A novel optic flow pattern speeds split-belt locomotor adaptation

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Finley JM, Statton MA, Bastian AJ. A novel optic flow pattern speeds split-belt locomotor adaptation. J Neurophysiol 111: 969–976, 2014. First published December 11, 2013; doi:10.1152/jn.00513.2013.—Visual input provides vital information for helping us modify our walking pattern. For example, artificial optic flow can drive changes in step length during locomotion and may also be useful for augmenting locomotor training for individuals with gait asymmetries. Here we asked whether optic flow could modify the acquisition of a symmetric walking pattern during split-belt treadmill adaptation. Participants walked on a split-belt treadmill while watching a virtual scene that produced artificial optic flow. For the Stance Congruent group, the scene moved at the slow belt speed at foot strike on the slow belt and then moved at the fast belt speed at foot strike on the fast belt. This approximates what participants would see if they moved over ground with the same walking pattern. For the Stance Incongruent group, the scene moved fast during slow stance and vice versa. In this case, flow speed does not match what the foot is experiencing, but predicts the belt speed for the next foot strike. Results showed that the Stance Incongruent group learned more quickly than the Stance Congruent group even though each group learned the same amount during adaptation. The increase in learning rate was primarily driven by changes in spatial control of each limb, rather than temporal control. Interestingly, when this alternating optic flow pattern was presented alone, no adaptation occurred. Our results demonstrate that an unnatural pattern of optic flow, one that predicts the belt speed on the next foot strike, can be used to enhance learning rate during split-belt locomotor adaptation.

motor learning; optic flow; locomotion; adaptation

VISUAL INFORMATION informs us of how our bodies move with respect to objects in our environment and enables us to modify our walking pattern accordingly. Optic flow, which involves radial expansion of the visual scene (Gibson 1950), is naturally generated as we move through our environment and contributes to our perception of self-motion (Perrone and Stone 1994), helps us navigate toward targets in the environment (Berard et al. 2011; Chou et al. 2009; Sarre et al. 2008; Warren et al. 2001), and helps us to avoid obstacles (Sun et al. 1992). These studies highlight the fact that visual information is naturally used to modify our walking pattern and represent a potential sensory pathway that could be targeted to selectively elicit changes in locomotor coordination.

Although optic flow is most commonly generated during translation with respect to the environment, artificial generation of optic flow can have a significant impact on the perception of self-motion and lead to changes in the spatiotemporal aspects of gait. For example, through use of a front-to-rear moving stimulus of horizontal stripes, artificial optic flow can be used to directly trigger locomotion in lobsters, crayfish, and blowflies (Davis and Ayers 1972). In humans, if optic flow is simulated by projecting a radially expanding scene on a display while subjects walk on a treadmill, the subjects perceive that they are translating through space, even if they hold on to a handrail providing a clear ground reference (Lackner and DiZio 1993). Furthermore, if the speed of optic flow is increased (decreased) relative to their actual walking speed, they will decelerate (accelerate) to try and drive the visually perceived speed toward the actual walking speed (Konczak 1994; Prokop et al. 1997). Interestingly, these changes are preferentially driven by changes in stride length, not cadence (Prokop et al. 1997).

Since discrepancies between optic flow speed and actual walking speed preferentially affect stride length, it may be possible to use optic flow to generate targeted changes in step length on a step-to-step basis. A potential application for this approach is the modification of step length asymmetries in hemiparetic individuals, who often walk with steps of unequal length (Balasubramanian et al. 2007; Chen et al. 2005; Hsu et al. 2003). These individuals would perceive a pattern of optic flow that varies in speed from step to step if there are asymmetries in step velocity. This would occur in individuals whose asymmetries in step length and step time oppose one another (Roerdink et al. 2007) or if the quotient of step length and step time (step velocity) varies between the paretic and nonparetic limbs. Thus, if the visuomotor effects of optic flow are generated within a step cycle, it may be possible to modify asymmetry by introducing patterns of optic flow that vary in speed at each foot strike.

Here, we introduced optic flow while healthy individuals adapted to walking on a split-belt treadmill to determine whether step-to-step changes in the speed of optic flow could be used to modify step length symmetry. We assumed that the effects of optic flow would depend on the congruency between the speed of optic flow and the speed of the belt under the stance leg. Therefore, we introduced two different polarities of optic flow. In our Stance Congruent group, optic flow speed was matched to the speed of the belt under the stance leg. In our Stance Incongruent group, optic flow speed was matched to the speed of the belt opposite the stance limb. We hypothesized that these types of optic flow would have opposing effects on symmetry, with the Stance Congruent flow speeding adaptation and the Stance Incongruent flow slowing adaptation. To our surprise, our results showed the opposite. These findings extend our understanding of how visual information is used in the context of locomotor adaptation and may have implications for the use of virtual reality environments during locomotor rehabilitation for individuals with gait asymmetries.
METHODOLOGY

Ethical approval. Fifty-seven individuals participated in this study (27 men, 30 women; 24 ± 4 yr old). The experimental protocol was approved by the Johns Hopkins Medicine Institutional Review Board and conformed to the standards set by the Declaration of Helsinki. All participants provided written informed consent before testing.

Primary experiment. We explored the effects of asymmetric optic flow patterns on the acquisition of a symmetric gait pattern during adaptation to walking on a split-belt treadmill. Participants adapted their walking pattern on a custom split-belt treadmill (Woodway USA, Waukesha, WI) capable of moving each leg at different speeds. Participants held on to a handrail in front of the treadmill during all phases of the experiment to prevent them from drifting backward and to better represent the conditions used when stroke survivors train on a split-belt treadmill. Although this provides participants with a ground reference, they perceived that both they and the handrail moved through space, similar to the illusion that has been reported during walking on a circular treadmill (Lackner and DiZio 1993). All participants began the experiment with four baseline walking trials. The first trial involved walking at 1 m/s with both belts moving at the same speed. This was followed by a brief (15 s) exposure to walking with the fast and slow belts moving at 1.5 m/s and 0.5 m/s, respectively. This brief exposure served to minimize any potential startle effects that may be present during the early portion of the adaptation period. The initial exposure was followed by a 1-min washout period with the belts moving at the same speed. Each of these initial periods was conducted in the dark. Participants then walked for 2 min with both belts moving at 1.0 m/s while watching either a static visual scene (n = 12) or a scene that moved toward the participant at 1.0 m/s (n = 45). This portion of the experiment served to acclimate the participants to the type of visual stimulus they would receive during the subsequent adaptation period (i.e., the correspondence between flow speed and belt speed). During adaptation, participants walked for 15 min while the left and right belts were driven at 0.5 m/s and 1.5 m/s, respectively. During adaptation, participants watched one of three types of visual displays designed to assess the effects of optic flow on adaptation. The experiment concluded with a postadaptation period in which participants walked for 15 min with both belts moving at 1.0 m/s.

Optic flow paradigm. Participants in the primary experiment were divided among three groups who each adapted while watching one of three types of visual scenes. The belt speeds and visual scene used for each group are illustrated in Fig. 1. The scene was composed of a field of gray pyramids uniformly distributed over a black background, and its displacement was controlled with the Vizard VR Toolkit (WorldViz, Santa Barbara, CA). We chose to use this type of scene because these high-contrast visual stimuli are known to be effective at driving locomotor and postural response (Logan et al. 2010; Oie et al. 2002; Prokop et al. 1997). The scene was displayed on a large monitor (1.25 m by 0.69 m) placed at eye level 0.71 m in front of the treadmill. Participants wore custom goggles that obscured their peripheral vision such that their view was restricted to the visual display. They were also instructed to look straight ahead at the center of the screen for the entire study. The experimenter watched the participants throughout the study, and if any overt head movements were noticed the participants would be reminded to focus on the center of the screen. For the Static condition (n = 12, 5 men, 7 women; 25 ± 6 yr), the pyramids were distributed throughout the virtual space and their position remained constant (i.e., no displacement) while the participants walked. For each of the asymmetric optic flow conditions, the speed of the visual scene changed instantaneously at each foot strike. The time of each foot strike was determined based on vertical force signals from load cells underneath each belt. A thin board was placed between the belts to prevent participants from crossing over onto the opposite belt. For the Stance Congruent condition (n = 12, 6 men, 6 women; 25 ± 3 yr), the scene moved toward the participants at 1.5 m/s at foot strike on the fast belt and at 0.5 m/s at foot strike on the slow belt. The opposite was true for the Stance Incongruent condition (n = 12, 6 men, 6 women; 24 ± 4 yr). The scene moved at 0.5 m/s at foot strike on the fast belt and at 1.5 m/s at foot strike on the slow belt. We used opposing patterns of optic flow to determine whether there were polarity-specific effects of asymmetric optic flow on split-belt treadmill adaptation.

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<th>Group</th>
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<td>Incongruent Post Only</td>
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Fig. 1. Experimental paradigm. A: experimental conditions for the adaptation and postadaptation periods for each group. The durations of each period, as well as the corresponding belt speeds and optic flow conditions, are indicated for each phase of the study. B: screenshot of the virtual environment displayed on the monitor in front of the participants. The environment consisted of 3,000 pyramids, and the displacement of these pyramids was controlled via custom code written in Python. C: diagram of the marker configuration used for kinematic analysis. The markers were placed bilaterally on each of the bony landmarks illustrated. AP, acromion process; IC, iliac crest; GT, greater trochanter; LE, lateral femoral epicondyle; LM, lateral malleolus; MT, 5th metatarsal head.
Secondary experiments. In addition to the primary experiment, we also tested the hypothesis that asymmetric optic flow, in the absence of a discrepancy in belt speeds, could induce asymmetry. This Vision Only group (n = 7, 2 men, 5 women; 25 ± 4 yr) followed the same protocol as the Stance Incongruent group but walked with both belts moving at 1.0 m/s during the adaptation period. This group allowed us to determine whether the effects of optic flow on symmetry during split-belt adaptation were additive or if the effects relied on a nonlinear interaction between asymmetries in optic flow and belt speeds.

Finally, we investigated whether we could modify the unlearning process by providing optic flow during the postadaptation period. We tested the Stance Incongruent flow only based on our findings in the prior experiments (i.e., it was most effective at speeding adaptation). As such, we thought that it might affect unlearning by reinforcing the coordination pattern (foot placement and timing) acquired during adaptation. Two groups of individuals participated in this portion of the study. Both groups experienced the same visual stimulus during postadaptation: optic flow at 1.5 m/s at foot strike on the right belt and optic flow at 0.5 m/s at foot strike on the right belt. This was the equivalent of the Stance Incongruent optic flow experienced during adaptation. The Stance Incongruent Post group (n = 7, 3 men, 4 women; 23 ± 3 yr) experienced the same optic flow during both adaptation and postadaptation, while the Stance Incongruent Post Only group (n = 7, 4 men, 3 women; 23 ± 5 yr) adapted in the dark and received optic flow during postadaptation only.

Kinematics. Kinematic data were acquired with a digital camera system (Optotrak Certus, Northern Digital, Waterloo, ON, Canada) at 100 Hz. Infrared-emitting markers were placed on the following anatomical landmarks bilaterally (Fig. 1C): acromion process (shoulder), iliac crest (pelvis), greater trochanter (hip), lateral femoral epicondyle (knee), lateral malleolus (ankle), and fifth metatarsal (toe). Foot strike and liftoff were estimated by the peak anterior and posterior positions of the toe marker on each limb as described previously (Zeni et al. 2008).

Data analysis. We calculated kinematic parameters associated with locomotor adaptation, using the recorded marker positions. Step length symmetry was used as a primary measure of adaptation as it has been shown to adapt robustly across multiple speed ratios (Malone and Bastian 2010; Reisman et al. 2005, 2007). Step length symmetry (SS) was defined as the normalized difference between the step lengths of each limb (Eq. 1).

\[
SS = \frac{SL_{fast} - SL_{slow}}{SL_{fast} + SL_{slow}}
\]

Step length (SL) was defined as the anterior-posterior distance between the markers on the lateral malleolus of each leg at foot strike. Fast step length was measured at foot strike of the limb on the fast belt, and slow step length was measured at foot strike of the slow limb. Positive values for step length symmetry indicate a larger fast step, and the converse holds for negative values. A step length symmetry value of zero indicates that the fast and slow steps are of equal length and therefore represents symmetry. The average step symmetry during the last five strides of the first baseline walking period was subtracted from all subsequent measures of step symmetry.

Step length symmetry can be modified by making changes to either spatial or temporal aspects of the walking pattern (Fig. 2). The spatial change in the axis about which each limb oscillates was quantified as the center of oscillation difference (Malone and Bastian 2010). Limb angle was defined as the angle between vertical and a vector extending from the hip to the fifth metatarsal head (Fig. 1C). Positive values indicated limb flexion, while negative values indicated limb extension. The center of oscillation for each limb was computed by averaging the limb angles at foot strike and liftoff. The center of oscillation difference was quantified as the difference between the center of oscillation of the slow limb and the center of oscillation of the fast limb. Positive values indicate that the slow limb oscillates in a more flexed position, and the converse is true for negative values. Changes in the temporal component of adaptation were assessed by computing interlimb phasing. Phasing was quantified as the peak lag of the cross-correlation function between limb angle trajectories for a single cycle. This lag was normalized to stride time and thus ranged from [0,1].

We characterized the learning and unlearning processes by quantifying the time course over which each of our parameters changed and by computing the average values of each parameter during early and late phases of adaptation and postadaptation. The time courses of learning (adaptation) and unlearning (postadaptation) were assessed by computing the number of strides from the beginning of each phase until the respective parameter remained within the plateau range for 30 strides. The plateau range for each parameter was defined as the mean ± 2 standard deviations of the last 100 strides. The values for each parameter during the early and late phases of adaptation and postadaptation were computed by averaging over the first five and last five strides, respectively, for each phase.

Statistics. We tested the effect of optic flow group on each of our parameters with a one-way ANOVA. For the Vision Only group, we used single-sample t-tests to determine whether the asymmetry values during the early and late phases of adaptation and postadaptation were significantly different from zero. All summary statistics are presented as means ± SE. Significance was assessed at the 5% level, and all statistical procedures were performed with STATISTICA (StatSoft, Tulsa, OK).

Fig. 2. Example of spatial and temporal strategies to adjust symmetry. Each plot includes a representative time series of the fast limb angle (dashed lines) and the slow limb angle (solid lines). Positive values indicate limb flexion, while negative values indicate limb extension. Foot strike times for 2 consecutive steps are indicated by small circles. The vertical lines on each plot represent the angular spread between the limbs at foot strike, which serves as an analog of step length. The actual angular spread values are presented to right of the time series data for each plot. A: example of initial asymmetry during the early phase of adaptation. B: spatial strategy to reduce asymmetry. A positive, vertical shift of the fast limb’s center of oscillation is capable of reducing the asymmetry in angular spread. C: temporal strategy to reduce asymmetry. Introducing a phase lag in the slow limb (solid line) can also result in a more symmetric stepping pattern.
RESULTS

The two types of optic flow presented to our participants had opposing effects on the rate of learning (Fig. 3A). Over the course of adaptation, all groups adapted to have steps of equal length, but the number of steps taken before participants reached symmetry varied between the groups. Contrary to our hypothesis, the Stance Incongruent group, who received optic flow that was not matched to the speed of the stance leg, adapted most rapidly. Results from our ANOVA (Fig. 3B) revealed a significant effect of group on the number of strides to reach plateau \( F(2,33) = 6.57, P < 0.01 \). Specifically, the Stance Incongruent group required fewer strides to reach plateau than the Stance Congruent group (Incongruent: 126 ± 28, Congruent: 282 ± 24, \( P = 0.003 \)). There was also a tendency for the Stance Incongruent group to adapt more quickly than the Static group; however, this difference did not reach statistical significance (Incongruent: 126 ± 28, Static: 208 ± 38, \( P = 0.15 \)).

The differences in adaptation rates were not due to differences in the initial perturbation or the final symmetry values reached during late adaptation. The initial perturbations were not different among the groups tested [Static: \(-0.20 ± 0.02\), Stance Congruent: \(-0.26 ± 0.04\), Stance Incongruent: \(-0.20 ± 0.04\), \( F(2,33) = 1.2, P = 0.31 \)], and each group plateaued at comparable symmetry values [Static: \(-0.013 ± 0.018\), Stance Congruent: \(-0.022 ± 0.019\), Stance Incongruent: \(0.0067 ± 0.017\), \( F(2,33) = 0.96, P = 0.39 \)]. Thus Stance Incongruent optic flow changed how participants used sensory information about their asymmetry to reach overall symmetry more quickly. However, differences in the rate of adaptation could be preferentially driven by changes in the length of the fast or slow step. Our data suggest that optic flow primarily drives changes in the fast step. Since the initial perturbation results in a larger step on the slow belt, one could reduce asymmetry by either increasing the length of the fast step or reducing the length of the slow step. We found that both of these strategies were used to different extents (Fig. 3, C and E). During early adaptation, the fast step length decreased by \(-20\) cm for each group. As adaptation progressed the fast step length approached baseline values for each group, but the time course of this change varied between groups (Fig. 3D). We found a significant effect of group on the number of strides until the fast step length plateaued \( F(2,33) = 3.96, P = 0.029 \), with the Stance Incongruent group requiring fewer steps to plateau than the Stance Congruent group (Congruent: 281 ± 32; Incongruent: 156 ± 35, \( P = 0.015 \)). Although each group gradually reduced the length of the slow step over the course of adaptation (Fig. 3E), there was no significant effect of optic flow on the time for the slow step length to reach a plateau [Fig. 3F; \( F(2,33) = 1.34, P = 0.28 \)]. Thus the effects of optic flow on the adaptation of step symmetry were primarily due to changes in the fast step length. We discuss postadaptation effects in a later section.

Optic flow preferentially affects spatial adaptation. Stance Incongruent optic flow sped the acquisition of symmetry by influencing spatial characteristics of locomotor adaptation. This was quantified by looking at the difference between the axes about which each limb oscillated (Fig. 4A). During early adaptation, the slow limb oscillated in a more flexed position than the fast limb, leading to a large positive center of oscillation difference. Over the course of adaptation, the placement of the fast limb occurred in an increasingly flexed position, leading to a reduction in the center of oscillation difference. Consistent with the observed changes in step symmetry, we found that there was a significant difference in the rate at which each group adapted their center of oscillation [Fig. 4B; \( F(2,33) = 4.21, P = 0.024 \)]. Post hoc

![Fig. 3. A, C, and E: adaptation curves for step symmetry (A), fast step length (C), and slow step length (E). Step length data are expressed as the change in step length relative to baseline walking at 1.0 m/s. Positive values indicate longer steps relative to baseline, while negative values correspond to shorter step lengths. Shaded areas around each line represent SE across subjects. Error bars at the beginning of adaptation represent the average initial perturbation to each parameter across subjects, and error bars at the end of adaptation represent the final values reached at the conclusion of adaptation. B, D, and F: number of strides required to plateau for step symmetry (B), fast step length (D), and slow step length (F). Error bars represent SE. *Significant differences at the 5% level.](http://jn.physiology.org/)
analyses revealed that the Stance Incongruent group adapted their center of oscillation difference more rapidly than both the Static (Static: 180 ± 96, Stance Incongruent: 77 ± 56, $P = 0.04$) and Stance Congruent (Stance Congruent: 179 ± 132, Stance Incongruent: 77 ± 56, $P = 0.04$) groups. In contrast to the changes in the rate of adaptation of the center of oscillation, no differences were observed in the rate at which interlimb phasing was adapted (Fig. 4, C and D). These results indicate that the effects of optic flow on adaptation are isolated to spatial changes in the walking pattern and not changes in timing.

**Effects of asymmetric optic flow on symmetry in the absence of a perturbation.** We found that asymmetric optic flow had only marginal effects on step symmetry in the absence of an asymmetric treadmill perturbation (Fig. 5). Here, participants walked with the belts moving at equal speeds while watching the same optic flow stimulus as the Stance Incongruent group, i.e., at foot strike of the right limb they received optic flow at a speed of 0.5 m/s and at foot strike of the left limb they received optic flow at a speed of 1.5 m/s. Step symmetry was assessed as the normalized difference between the right and left step lengths to maintain the same convention as the groups who adapted with the belts moving at different speeds. During early adaptation, six of seven participants had a small, positive asymmetry (average: 0.02 ± 0.01), which indicates that asymmetric optic flow alone can have modest effects on symmetry. However, this asymmetry was not found to be statistically different from zero (single-sample $t$-test, $P = 0.11$). Step symmetry was also found to be no different from zero during late adaptation ($P = 0.29$), early postadaptation ($P = 0.38$), or late postadaptation ($P = 0.91$). This demonstrates that optic flow alone has only marginal and transient effects on step symmetry and leaves no lingering effects when the visual stimulus is removed.

No differences observed in the rate of washout during postadaptation. Despite differences in the rate of adaptation, all groups washed out their learning at similar rates (Fig. 6A). In addition to the groups from the primary experiment, we included two groups in a secondary experiment to test whether adding optic flow during the postadaptation period could modify unlearning. The Incongruent Post group received the Stance Incongruent visual stimulus during adaptation and postadaptation, while the Incongruent Post Only group adapted in the dark and was then exposed to the same visual stimulus as the Incongruent Post group during postadaptation. We found that neither maintaining optic flow from adaptation to postadaptation nor introducing Incongruent optic flow during postadaptation had an effect on the rate of unlearning. There were no differences in the number of strides taken until each group reached their plateaus [Fig. 6B; $F_{(4,45)} = 1.38$, $P = 0.46$]. There were also no significant differences in the size of the aftereffect [$F_{(4,45)} = 0.73$, $P = 0.58$] or the final symmetry

Fig. 4. Adaptation curves for spatial and temporal parameters. A: center of oscillation difference. Positive values indicate that the slow limb oscillates at a more flexed position than the fast limb. C: interlimb phasing. Positive values indicate that the slow limb is phased advanced relative to the fast limb. Both center of oscillation difference and phasing are expressed relative to baseline. Shaded areas around each line represent SE across subjects. Error bars at the beginning and end of adaptation represent the average initial perturbation and the final value reached at the conclusion of adaptation, respectively. B and D: number of strides required to plateau for center of oscillation difference (B) and interlimb phasing (D) for each group. Error bars represent SE. *Significant differences at the 5% level.

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value \( F_{(4,45)} = 0.56, P = 0.70 \) across groups. Therefore, although optic flow could be used to modify adaptation, we were unable to leverage visual information to change deadaptation.

**DISCUSSION**

The goal of this study was to determine whether asymmetric patterns of optic flow could be used to enhance the acquisition of a symmetric walking pattern during split-belt treadmill adaptation. Contrary to our expectations, we found that providing optic flow that was incongruent with speed of the stance belt reduced the time required to learn a symmetric walking pattern relative to congruent optic flow. This shows that neural pathways responsible for using optic flow to modify the walking pattern are capable of modifying interlimb asymmetry. This leads to the interesting possibility that optic flow could be combined with locomotor training to help alleviate asymmetry in clinical populations with asymmetric gaits.

There are at least two possible explanations for how Stance Incongruent optic flow could speed the adaptation process. First, it is possible that individuals used optic flow in a predictive manner to help determine when and where to place their feet. When walking on a treadmill, step length and cadence can be selected based on a combination of past experience and current sensory information. Past experience allows for rapid selection of an appropriate gait pattern and is most useful when walking in contexts that one has been exposed to previously. For example, when individuals are exposed to changes in speed on a standard treadmill, most of the transient change in step frequency requires only a few seconds (Snaterse et al. 2011). This rapid switching likely occurs because individuals can use sensory information from both legs to estimate speed and select step lengths. However, when individuals are exposed to walking on a split-belt treadmill, their past treadmill experience may not be as helpful for selecting an appropriate gait pattern, and they must therefore rely on available sensory information. In the absence of optic flow, this sensory information comes primarily from the mechanical interaction between each foot and its respective belt. During early learning, it is possible that the nervous system initially relies on an assumption of symmetry based on prior experience on treadmills and therefore uses the sensory state of the stance leg to inform the upcoming placement of the swing leg. Providing optic flow that is incongruent with the stance leg but congruent with the upcoming speed for the swing leg may improve the ability to predict where the next foot strike should occur and speed adaptation. Conversely, Stance Congruent optic flow may slow learning by reinforcing the incorrect assumption that the sensory state of the stance leg can be used to set the location of the subsequent swing leg foot strike.

The influence of optic flow on symmetry could also be tied to the congruency between the speed of flow and the speed of the swing leg, particularly since the swing leg is unconstrained and free to make adjustments for the next step. Consistent with this idea, single-cell recordings in area 5 of the posterior parietal cortex have identified populations of neurons that fire immediately prior to and during the swing phase when gait modifications are visually triggered by a looming obstacle (Andujar et al. 2010). This suggests that gait modifications are most sensitive to visual information that is presented during preswing and the swing phase, similar to how the visual stimulus was presented in the present study. Given this perspective, our Stance Incongruent stimulus might be considered Swing Congruent, while our Stance Congruent stimulus would be Swing Incongruent.

An alternative explanation is that subjects change their step length to resolve the discrepancy between the velocity of the virtual environment and walking speed on a step-to-step basis. If the speed of optic flow is controlled to be slower than actual walking speed, individuals will take larger steps and walk more quickly (Prokop et al. 1997). This behavior is thought to result from a strategy that attempts to drive the speed of optic flow toward actual walking speed. If this same behavior is used during split-belt adaptation, it would result in subjects taking longer steps when optic flow is slower than the speed of the belt under the stance leg and shorter steps when flow is faster than would be expected. This is precisely what occurred during early adaptation in our Stance Incongruent group and could explain why participants in this group adapted more rapidly. Although this strategy may explain our observations during split-belt walking, it would also predict that asymmetries in
Optic flow would modify the walking pattern when both treadmill belts move at the same speed; however, this was not what we observed. Interestingly, we found that optic flow most strongly modulated changes in learning rate for the fast step, with negligible changes in the slow step. This may be explained by the observation that the fast step undergoes the largest change in length during adaptation and therefore presents a wider dynamic range within which optic flow can modify step length. This explanation is also thought to explain why discordant optic flow led to preferential changes in stride length and not cadence (Prokop et al. 1997). The authors suggested that changes in the spatial control of walking were an identifying characteristic of the supraspinal contribution to the locomotor pattern. Consistent with this interpretation, a recent study exploring the role of conscious strategies during split-belt adaptation also found a preferential modification of spatial versus temporal components of adaptation when the effects of conscious strategies were reduced through dual-task performance (Malone and Bastian 2010). Thus it is possible that the effects of optic flow on adaptation were mediated by supraspinal networks that preferentially influence spatial control.

Effects of optic flow on symmetry require an asymmetric environment. We also found that the effects of optic flow on step symmetry were only evident when the visual stimulus was combined with an asymmetric treadmill perturbation. In our Vision Only group, subjects walked on the treadmill with both belts moving at the same speed but received optic flow that changed speed at each foot strike. This stimulus did not result in any significant modification of asymmetry despite the fact that it was the same stimulus that produced a more rapid adaptation of step symmetry when the belts moved at different speeds. We also found that the rate of unlearning was unaffected by optic flow regardless of whether flow was presented during adaptation, postadaptation, or both. Each of these results suggests that if the sensory information provided by the treadmill is symmetric, then it may result in a down-weighting of visual input. If this is true, then the observed changes in asymmetry in the Incongruent group may have been mediated by circuits that resolve discordant somatosensory information through integration of sensory input from other modalities such as vision. The vestibular nuclei are one possible locus for this multimodal sensory processing, and they also project to motor areas involved in locomotion (Boyle et al. 1985; Waespe and Henn 1977a, 1977b, 1979).

Clinical implications. The addition of optic flow to split-belt treadmill training could serve multiple purposes in the context of rehabilitation. For example, the addition of optic flow within a rich virtual environment may better engage patients during rehabilitation and reduce boredom during training. Optic flow may also help facilitate the transfer of learning on the treadmill to overground walking by providing visual cues during learning that are consistent with the type of optic flow received during overground gait. Device-based training often leads to limited transfer of learned motor patterns to movements outside of the device (Cothros et al. 2006; Kluzik et al. 2008; Reisman et al. 2009), and this may result from contextual differences between movements performed on and off the device. In support of this possibility, it was recently demonstrated that transfer of split-belt adaptation to overground walking is enhanced when the visual context between treadmill and overground walking is matched by having participants close their eyes in both conditions (Torres-Oviedo and Bastian 2010). What remains to be determined is how optic flow is processed in patient populations and how this processing impacts the effectiveness of artificial optic flow in mediating improvements in gait asymmetry.

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DISCLOSURES
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AUTHOR CONTRIBUTIONS
Author contributions: J.M.F. and A.J.B. conception and design of research; J.M.F. and M.A.S. performed experiments; J.M.F. and M.A.S. analyzed data; J.M.F., M.A.S., and A.J.B. interpreted results of experiments; J.M.F. prepared figures; J.M.F. drafted manuscript; J.M.F. and A.J.B. edited and revised manuscript; J.M.F., M.A.S., and A.J.B. approved final version of manuscript.

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