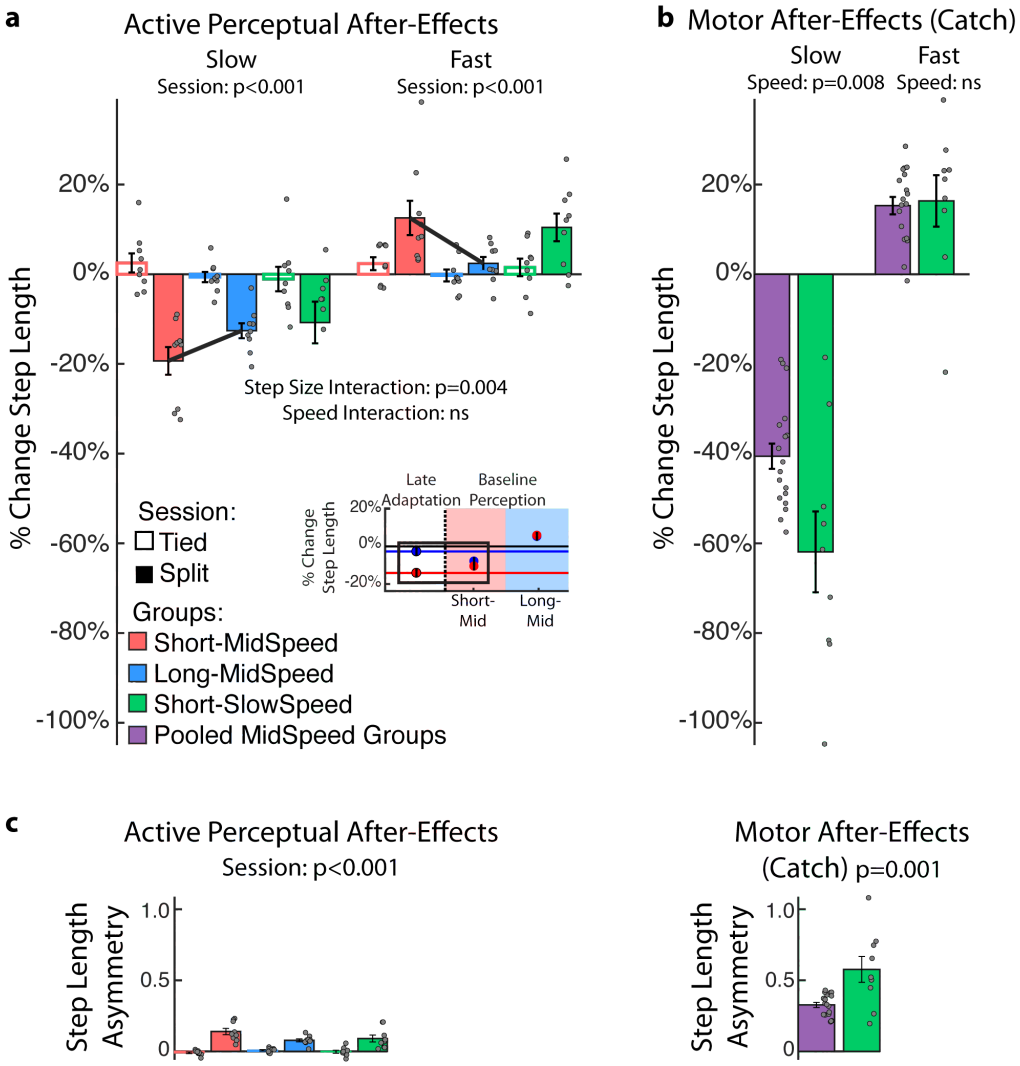

Figure 2 Split-belt walking induces changes in active perception | (a) Step Length Active Perception After-Effects: Bars' height indicates group mean changes in step length before and after the Adaptation epoch, which consisted of tied (empty bars) or split walking (filled bars). These changes were expressed as a percentage of each subject's mean step length during the baseline active perceptual task tested at the specific step length size and walking speed for each group. For example, we used the mean step lengths during the baseline perceptual task aiming at short step lengths and walking at slow speed for the Short-SlowSpeed group. Negative or positive values indicate that subjects either undershot or overshot the target step lengths, respectively because they perceived step lengths to be longer or shorter than the actual value. The insert illustrates the %Change in Step Length that was executed by the slow (red dot) and fast (blue dot) step lengths at steady state during split-belt walking (Late Adaptation; white background). We also show the target step lengths (red and blue dots) for probing active perception during baseline in the Short-MidSpeed group (red background) and the Long-MidSpeed group (blue

background). Standard errors are displayed in all plots. **(b) Step Length Motor After-Effects:** Bars' height indicates group mean changes in step length relative to baseline walking during the Catch trial tested at either 1.0m/s (Short-MidSpeed and Long-MidSpeed) or 0.5 m/s (Short-SlowSpeed). The mid speed groups were pooled for this analysis since these two groups experienced exactly the same protocol prior to the catch trial. **(c) Step Length Asymmetry Perceptual and Motor After-Effects:** Bars' height indicates group mean changes in step length asymmetry relative to baseline walking during the Perceptual trials and during the Catch trials. The left panel illustrates the mean step length asymmetry that results from the change in individual step lengths during the active perceptual task for each group. The right panel illustrates the mean step length asymmetry that results from changes during the Catch trial tested at the Mid (1.0 m/s) or Slow (0.5 m/s) walking speed. Standard errors are displayed in all plots.

compared to those during the Catch trial (colored dotted lines in Figure 3b). Two-way repeated measures ANOVAs (factors: epoch and speed) were used for each step length to show that motor after-effects are present after perceptual after-effects are washed out and that the motor after-effects are influenced by speed. Specifically, the slow and fast leg had significant resurgence of the motor after-effects following perceptual testing (Figure 3b: slow step length: $p_{epoch}<0.001$; fast step length: $p_{epoch}<0.001$) and the magnitudes of after-effects were regulated by walking speed (Figure 3b: slow step length: $p_{speed}=0.04$, $p_{speed\#epoch}=0.018$; fast step length: $p_{speed}=0.041$, $p_{speed\#epoch}=0.43$). In summary, active perception after-effects decayed as subjects walked, but this did not fully washout motor after-effects.

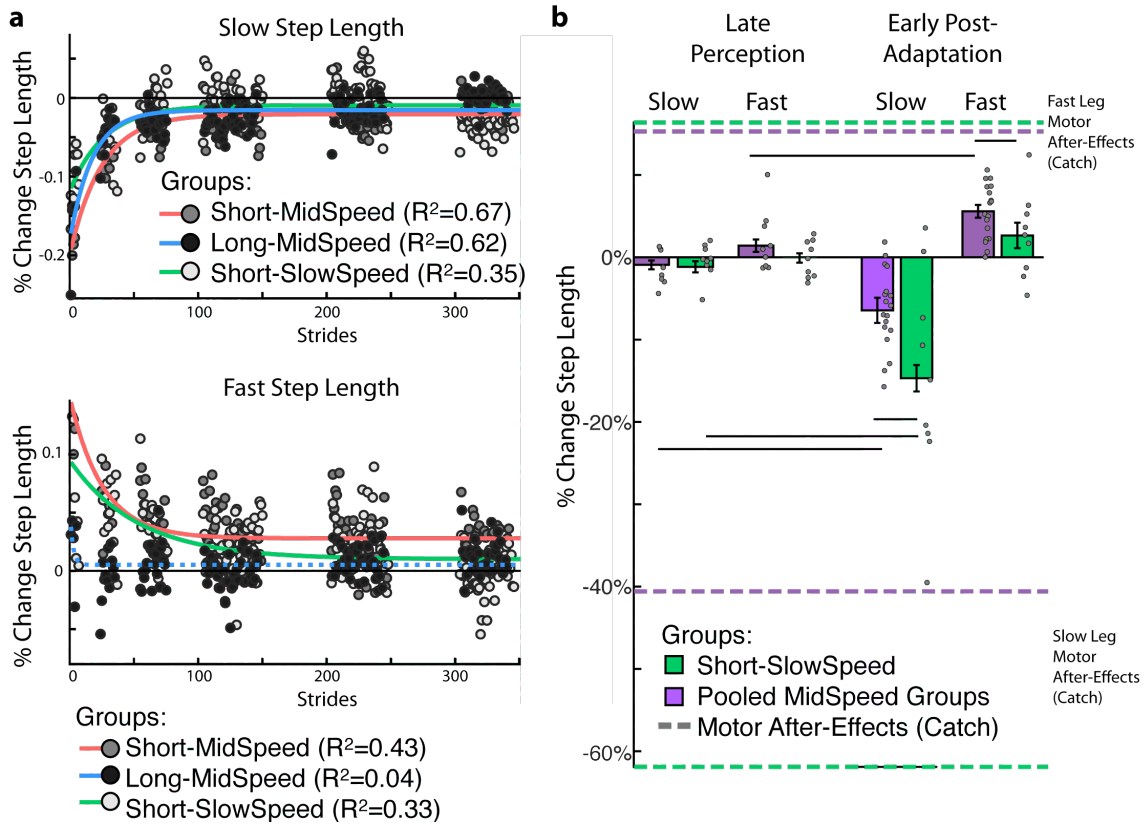

Figure 3 Active perception after-effects, but not motor after-effects, are fully washed out by the end of the perceptual task | (a) Decay of active perception after-effects. We show the %Change in Step Length (i.e., after-effects) for the slow (Top panel) and fast step length (Bottom Panel) over the course of the active perceptual task. Note that all groups exhibit an exponential decay of active perception after-effects in both legs except for the fast leg in the Long-MidSpeed group whose τ was not significantly different from zero (lack of significance indicated with a dotted line). This further indicates that subjects did not have significant fast step length perceptual shifts when probed with long step lengths. Perceptual after-effects assessed at target step lengths that were different from the initial probe were not included in the analysis (white spaces). **(b) Remaining motor after-effects following the active perceptual task.** Colored lines indicate the motor after-effects recorded during the Catch trial (prior to the active perceptual task, Figure 2b). Bars indicate group means for the slow and fast %Change Step Length at the end of the perceptual task (Late Perception) and at the beginning of the Post-Adaptation period (Early Post-Adaptation). Black lines indicate Fisher's LSD post Hoc results. Subjects walked at the exact same tied-belt speeds during the Late Perception and Early Post-Adaptation periods. The only difference in these time points was that subjects were prompted to take their comfortable step length during Late Perception, but during Early Post-Adaptation subjects walked unconstrained (i.e., without any specific instruction of where to

step). Standard errors are displayed in all plots. Note that the mid speed groups are pooled for this analysis since they experienced the same Adaptation protocol and target step lengths during Late Perception.

Active Perception After-Effects are Mediated by Changes in Trailing Leg Perception

Step lengths during active perceptual trials were further decomposed into perceived leading (α) and trailing (X) leg positions (Figure 4a) to determine which leg's position perception underlies changes in step length perception following split-belt adaptation. Our results show that only the trailing leg's position (X) exhibited active perception after-effects (Figure 4b). These were quantified with symmetry measures of each leg's X, such that values different from zero indicated active perception after-effects. We separately characterized α and X perceptual after-effects for short and long target step lengths with single exponential fits ($y = c + ae^{(-x/\tau)}$). A separate fit was performed for individuals walking slow vs. those walking at mid speeds. Fits of the data indicate that only the trailing leg position experiences large changes in perception that decayed as subjects experienced the active perceptual task. This is indicated by the decay of perceptual after-effects probed at either the short step length target (Figure 4b: τ [95% CI]; Short Target: MidSpeed= 12.5 [10.8, 14.9], SlowSpeed=36.9 [32.6, 42.7]) or long step length target (MidSpeed=37.5 [33.4, 42.8], SlowSpeed=41.0 [33.5, 52.9]). In contrast, the leading leg's position exhibited perceptual after-effects that were very short lived, regardless of whether they were probed with the short step length target (Figure 4c: τ [95% CI]; Short Target: MidSpeed= 8.4 [6.4, 12.4], SlowSpeed=1.2 [-0.01, 2.4]) or the long step length target (MidSpeed=7.2 [4.7, 15.2], SlowSpeed=7.3 [3.8, 90.0]). Taken together, these

results indicate that active perception shifts in step lengths are due to changes in the perception of the trailing leg's position, and not the leading leg's position.

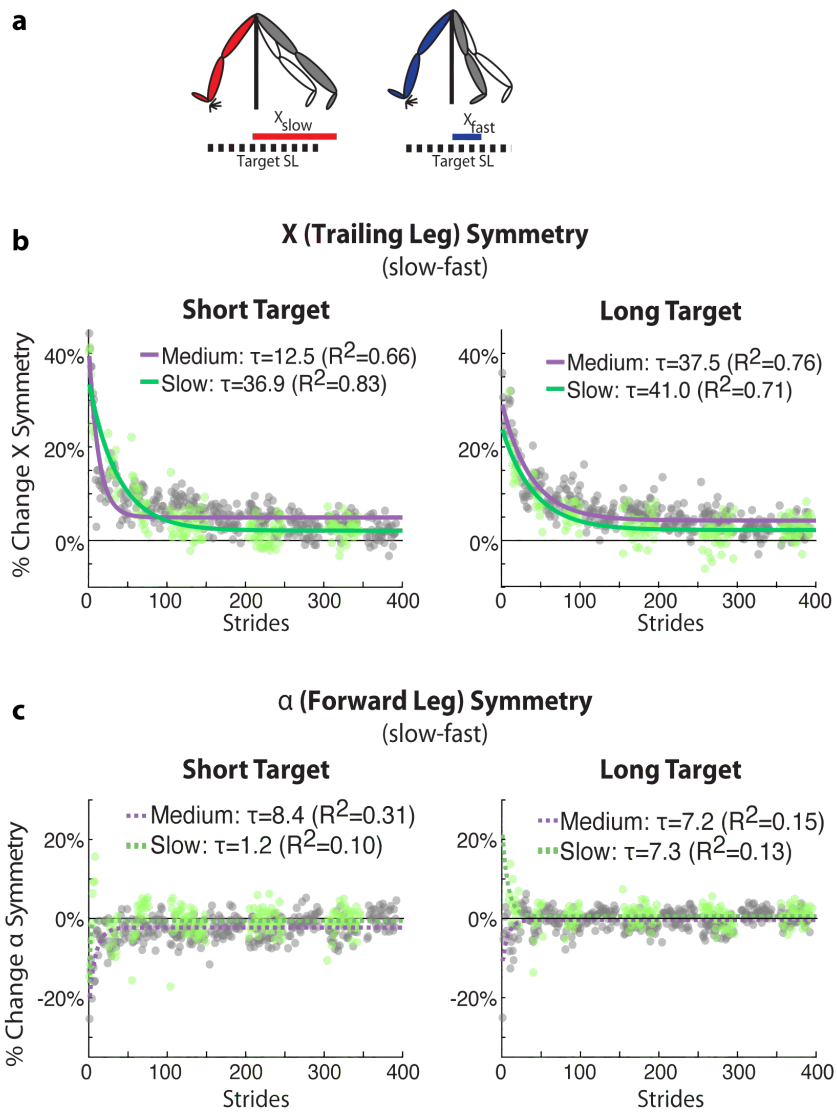

Figure 4 Split-belt Walking Induces Active Perception Changes in the Trailing Leg Position | (a) Schematic of the decomposition of step length into the leading (α) and trailing (X) leg relative to the hips. Both α and X are normalized by the speed specific baseline walking behavior, such that positive values mean the distance from the body is greater following Adaptation and vice versa. Symmetry measures were computed for both X **(b)** and α **(c)** and were defined as the differences between these measures on two consecutive steps (slow leg - fast leg). Thus, positive values of %Change X Symmetry here indicates that the slow leg (X_{slow}) is trailing farther behind than fast leg (X_{fast}) relative to baseline behavior. Similarly, positive values of %Change α Symmetry would

indicate that the slow leg (α_{slow}) is farther in front of the body than the fast leg (α_{fast}) relative to baseline behavior. Note that the X position perception is altered following split-belt walking, but that the α position perception is not altered, as indicated by negligible %Changes in α Symmetry following split-belt walking.

Discussion

Summary

We investigated the effects of locomotor adaptation on passive and active step length perception. We observed active, but not passive, perceptual after-effects of step length. Thus, locomotor adaptation did not induce sensory shifts, but altered the estimation of limb position based on integration of afferent and updated efferent information. In addition, we found that active perception after-effects were only observed on the trailing limb's position, indicating that the perceived position of the trailing, but not the leading leg, with respect to the body is recalibrated after locomotor adaptation. Moreover, perceptual and motor after-effects were regulated by how they were tested. Specifically, perceptual after-effects were altered by step length size, whereas motor after-effects were altered by walking speed. Lastly, the observed perceptual after-effects decayed as subjects walked in the active perceptual task, but motor after-effects remained, raising the possibility that after-effects in these two domains are originated by partially distinct processes.

Motor recalibration in locomotion induces changes in active, but not passive perception of limb position.

Our results show that the perception of limb position is altered following motor adaptation in locomotion, which supports prior findings that the perception of limb position is susceptible to motor adaptation (e.g., [5,6,15,7–14]). However, we only observed perceptual after-effects when subjects actively generated motor commands and not when their legs were passively moved, which is consistent with prior work indicating that afferent signals encoding position remain intact following split-belt walking [16]. These findings contrast multiple reports of shifts in the estimation of hand position following motor adaptation when the arms are moved by the experimenter (e.g., [5–12]). We believe that this discrepancy between reaching and locomotion suggests that sensory changes post-adaptation arise from mismatched position estimates from different sensory sources (i.e., proprioception and vision), which is less prominent in walking. We also found that active perceptual effects were not observed in the leading leg's position, as previously reported [16], but they were clearly observed in the trailing leg's position, which had not been assessed before. We posit two potential explanations for the altered estimation of the trailing leg's position. First, subjects might maintain the expectation that one leg will move faster than the other post-adaptation. As a result, they will stand longer on the leg that walked slow compared to the other as they take steps in the active perceptual task, leading to differences in trailing leg position that are consistent to the ones we see (i.e., $X_{slow}>X_{fast}$). Alternatively, the shifts in position might be due to changes in how subjects perceived the environment. It is known that the perception of symmetric walking speeds

370 is shifted following split-belt walking [16,25]. More specifically, individuals during post-
371 adaptation perceive the fast leg to move slower and the slow leg to move faster than their
372 actual speed. Subjects might act according to this perception by standing longer on their
373 trailing leg when taking steps with the fast leg and vice versa for steps with the slow leg,
374 resulting in the observed larger X_{slow} than X_{fast} values. In sum, subjects' estimation of
375 limb position is altered following sensorimotor adaptation. This shift is not due to
376 changes to afferent information, but might be due to updated motor commands or altered
377 perception of the environment following adaptation.
378
379 *Motor and perceptual after-effects are susceptible to how they are tested.*
380
381 It has been shown that split-belt motor after-effects are sensitive to walking speed [20] and
382 perceptual after-effects are sensitive to movement distance [18]. Thus, our observations that
383 motor after-effects are regulated by walking speed and perceptual after-effects are
384 regulated by step length are consistent with previous literature. However, it should be
385 noted that walking speed and step length are not independent (e.g., [22,23]) raising the
386 possibility that step length is the factor that regulates both motor and perceptual after-
387 effects. Should that be the case, we speculate that similarity in step lengths sizes during
388 training and testing is a critical feature to maximize after-effects, given the well-known
389 effect of similarity on the generalization of learned movements across conditions [26–28]. In
390 sum, our results highlight the importance of considering how both motor and perceptual
391 after-effects are tested.
392

393 *Why did motor after-effects remain after perceptual ones were fully washed out?*

394

395 It is interesting that walking in the active perceptual task did not fully eliminate motor
396 after-effects. We believe this could be due to three possible reasons. First, the perceptual
397 and motor effects were tested under different peripheral vision because subjects were
398 wearing a virtual reality headset in the active perceptual task. This distinct situation
399 constitutes a contextual difference known to reduce the washout of the pattern specific to
400 the split-belt treadmill by walking in a symmetric environment [29]. Second, the
401 constrained nature of walking in the perceptual task might also influence the remaining
402 motor after-effects. Namely, perceptual after-effects were tested by instructing subjects
403 "where" to step, whereas motor after-effects were tested in unconstrained walking.
404 Constrained and unconstrained movements are thought to be differently controlled (e.g.
405 [30]). Thus, the fact that individuals were aiming to a target in the perceptual task might
406 have altered the extent to which implicit actions were washed out. Lastly, the limited
407 washout of motor after-effects could also indicate that motor and perceptual after-effects
408 are originated by partially distinct processes. This is supported by previous research
409 showing that motor and perceptual effects exhibit different patterns of saving [25] and
410 retention [11], distinct adaptation rates [6,15] and uncorrelated amounts of adaptation [8,9,12,13].
411 They also exhibit different patterns of generalization to other limbs [17] or novel targets
412 [18,19]. Thus, while the limited washout of motor after-effects by the perceptual task might
413 be due to testing differences, it could also indicate that the processes underlying motor
414 and perceptual after-effects might be partially independent.

415

Clinical implications

The split-belt walking may be a viable tool to address perceptual deficits associated with stroke. Notably, stroke survivors' inability to perceive that their gait is asymmetric is associated with limited recovery of symmetric gait [21]. Our results indicate that active perception of step lengths can change following split-belt walking, suggesting that a similar effect might be observed post-stroke. It has been shown that split-belt training can correct motor deficits [31,32] and it would be interesting to determine if it also corrects perceptual deficits as well. Of note, recent work indicates that perceptual changes in the estimation of speed are reduced with repeated exposure to the split condition [25], suggesting that similar reduction would be observed in the shifts of limb position. Thus, there might be a limited long term effect of split-belt walking on perceptual changes. Therefore, future work is needed to understand if split-belt walking has similar effects in the lesioned motor system and whether training protocols could lead to long lasting improvements in motor, as well as, perceptual deficits post-stroke.

Methods

The influence of split-belt walking on passive (Experiment 1: n=8, 2 females, 24.8±4.8 yrs.) and active (Experiment 2: n=27, 16 females, 25.1±5.4 yrs.) step length perception was characterized in separate groups of subjects. This study was approved by the University of Pittsburgh Institutional Review Board, was carried out in accordance with the approved guidelines, and all subjects provided written informed consent.

439

440 **Experiment 1: Passive Perception**

441

442 We tested subjects' perception of their limb position by moving their legs in order to
443 determine if afferent information was altered by split-belt walking. This was done before
444 and after a tied and a split session, which occurred on different days. Both the tied and
445 split sessions included perceptual and locomotor epochs (Figure 5a).

446

447 *Locomotor Task*

448

449 Subjects experienced a tied and split session that differed only in the locomotor
450 Adaptation and Re-Adaptation epochs (Figure 5a). The first session was used to
451 determine if an extended period of tied belt walking (i.e., walking with both belts moving
452 1.0 m/s) during the Adaptation epoch changed subjects' passive perception of step length.
453 During the second session, subjects walked with the legs moving at different speeds
454 during the Adaptation epoch to determine if locomotor adaptation altered subjects'
455 passive perception of step length. The split-belt perturbation was gradually introduced
456 during the Adaptation epoch for consistency with prior work studying passive perception
457 (e.g., [6,8,9,12,33]). More specifically, belts started at 1.0 m/s and linearly diverged for 600
458 strides until a 3:1 split-belt ratio (i.e., 1.5 m/s: 0.5 m/s) was achieved and maintained for
459 200 strides resulting in a total of 800 strides for the Adaptation epoch. Subjects' passive
460 perception of step length was assessed immediately before and after the Adaptation
461 epoch. We re-exposed individuals to either the tied condition (i.e., both legs at 1 m/s) or

462 split condition (i.e., 1.5 m/s: 0.5 m/s) during a Re-Adaptation epoch to subsequently
463 evaluate motor after-effects in each subject. We chose to evaluate motor after-effects
464 following the perceptual task to avoid changes in perception due to multiple transitions
465 between tied and split environments, which are known to alter perceptual effects [25]. The
466 Re-Adaptation epoch lasted 300 strides to ensure individuals reached a similar steady
467 state as in the Adaptation epoch prior to assessing motor after-effects. Then, we evaluated
468 motor after-effects during a Post-Adaptation epoch (450 strides) when the two legs
469 moved at the same speed (1 m/s). Subjects walked in this tied environment for 450 strides
470 to fully wash out any split-belt after-effects before testing subjects' retention of the
471 mapping between the imposed step lengths and the analog scale used in the perceptual
472 task (see section below).
473
474 *Passive Perceptual Tasks*
475
476 During the passive perception task, subjects wore a virtual reality headset (Oculus,
477 Facebook Technologies, Irvine, CA, United States) while standing with their weight
478 evenly distributed between the two feet and with each foot placed on one belt of the split-
479 belt treadmill. The sequence of a passive perceptual trial is shown in Figure 5b. First, legs
480 were passively moved to a specific step length value (ankle to ankle distance) (Figure 5b,
481 first panel). Then, belts were stopped and subjects were asked to distribute their weight
482 equally between their feet by maintaining their center of pressure (green dot) within a
483 target region (blue rectangle) (Figure 5b, second panel). Subjects maintained this
484 balanced position for 5 seconds during which they had to indicate their perceived step

length using a clicker that moved a cursor (red dot) along an analog scale displayed in the virtual reality headset (Figure 5b, third panel). Then, a new perceptual trial was initiated by moving the legs to a different step length value (Figure 5b, fifth panel). Subjects received feedback of the actual step length in the analog scale (dark green dot) only during perceptual training (see full description below) (Figure 5b, fourth panel). Subjects did not lift their feet off the belts when the belts were moving or still. We alternated the leg that was placed forward after every perceptual probe/trial.

Perceptual Training

Subjects trained extensively on the passive step length task to learn the mapping between the imposed step lengths and the analog scale. Training occurred at the beginning of every session. Three out of the 8 participants had an additional session with only training trials prior to the tied session to determine if improved accuracy at the task would allow us to identify small perceptual shifts. The analog display observed by all subjects is shown in Figure 5b The middle of the analog scale corresponded to a medium size step length computed as 75% of each subject's averaged step length during baseline walking at 1.0 m/s. Subjects additionally trained on targets 8 cm shorter (short step length) and longer (long step length) than the medium size step length. Six out of the eight participants on this task also trained with step lengths that were 4 cm shorter and longer than the medium size step length. During training, subjects experienced the same perceptual probe sequence as during testing: 1) legs were passively moved to one of the target step length values (e.g., medium, short, and long step length sizes), 2) subjects

508 indicated their perceived step length while maintaining an equal distribution of their
509 weight between their feet, and 3) subjects received feedback on their actual step length
510 along the same analog scale. Subjects experienced 10 or 20 iterations of each of the target
511 step lengths in a random order. Our results did not change when either more step length
512 sizes were assessed (e.g., 3, rather than 5, target step lengths) or more instances of each
513 step length size were tested (e.g., 21, rather than 10).
514
515 Perceptual Trials
516
517 We evaluated subjects' capacity to classify step length sizes with the analog scale
518 immediately following training (i.e., Baseline Perceptual epoch) and right after the
519 Adaptation epoch during each session (i.e., Post-Adaptation epoch). Each epoch
520 consisted of several iterations (10 or 21) of the target step sizes presented in a random
521 order. Subjects performance was computed as the mean value that they selected in the
522 analog scale across all perceptual trials at each target size. In all trials, subjects were told
523 that they would experience step lengths all along the analog scale, including values that
524 were shorter or longer than those they experienced during training. In reality, subjects
525 were only exposed to the step length values that they trained on. Feedback was not
526 provided in any trial. The performance of the perceptual trials for each leg were used to
527 determine if subjects could differentiate the distinct step length sizes with the analog
528 scale (i.e., Baseline Perceptual epoch performance), and if passive perception of step
529 length was altered by the Adaptation epoch (Baseline Perceptual vs. Post-Adaptation
530 epoch performance). First, the Baseline Perceptual performance for each leg was

compared across all target sizes and sessions to determine if subjects could differentiate the distinct step length sizes with the analog scale for each session. Figure 5c indicates that subjects learned to discern the three step length values they experienced when their legs were passively moved (Figure 5c: two-way repeated measures ANOVA testing the effect of target and session on perceived step length; Slow Leg: $p_{target}<0.001$, $p_{session}=0.59$, $p_{target\#session}=0.56$; Fast Leg: $p_{target}<0.001$, $p_{session}=0.32$, $p_{target\#session}=0.71$). Next, it was determined if passive perception of step length size was altered by split belt walking by comparing the Baseline Perceptual performance and Post-Adaptation performance (see results). Lastly, we probed subjects' passive perception at the very end of the split session in a Post-Washout epoch, during which subjects' perception of the short and long step length were probed 7 or 10 times each. This was done to ensure that changes in the reported step length with the analog scale were due to perceptual changes, rather than forgetting of the mapping between the sensed step length and the analog scale. Thus, subjects' perception of the short and long step lengths were compared between the Baseline Perceptual and Post-Washout epochs. We found no differences between epochs or target step lengths (Figure 5c: two-way repeated measures ANOVA testing the effect of epoch and target on perceived step lengths: Slow Leg: $p_{epoch}=0.80$, $p_{target}<0.001$, $p_{epoch\#target}=0.13$; Fast Leg: $p_{epoch}=0.88$, $p_{target}<0.001$, $p_{epoch\#target}=0.83$). This indicated that individuals could classify well the distinct step length values throughout the duration of the experiment.

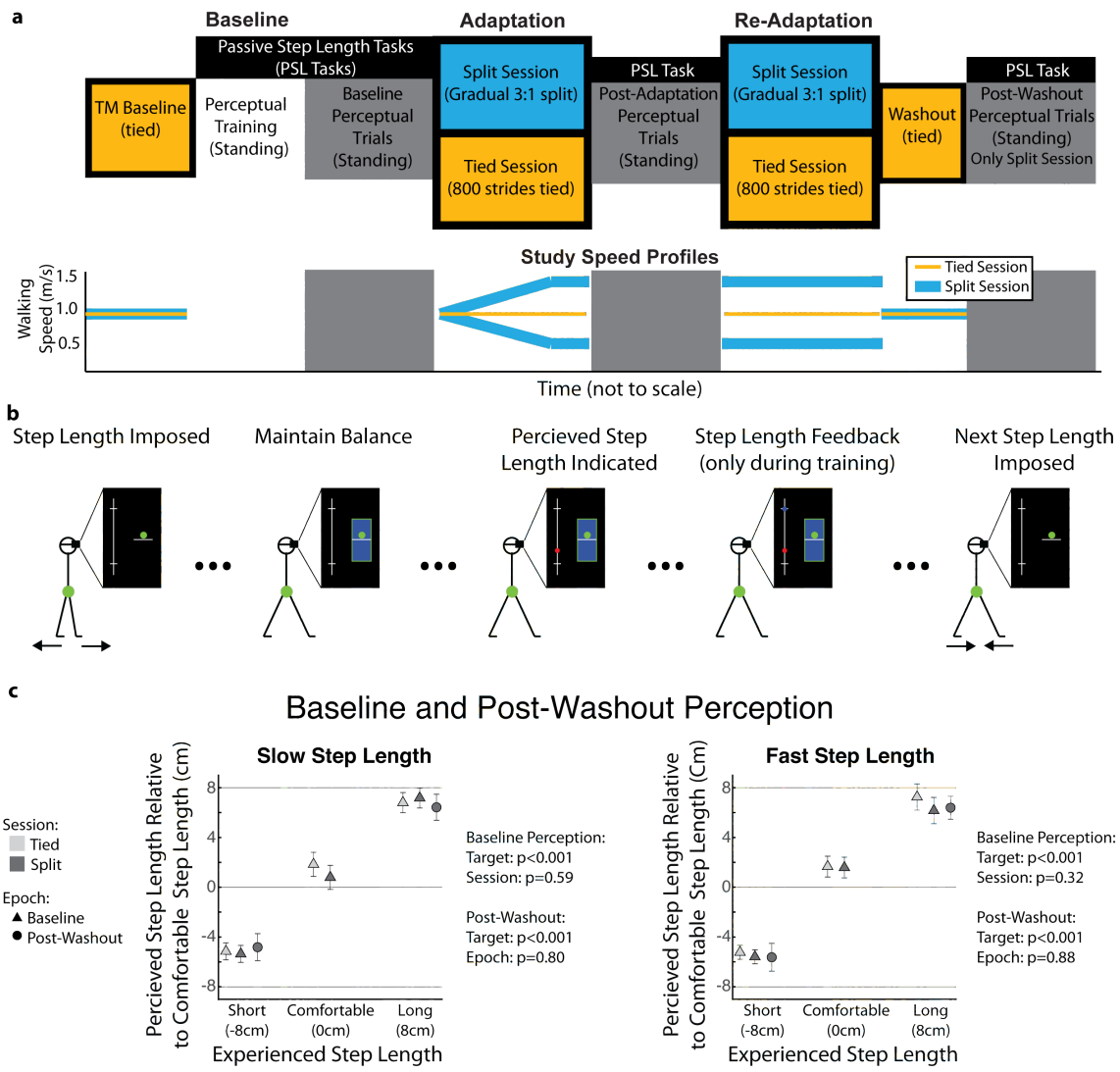

Figure 5 Locomotor and Passive Perception Protocol | (a) Locomotor epochs (colored blocks) and Passive Perceptual epochs (grey scale blocks) were included in both the control and testing session. Note that subjects were standing during the passive perceptual trials and walking during the locomotor trials. **(b) Passive Step Length Tasks:** Subjects' legs were passively moved to a target step length. Subjects maintain an equal distribution of their weight between their feet using visual feedback displayed in the virtual reality headset. Subjects indicated their perceived step length size using an analog scale that was also displayed. Only during training, participants received feedback on their perceived vs. actual step length along the analog scale. This was done such that individuals could learn the mapping between what they felt and what was displayed in the analog scale. **(c) Baseline and Post-Washout Perceptual Trials:** Subjects' performance during the Baseline Perceptual Trials for both sessions and the Post-Washout Trials for the split session are shown for each leg. Note that subjects could discern three distinct step lengths from the beginning (Baseline) until the end (Post-Washout) of the experiment. Thus, any performance changes between the Baseline vs.

Post-Adaptation epochs were attributed to shifts in subjects' passive perception of step length, rather than subjects' inability to maintain the mapping between the imposed step lengths and the analog scale.

Experiment 2: Active Perception

Subjects' estimation of step length upon active motion of their legs was evaluated to determine if this estimation was altered by split-belt walking. This was done before and after a tied and a split session, which occurred on different days. Both the tied and split sessions included perceptual and locomotor epochs (Figure 6a). Importantly, perceptual and motor after-effects were tested under distinct walking speeds (i.e., mid and slow) since this factor has been shown to modulate the generalization of sensorimotor recalibration across walking conditions [20]. Moreover, speed naturally regulates the magnitude of step lengths [22,23]. Therefore, we evaluated the possibility that active perception of step length would be distinct for different step length sizes (i.e., long and short). Of note, both step length sizes were tested in all groups, but we altered the order at which the perception of step lengths were probed (i.e., long first vs. short first) given our expectation that active perceptual after-effects would decay as subjects performed the active perceptual task. In sum, motor and active perceptual after-effects were tested at either a slow (0.5 m/s) or mid (1 m/s) walking speeds, and active perceptual after-effects were first measured at either short or long step lengths. These experimental conditions resulted in three groups designated first by testing speed and second by the first step length size at which active perception was probed (Long-MidSpeed, Short-MidSpeed, Short-SlowSpeed).

Locomotor Task

Similar to Experiment 1, subjects experienced a tied and split session that differed only in the locomotor Adaptation and Re-Adaptation epochs (Figure 6a). The first session ensured that tied walking (i.e., walking with both belts moving 1.0 m/s) during the Adaptation and Re-Adaptation epochs did not induce active changes in step length perception. During the second session, subjects walked for 600 strides at a 3:1 split-belt perturbation (1.5 m/s and 0.5 m/s) during the Adaptation epoch. Unlike Experiment 1, we introduce the split-belt perturbation abruptly because it has been shown that active perception adapts more slowly than motor recalibration [15]. Thus, we wanted to maximize the exposure of the full split condition before assessing perceptual after-effects. Motor after-effects were characterized in a short tied Catch trial at the group-specific walking speed. During the split session's Re-Adaptation epoch, subjects again experienced 3:1 split-belt walking for 300 strides in order to return subjects to steady state split-belt walking before testing active perception of step length in the Post-Adaptation epoch. Following the active perceptual assessment during the Post-Adaptation epoch, subjects walked for 150 strides at the group-specific walking speed in order to evaluate any remaining motor after-effects. Once these motor after-effects were fully washed out, we performed one last active perceptual task without feedback to assess subjects' retention of the map between the target and executed step lengths.

General Approach for all Active Perception Trials

Subjects wore a virtual reality headset (Oculus, Facebook Technologies, Irvine, CA, United States) to eliminate the possibility of using visual information to bias subjects' estimate of step length based on their body motion with respect to the treadmill. Subjects received limited feedback on their step length on a numbered grid that was displayed in the virtual reality headset (Figure 6). Each grid line corresponded to 2 cm in real space. The cursors on the screen indicated the step length when taking a step with the right (orange cursor) or left leg (green cursor). The cursor position for each leg was only updated at heel-strike. The target step length was indicated with the blue highlighted line on the grid. The comfortable step length (grid #10) corresponded to the average step length during the speed-specific baseline walking. Subjects were also prompted to take a short (grid #7, 6 cm shorter than comfortable step length) and long (grid #13, 6 cm longer than comfortable step length) target step lengths. Importantly, the short and long step lengths used in the perceptual task were different from those regularly taken during baseline walking or during the catch trail. This was done to test active perceptual effects with step lengths that were distinct from those that subjects would normally take when assessing motor after-effects. Subjects performed the active perceptual task as they walked while lightly touching (<2N, enforced with verbal feedback) an instrumented handrail located in front of the treadmill. This was done to ensure that individuals would maintain their position on the treadmill while walking with the virtual reality headset [34]. Recall that the Short-MidSpeed and Long-MidSpeed groups performed the step length

639 tasks at a mid-walking speed (1.0 m/s), whereas the Short-SlowSpeed group performed
640 the step length tasks at a slow walking speed (0.5 m/s).
641
642 Training for active perceptual testing
643
644 A step length Training epoch was first conducted in order to train subjects to take three
645 distinct step lengths. During training, subjects received feedback on 100% of their step
646 length error, where step length error is defined as the distance between the target step
647 length and the executed step length. Subjects experienced targets in 4 sets where each set
648 included each of the three targets in a random order. Each presentation of the target
649 included 50 strides with visual feedback followed by 10 strides with no visual feedback.
650 This was done to habituate the subjects to performing the perceptual task without
651 feedback and favor the learning and retention process (e.g., [35]). In total, subjects trained
652 for 720 strides.
653
654 Map Test
655
656 Map Tests were used to ensure that subjects had successfully learned and maintained a
657 mapping between the target step lengths prompted by each number on the grid. During
658 this map test, subjects performed two sets of 25 strides for each target (total of 150
659 strides) without any feedback. This was done right before the Adaptation epoch and at the
660 end of each session following the extinction of any locomotor after-effects during the
661 Post-Adaptation epoch. The perceptual training protocol was effective as indicated by the

fact that subjects took distinct step lengths for each target step length value (Figure 6c: two-way repeated measures ANOVA testing the effect of target step length and session on step length for each leg; Slow Leg: $p_{Target}<0.001$, $p_{Session}=0.20$, $p_{Target\#Session}=1.00$; Fast Leg: $p_{Target}<0.001$, $p_{Session}=0.35$, $p_{Target\#Session}=0.80$) that were retained for the duration of each session except for the fast leg during the tied session (two-way repeated measures ANOVA with effect of target step length and epoch; Tied Session, slow step length: $p_{Target}=0.82$, $p_{Epoch}=0.79$, $p_{Epoch\#Target}=0.68$; Tied Session, fast step length: $p_{Target}=0.92$, $p_{Epoch}=0.009$, $p_{Epoch\#Target}=0.37$; Split Session, slow step length: $p_{Target}=0.89$, $p_{Epoch}=0.069$, $p_{Epoch\#Target}=0.80$; Split Session, fast step length: $p_{Target}=0.76$, $p_{Epoch}=0.13$, $p_{Epoch\#Target}=0.72$). While the mapping between prompted and taken step lengths was not well maintained for the fast leg during the tied session, qualitatively, subjects still maintained distinct step lengths. Therefore, any changes observed between the Baseline and Post-Adaptation Perceptual trials are due to changes in perception, rather than subjects forgetting of the step length value that they were required to take when prompted by each number on the grid.

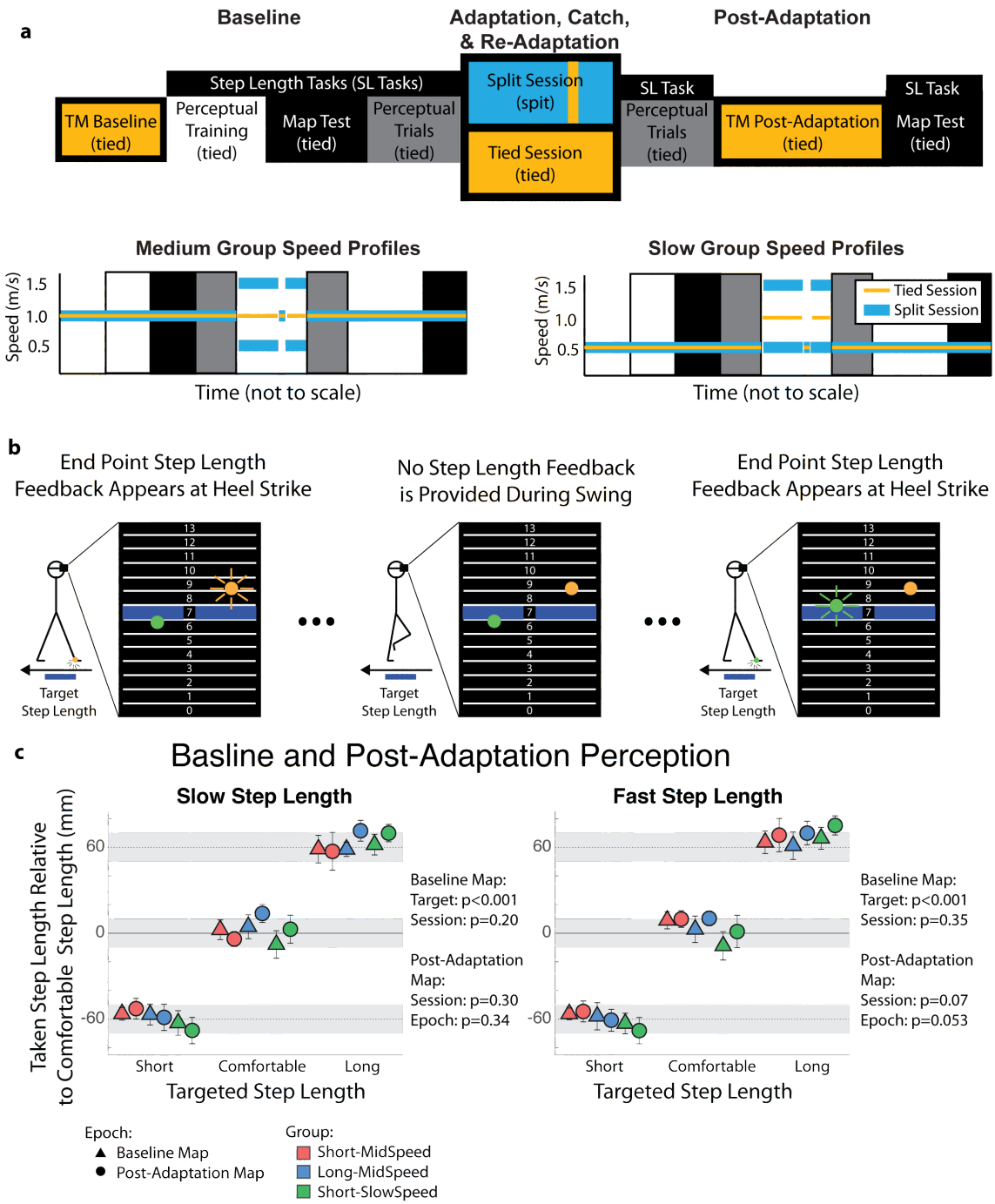

Figure 6 Locomotor and Active Perception Protocol | (a) Locomotor (colored blocks) and Active Perceptual (grey scale blocks) epochs were included in both the control and testing session. Note that subjects were walking during the active perceptual trials. **(b) Active Step Length Task:** Subjects walked on the treadmill while wearing a virtual reality headset. Note that subject's walking speed depended on the group. Subjects saw a grid where each grid corresponded to 2 cm in real space. The blue highlighted grid line indicated a target step length that subjects should take. Grid 7, 10, and 13 corresponded to

689 short, medium, and long step lengths, respectively. During training trials, subjects
690 received accurate endpoint feedback on each step length. During Map Tests, subjects did
691 not receive any feedback on their performance. During perceptual trials, subjects
692 received reduced error feedback (i.e., subjects only saw 35% of the error that they made).
693 **(c) Map Test:** Subjects performance during the Map Test indicated how well subjects
694 learned and retained the spatial mapping between step lengths prompted with
695 biofeedback and taken step lengths. Note that subjects learned distinct step lengths that
696 were well maintained from the beginning until the end of the experiment. Thus, any
697 changes in the active perception of step length are due to perceptual changes rather than
698 subject's inability to learn or maintain a mapping between prompted and taken step
699 lengths.
700
701 Active Perception Trials

702

703 To determine if active perception was altered, subjects needed to be able to have large
704 step length errors without receiving feedback that would illicit strategic movement
705 corrections that could override perceptual shifts. However, pilot data indicated that
706 subjects needed some feedback to stay on task for the duration of the perceptual trials.
707 Therefore, 35% of subjects step length error was projected during the active perceptual
708 trials directly before and after the Adaptation epoch without the subjects' knowledge in
709 order to observe active perceptual shifts and their natural decay (e.g., if subjects had a 10
710 cm step length error, the feedback only indicated that there was a 3.5 cm step length
711 error). Recall that the Short-MidSpeed and Short-SlowSpeed group started with short
712 targets whereas the Long-MidSpeed group started with long targets. Subjects alternated
713 between the short and long target step lengths in a predefined manner in order to
714 characterize the decay of any temporally persistent perceptual shifts (455 strides total: 10
715 strides first target, 15 strides of the second target, one set of the short and long target for
716 15 strides, one set of the short and long target for 25 strides, three sets of the short and
717 long target for 50 strides, 50 strides of the comfortable step length). Note that because all

718 groups took the same number of strides, that it took the group walking slow (0.5 m/s)
719 twice as long to complete the perceptual trials as the groups walking at the mid speed (1
720 m/s).
721
722 **Data collection**
723
724 Kinematic data were collected to characterize subjects' locomotor behaviors while
725 walking on the treadmill during locomotor and perceptual trials. A motion analysis
726 system (Vicon Motion Systems, Oxford, UK) was used to collect kinematic data at 100
727 Hz. A quintic spline interpolation was used to fill gaps in the raw kinematic data
728 (Woltring; Vicon Nexus Software, Oxford, UK). Subjects' movements were tracked via
729 passive reflective markers placed bilaterally over the hip (greater trochanter) and ankle
730 (lateral malleoulous) and asymmetrically on the thigh and shank to distinguish the legs.
731 The duration of treadmill trials was defined by real time kinetic detection of heel strikes.
732 Heel strikes were identified with raw vertical kinetic data collected from the instrumented
733 treadmill (Bertec, Columbus, OH, United States).
734
735 *Perceptual Task*
736
737 Custom written Vizard (WoldViz, Santa Barbara, CA, United States) and MATLAB (The
738 MathWorks, Inc., Natick, MA, United States) code was used to control the treadmill in
739 order to impose desired step lengths during the passive perception tasks and to provide
740 appropriate feedback during all perceptual tasks.

741 **Statistical Analysis**

742

743 The statistical analyses were performed as reported in the text. A significance level of α

744 = 0.05 was used for all analysis. Stata was used to perform all statistical analysis

745 (StataCorp LP, College Station, TX).

746

747 **Competing Interests**

748

749 The authors declare that there are no competing interests.

750

751 **Author Contributions**

752

753 G.T.-O. and C.S. were involved with the conception and design of the work. C.S. and

754 M.G.-R. collected and analyzed the data. C.S. and G.T.-O. interpreted the results. C.S.

755 drafted the manuscript, which was carefully revised by all authors. The final version of

756 the manuscript has been approved by all the authors who agree to be accountable for all

757 aspects of the work in ensuring that questions related to the accuracy or integrity of any

758 part of the work are appropriately investigated and resolved. All authors qualify for

759 authorship and all those who qualify for authorship are listed.

760

761 **Funding**

762

763 This work is funded by NSF1535036 and C.S is funded by a NSF fellowship (GRFP)

Bibliography

1. Vaziri, S., Diedrichsen, J. & Shadmehr, R. Why Does the Brain Predict Sensory Consequences of Oculomotor Commands? Optimal Integration of the Predicted and the Actual Sensory Feedback. *J. Neurosci.* **26,** 4188–4197 (2006).
2. Coslett, H. B., Buxbaum, L. J. & Schwoebel, J. Accurate reaching after active but not passive movements of the hand: Evidence for forward modeling. *Behav. Neurol.* **19,** 117–125 (2008).
3. Laufer, Y., Hocherman, S. & Dickstein, R. Accuracy of reproducing hand position when using active compared with passive movement. *Physiother. Res. Int.* **6,** 65–75 (2001).
4. Paillard, J. & Brouchon, M. Active and passive movements in the calibration of position sense. *Neuropsychol. Spat. oriented Behav.* **11,** 37–55 (1968).
5. Haith, A., Jackson, C. P., Miall, R. C. & Vijayakumar, S. Unifying the Sensory and Motor Components of Sensorimotor Adaptation. *Adv. Neural Inf. Process. Syst.* 593–600 (2009).
6. Mattar, A. A. G., Darainy, M. & Ostry, D. J. Motor learning and its sensory effects : time course of perceptual change and its presence with gradual introduction of load. *J. Neurophysiol.* **109,** 782–791 (2013).
7. Van Beers, R. J., Sittig, A. C. & Denier van der Gon, J. J. Integration of proprioceptive and visual position-information: An experimentally supported model. *J. Neurophysiol.* **81,** 1355–1364 (1999).
8. Cressman, E. K. & Henriques, D. Y. P. Sensory Recalibration of Hand Position Following Visuomotor Adaptation. *J. Neurophysiol.* **102,** 3505–3518 (2009).

9. Cressman, E. K. & Henriques, D. Y. P. Reach Adaptation and Proprioceptive Recalibration Following Exposure to Misaligned Sensory Input. *J. Neurophysiol.* **103,** 1888–1895 (2010).

10. t' Hart, B. M., Henriques, D. Y. P., Marius, B. & Henriques, D. Y. P. Separating predicted and perceived sensory consequences of motor learning. *PLoS One* **11,** 1–15 (2016).

11. Ostry, D. J., Darainy, M., Mattar, A. A. G., Wong, J. & Gribble, P. L. Somatosensory Plasticity and Motor Learning. *J. Neurosci.* **30,** 5384–5393 (2010).

12. Salomonczyk, D., Cressman, E. K. & Henriques, D. Y. P. Neuropsychologia Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. *Neuropsychologia* **49,** 3053–3062 (2011).

13. Salomonczyk, D., Henriques, D. Y. P. & Cressman, E. K. Proprioceptive recalibration in the right and left hands following abrupt visuomotor adaptation. *Exp. Brain Res.* **217,** 187–196 (2012).

14. Salomonczyk, D., Cressman, E. K. & Henriques, D. Y. P. The role of the cross - sensory error signal in visuomotor adaptation. *Exp. Brain Res.* **228,** 313–325 (2013).

15. Zbib, B., Henriques, D. Y. P. & Cressman, E. K. Proprioceptive recalibration arises slowly compared to reach adaptation. *Exp. Brain Res.* **234,** 2201–2213 (2016).

16. Vazquez, A., Statton, M. A., Busgang, S. A. & Bastian, A. J. Split-belt walking adaptation recalibrates sensorimotor estimates of leg speed but not position or force. *J. Neurophysiol.* **114,** 3255–3267 (2015).

17. Mostafa, A. A., Salomonczyk, D., Cressman, E. K. & Henriques, D. Y. P. Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand. *Exp. Brain Res.* **232,** 1639–1651 (2014).

18. Mostafa, A. A., Kamran, R., Bahari, G., Erin, K. & Henriques, D. Y. P. Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace. *Exp. brain Res.* **233,** 817–827 (2015).

19. Cressman, X. E. K. & Henriques, D. Y. P. Generalization patterns for reach adaptation and proprioceptive recalibration differ after visuomotor learning. *J. Neurophysiol.* **114,** 354–365 (2015).

20. Vasudevan, E. V. L. & Bastian, A. J. Split-belt treadmill adaptation shows different functional networks for fast and slow human walking. *J. Neurophysiol.* **103,** 183–91 (2010).

21. Wutzke, C. J., Faldowski, R. A. & Lewek, M. D. Individuals Poststroke Do Not Perceive Their Spatiotemporal Gait Asymmetries as Abnormal. *Phys. Ther.* **95,** 1244–1253 (2015).

22. Orendurff, M. S., Bernatz, G. C., Schoen, J. A. & Klute, G. K. Kinetic mechanisms to alter walking speed. *Gait Posture* **27,** 603–610 (2008).

23. Dewolf, A. H., Ivanenko, Y., Zelik, K. E., Lacquaniti, F. & Willems, P. A. Kinematic patterns while walking on a slope at different speeds. *J. Appl. Physiol.* **125,** 642–653 (2018).

24. Torres-Oviedo, G. & Bastian, A. J. Natural error patterns enable transfer of motor learning to novel contexts. *J. Neurophysiol.* **107,** 346–56 (2012).

25. Leech, K. A., Roemmich, R. T., Day, K. A. & Bastian, A. J. Movement and

833 perception recalibrate differently across multiple days of locomotor learning. *J.*
834 *Neurophysiol.* **114,** 608–623 (2018).
835 26. Bouton, M. E., Nelson, J. B. & Rosas, J. M. Stimulus generalization, context
836 change, and forgetting. *Psychol. Bull.* **125,** 171–186 (1999).
837 27. Spear, N. E. *The processing of memories: forgetting and retention*. (Hillsdale,
838 1978).
839 28. Tulvig, E. & Thomson, D. M. Encoding specificity and retrieval processes in
840 episodic memory. *Psychol. Rev.* **80,** 352–373 (1973).
841 29. Torres-Oviedo, G. & Bastian, A. J. Seeing Is Believing : Effects of Visual
842 Contextual Cues on Learning and Transfer of Locomotor Adaptation. *J. Neurosci.*
843 **30,** 17015–17022 (2010).
844 30. Desmurget, M., Jordan, M., Prablanc, C. & Jeannerod, M. Constrained and
845 Unconstrained Movements Involve Different Control Strategies. *J. Neurophysiol.*
846 **77,** 1644–1650 (1997).
847 31. Reisman, D. S., McLean, H., Keller, J., Danks, K. A. & Bastian, A. J. Repeated
848 split-belt treadmill training improves poststroke step length asymmetry.
849 *Neurorehabil. Neural Repair* **27,** 460–468 (2013).
850 32. Lewek, M. D., Braun, C. H. & Wutzke, C. The role of movement errors in
851 modifying spatiotemporal gait asymmetry post stroke: a randomized controlled
852 trial. *Clin. Rehabil.* **32,** 161–172 (2018).
853 33. Cressman, E. K., Salomonczyk, D. & Henriques, D. Y. P. Visuomotor adaptation
854 and proprioceptive recalibration in older adults. *Exp. Brain Res.* **205,** 533–544
855 (2010).

34. Forero, J. & Misiaszek, J. E. The contribution of light touch sensory cues to corrective reactions during treadmill locomotion. *Exp. Brain Res.* **226,** 575–584 (2013).

35. Winstein, C. J. & Schmidt, R. A. Reduced frequency of knowledge of results enhances motor skill learning. *J. Exp. Psychol. Learn. Mem. Cogn.* **16,** 677 (1990).