Adaptation to conflicting visual and physical heading directions during walking

Jeffrey A. Saunders   Department of Psychology, University of Hong Kong, Hong Kong SAR

Frank H. Durgin   Department of Psychology, Swarthmore College, Swarthmore, PA, USA

We investigated the role of global optic flow for visual–motor adaptation of walking direction. In an immersive virtual environment, observers walked to a circular target lying on either a homogeneous ground plane (target-motion condition) or a textured ground plane (ground-flow condition). During adaptation trials, we changed the mapping from physical to visual space to create a conflict between physical and visual heading directions. On these trials, the visual heading specified by optic flow deviated from an observer's physical heading by ±10°. This conflict was not noticed by observers but caused them to walk along curved paths to the target. Over the course of 20 adaptation trials, observers adapted to partially compensate for the conflicts, resulting in straighter paths. When the conflicts were removed post-adaptation, observers showed aftereffects in the opposite direction. The amount of adaptation was similar for target-motion and ground-flow conditions (20–25%), with the ground-flow environment producing slightly faster adaptation and larger aftereffects. We conclude that the visual–motor system can rapidly recalibrate the mapping from physical to visual heading and that this adaptation does not strongly depend on full-field optic flow.

Introduction

Visual control of actions requires accurate knowledge of transformations from visual to motor coordinates, and the brain has adaptive mechanisms for maintaining the calibration of these mappings. In the case of locomotion, observers are capable of accurately walking to a previously viewed target without vision (Loomis, Da Silva, Fujita, & Fukusima, 1992; Thomson, 1983), indicating good calibration. Even when vision is available, initiating locomotion in the correct direction requires knowledge of the mapping between motor commands and visual direction of self-motion. Some evidence suggests that online control of locomotion also involves aiming one's physical direction of motion toward the goal (Harris & Bonas, 2002; Harris & Carre, 2001; Rushton, Harris, Lloyd, & Wann, 1998), which would similarly require an accurate visual-to-motor mapping.

To study visual–motor adaptation, a standard technique is to present continued exposure to conditions with visual feedback that is not consistent with actions. One can then look for changes in performance and subsequent aftereffects that are indicative of recalibration. Previous studies have tested adaptation to conflicting visual feedback about direction of self-motion (Bruggeman & Warren, 2010;

Bruggeman, Zosh, & Warren, 2007; Morton & Bastian, 2004; Redding & Wallace, 1985, 1987) and speed of self-motion (Durgin & Pelah, 1999; Durgin et al., 2005; Mohler et al., 2007; Rieser, Pick, Ashmead, & Garing, 1995). The general finding is that conflicting visual cues to self-motion can produce adaptation over a short time span.

The focus of our study is locomotor adaptation to visual feedback about direction of self-motion. One method to create a conflict between visual and physical headings is through use of prism goggles. Displacement prisms change the mapping between physical and visual spaces, so that walking in one direction produces visual feedback consistent with walking in a different direction. Redding and Wallace (1985, 1987) found that experience with walking with prisms could produce changes in perceived straight ahead, as much as 10% of the visual displacement. They did not attempt to measure locomotion-specific recalibration. Morton and Bastian (2004) tested adaptation to walking with displacement prisms and measured the effect on walking performance, as well as other measures. Prior to adaptation, if an observer attempts to walk to a target while wearing displacement prisms, they tend to walk in the visual direction of the target (which is displaced), resulting in a curved path to the target (Harris & Bonas, 2002; Harris & Carre, 2001; Rushton et al., 1998). Morton

and Bastian found that after prolonged exposure subjects' paths became straighter and that the adaptation caused by walking partially generalized to open-loop reaching movements.

Some studies have used an immersive virtual environment to create similar conflicts between visual and physical directions of self-motion (Bruggeman & Warren, 2010; Bruggeman et al., 2007; Warren, Kay, Zosh, Duchon, & Sahuc, 2001), which allows greater control of the visual environment. Bruggeman et al. (2007) compared adaptation in a rich simulated environment that provided full-field optic flow to adaptation in a minimal environment that provided only a target drift signal. The rich environment produced rapid adaptation of both initial walking direction and online control, detectable within a few trials, and a corresponding aftereffect when the cue conflict was removed. Some adaptation was also observed in the minimal environment, but this adaptation was slower and produced a less robust aftereffect. These results suggest that global optic flow is required for strong and persistent locomotor adaptation. However, as discussed in the next section, there are other possible reasons that the minimal environment was not effective at driving adaptation (see also Rushton, 2008).

Bruggeman and Warren (2010) further tested whether such adaptation generalizes to other tasks besides walking, using similar virtual environment and conditions. They found no transfer to throwing or kicking tasks, suggesting that the observed adaptation was specific to locomotion rather than a generalized remapping of visual space. The lack of transfer contrasts with the results of Morton and Bastian (2004). Bruggeman and Warren suggest that the difference is due to use of prisms vs. virtual reality to introduce cue conflicts. The use of virtual reality allows the mapping from locomotion direction to visual heading to be isolated, while prisms produce a global displacement of the scene relative to the head, as well as various optical artifacts. Such differences could affect the locus of adaptation. For example, visual displacement that changes with head inclination (as in the case of prisms) might encourage head–eye or head–trunk recalibration rather than locomotor-specific recalibration.

Global motion error vs. target-relative motion error

The purpose of the present study was to further investigate how optic flow contributes to locomotor adaptation when visual and physical heading directions are conflicting. Specifically, we tested whether the crucial visual feedback is the discrepancy in heading specified by global optic flow or whether discrepancy in observer motion relative to the target destination is sufficient.

The global pattern of optic flow produced when moving through a rigid environment provides a strong cue to observer heading. It is well established that observers can perceive heading from optic flow in an accurate and robust manner (Warren, Blackwell, Kurtz, Hatsopoulos, & Kalish, 1991; Warren, Morris, & Kalish, 1988; Warren & Saunders, 1995), and there are neural mechanisms selective for optic flow patterns (for a review, see Britten, 2008; Lappe, 2000).

If visual heading does not match the heading expected based on motor commands, or the heading specified by non-visual information (e.g., proprioceptive or vestibular signals), this error provides a potential feedback signal for calibration. Thus, when optic flow is available, the visual–motor system would have access to a reliable visual heading cue that could be compared to motor expectations for purposes of calibration. Bruggeman et al. (2007) interpret the role of optic flow during adaptation in this manner, following Held and Freedman (1963).

Alternatively, calibration might be dependent on visual feedback about the progress of the observer toward their target destination. When an observer is trying to get to some location, which is the typical situation, the motion of the target relative to the observer provides a measure of movement error. Discrepancies between the observed and expected motion of the target might therefore be the crucial feedback signal for calibration rather than discrepancy between observed and expected heading directions (Rock, 1966). In the case of hand movements, feedback only about endpoint error is sufficient to cause adaptation to prism displacement (e.g., Bedford, 1989). Similarly, feedback about an observer's progress toward the goal might be sufficient for locomotor adaptation.

Of the few previous studies that have tested adaptation to conflicting visual feedback about direction of self-motion, Bruggeman et al. (2007) is the only study that also manipulated the optic flow provided by the environment. Bruggeman et al. found that the rich flow environment produced much more adaptation, which suggests that global motion error is the basis for adaptation. However, their minimal and rich flow conditions differed in other important ways.

In the minimal flow condition tested by Bruggeman et al. (2007), the 3D position and relative motion of the target was poorly defined by visual information, so the potential error signal provided by target-relative motion was degraded. The simulated target was an infinitely tall post in empty space. The absence of a ground surface is highly unnatural, and the only information about target distance was provided by binocular convergence. In these conditions, the relative position and 3D motion of the target would have been difficult to perceive (Regan & Gray, 2000; Welchman, Tuck, & Harris, 2004). Thus, the target-only condition of Bruggeman et al. not only lacked global optic flow but also provided a degraded target-motion signal. A post in empty space provides a "target drift" signal but not necessarily provide a good signal for the 3D motion of the target relative to the observer.

Another potential confounding factor in the conditions tested by Bruggeman et al. (2007) is pre-adaptation performance. In their target-only condition, observers tend to walk on curved paths with their physical heading aligned with the visual direction of the target. In the rich flow condition tested by Bruggeman et al., observers are capable of using optic flow to walk on straighter paths even when the direction of perturbation is randomized to prevent learning (Warren et al., 2001). Thus, pre-adaptation performance was not matched across these conditions. Conflicting optic flow contributed to online visual guidance in the rich flow condition but not the target-only condition, which could affect adaptation. There was also a difference in performance error, because observers made more online correction in the rich flow conditions.

Present study

We compared adaptation to conflicting visual and physical heading directions for environments that either provided only target-relative motion or both target-relative motion and global motion. To manipulate visual information about self-motion, we used an interactive virtual reality environment, illustrated in Figure 1. Our conditions were specifically designed to: (1) isolate the target-relative motion signal without also degrading it and (2) produce similar performance prior to adaptation.

In the *target-motion* condition, the simulated environment consisted of circular target lying on a homogeneous ground plane, with a visible horizon line. The only optic flow produced in this environment is due to the target.
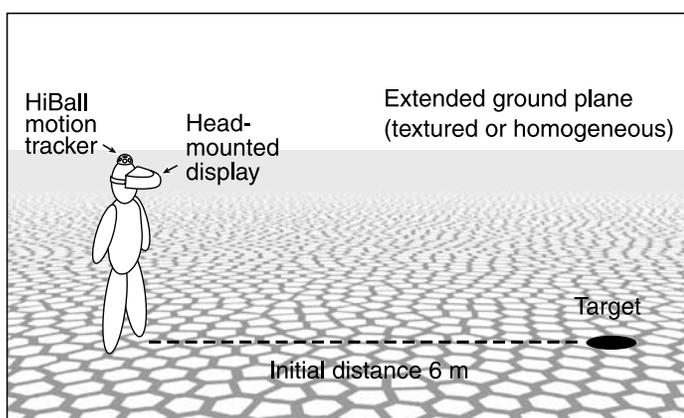

Figure 1. Illustration of the virtual environment. Stereo images were presented with a head-mounted display and were updated in real time using data from an optical tracking system. The simulated ground plane extended to the horizon and was either textured by a Voronoi pattern out to 30 m or was homogeneous (not shown). The walking target was indicated by a 50-cm diameter filled circle.

However, compared to the target-only condition of Bruggeman et al. (2007), the relative position and motion of the target are better specified. The inclination angle of the target relative to the horizon provides a cue to distance, and the retinal motion of the target relative to the horizon provides a cue to the rate of approach and relative heading error, which is sufficient to compute relative 3D motion (Rushton, Wen, & Allison, 2002). Despite being minimal, this environment also creates subjective sense of walking toward an object in a 3D scene.

As a comparison condition, we tested an environment that was identical except that the ground plane was covered with visual texture. We will refer to this as the *ground-flow* condition. Optic flow from a ground plane is sufficient for accurate judgments of visual heading (e.g., Warren et al., 1988), so this condition potentially provides a strong global motion error signal for calibration. However, unlike the rich flow condition tested by Bruggeman et al. (2007), walking performance during initial adaptation trials would be similar to that of our target-motion condition. Warren et al. (2001) found that when only a textured ground is present, walking with displaced vision produced highly curved paths. Thus, the ground-flow condition provides a good comparison condition for isolating the contribution of global motion error. Visual heading is well specified by global optic flow in the ground-flow condition, yet performance prior to adaptation would be similar to the target-motion condition.

Figure 2 illustrates the sequence of trials used to test for visual–motor adaptation. Subjects were first exposed to pre-adaptation baseline trials, in which visual feedback accurately reflected subjects' physical motion, and visual and physical headings coincided (Figure 2a). These were followed by adaptation trials, in which visual space was rotated by ±10° relative to physical space, around an axis centered at the observer's head and perpendicular to the ground. In this condition, aiming one's physical direction of the motion toward the target causes the visual heading to be displaced from the target (Figure 2b). If a subject walks so that their physical heading remains aligned with the target, the result is a curved path with a constant 10° difference between the visual heading and the target. With exposure to adaptation trials, subjects could learn to compensate for the visual displacement by walking in an offset direction, so that visual heading is closer to the target (Figure 2c). This would result in straighter paths on later adaptation trials. After the adaptation trials, subjects were again presented with baseline trials with no conflicts to measure any post-adaptation aftereffects (Figure 2d). If improved performance in late adaptation trials is due visual–motor recalibration, one would expect aftereffects of the same direction and magnitude as the change across the adaptation trials. Thus, adaptation would be observed as a change in performance from early to late adaptation trials and between pre-adaptation and post-adaptation baseline trials.
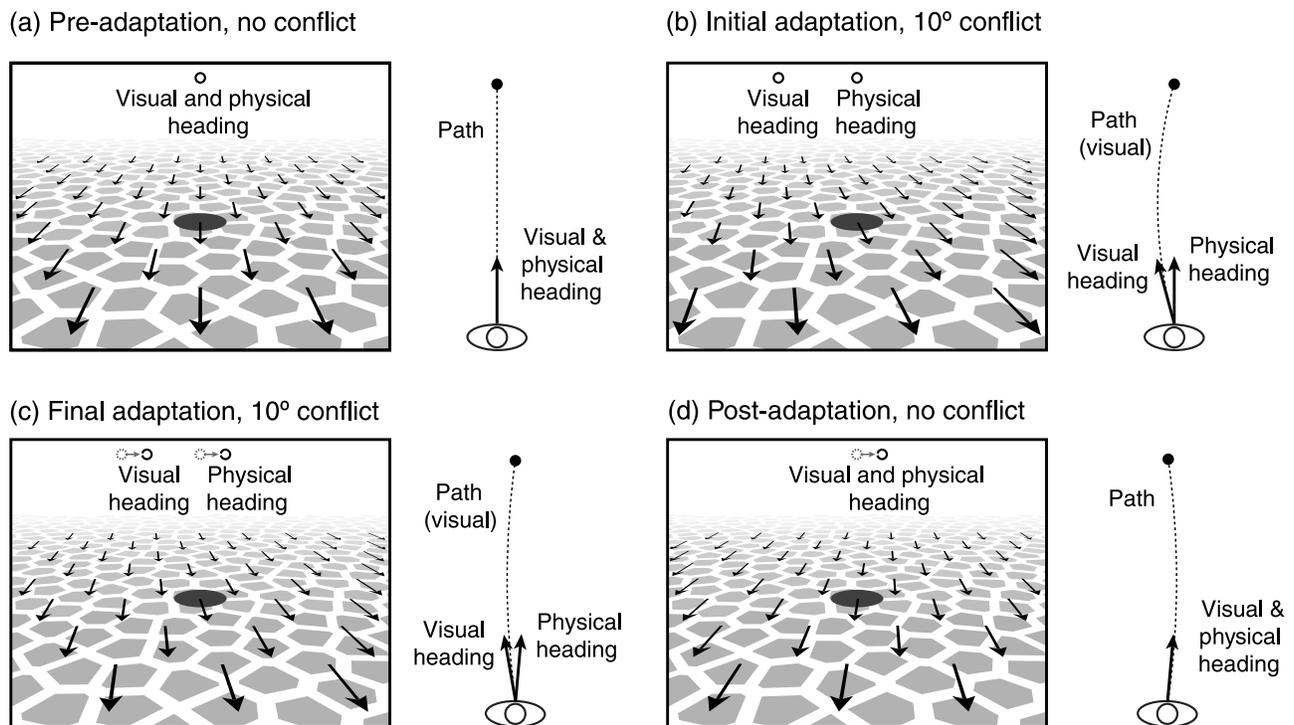
Figure 2. Adaptation trial sequence. Each phase is illustrated with (left) perspective and (right) top-down views. (a) Pre-adaptation trials with no conflict. Optic flow (arrows) radiates from a focus of expansion that coincides with the physical heading direction. (b) Initial adaptation trials. Visual heading is offset from physical heading by a 10° rotation. If a subject aims their physical motion toward the target, the target will drift away from the visual heading, resulting in a curved path. (c) Final adaptation trials. After repeated exposure to the 10° conflict, subjects may adapt to align their visual heading more closely with the target, resulting in straighter paths. (d) Post-adaptation trials with no conflict. If adaptation persists, subjects would be expected to continue aiming their physical heading away from the visual direction of the target, resulting in curved paths in the opposite direction.

If locomotor calibration is primarily driven by mismatch between observed and expected visual headings, then only the ground-flow condition should be effective at eliciting adaptation. On the other hand, if calibration is primarily driven by the mismatches between observed and expected relative motion of the target, performance in the two optic flow conditions should be comparable.

Methods

Apparatus and display

Subjects walked in a virtual reality environment, illustrated in Figure 1. The physical space available for walking was a 2-m-wide hallway. Perspective views of the simulated environment were rendered with OpenGL and presented with an nVis head-mounted display (HMD) system. The position and orientation of a subject's head were tracked at 60 Hz using a 3rd Tech HiBall optical tracking system, and these parameters were used to update the visual displays in real time. For each eye's view, the video display subtended a visual angle of 44 by 36 degrees of visual angle and had a resolution of 1280 by 1024 pixels. The nominal FOV of the nVis is 60° diagonal; our numbers are based on careful matching between presented images and known visual angles. Image geometry was pre-distorted in software to compensate for optical pincushioning in the display. The refresh rate of the displays was 60 Hz, and the overall latency between movement and visual updating was no greater than 50 ms.

The simulated environment consisted of the ground plane and 50-cm diameter target disk. The ground texture, when present, was a Voronoi tiling, with elements that were 33 cm wide on average and separated by 16-cm gaps. The luminance of the texture was faded with distance, disappearing at 30 m away. On target-motion trials, the ground plane was uniformly dark. In both conditions, a "sky" was simulated as a uniform gray region, lighter than the ground, with a border at the horizon.

Procedure

Subjects performed a task that involved walking to a visible target on the ground. Although the walking itself was of principal experimental interest, it was embedded as part of a visual memory task intended to conceal the true nature of the experiment. At the start of a trial, subjects were positioned at one end of the rectangular workspace, facing the open direction. Subjects began the trials by turning in place 180 degrees and viewing a configuration of four colored dots on the ground plane. They then turned back around in place and walked to a visible target location on the ground, which was described as the "second viewing location." The target was 6 m away from the initial position along the main axis of the workspace After arriving at the second location, subjects stopped and turned in place again. The configuration of the four colored dots was presented a second time at the same location in virtual space as before but with one of the dots shifted by a random amount along the ground. Subjects were asked to judge which of the four dots had moved. At the end of a trial, subjects were positioned at the opposite side of the workspace and facing in the opposite direction. After responding, subjects initiated the next trial by turning in place to view a new configuration of colored dots.

Subjects performed two experimental sessions on separate days, one in which the ground plane was always textured (ground-flow condition) and the other in which the ground plane was always homogeneous (target motion). In each session, subjects performed two blocks of 40 trials. Each block consisted of 10 pre-adaptation trials in which visual and physical spaces were aligned, 20 adaptation trials in which visual space was rotated relative to physical space by 10°, and 10 post-adaptation trials with no conflict (see Figure 2 for illustration). The sign of conflict was reversed for the two blocks within a session, and the order of presentation was counterbalanced across subjects. The order of the ground-flow and target-motion sessions was also counterbalanced. The interval between sessions varied between 1 and 8 days.

During debriefing, subjects were asked whether the virtual world appeared to pass by them in a normal manner when they were walking and whether they noticed any times when the motion seemed inconsistent. After the conditions were explained, subjects were also asked directly whether they thought they had noticed the discrepancy between physical and visual headings. None of the subjects indicated being aware of the conflict.

We analyzed only the intermediate, online control portion of walking movements. Because of our cover story, subjects were not focused on minimizing endpoint error, so the endpoints had variability that does not reflect ideal performance. The mean horizontal error at the end of movement, averaged across subjects, was 11 cm for baseline trials and 24 cm for adaptation trials, and there was no significant difference in endpoint error between ground-flow and target-motion conditions.

Participants

Twelve undergraduate students at Swarthmore College were paid to participate in the experiment. All subjects had normal or corrected-to-normal vision. Participants gave informed consent in accordance with ethical standards of the APA.

Results

Figure 3 plots mean heading errors as a function of time, averaged across subjects ($N = 12$), for the ground-flow condition (top) and the target-motion condition (bottom). The four lines on each graph correspond to different subsets of the trial sequence, as described below. For averaging across trials, the raw data series were aligned at the point where subjects were halfway to the target, so the time axis represents time before or after reaching the midpoint. Data series were also smoothed with a 5th-order Butterworth filter with 8-Hz cutoff frequency to remove high-frequency noise. Blocks with positive and negative conflicts were combined in the analysis, with the signs of heading errors reversed for the negative conflict blocks. The time series data from ground-flow and target-motion conditions were similar and will be discussed together.

Thin gray lines show mean heading errors for the last five trials in the pre-adaptation phase. In these trials, there is no reason to expect systematic bias; subjects would be expected to aim their movement toward the target, corresponding to zero visual heading error on average. The observed data are consistent with this.

The thin black lines show mean heading errors for the first five adaptation trials with conflicting visual and physical headings. In adaptation trials, aiming physical motion toward the target would cause visual heading to be offset by 10°. Subjects' performance in the initial adaptation trials was consistent with this strategy: average visual heading error was approximately constant over a 2- to 3-s period of the trials and close to 10°. There was no indication that subjects made online corrections to reduce visual heading error over the course of a trial, in either the ground-flow or target-motion condition. Thus, performance during initial adaptation trials was approximately matched. In both conditions, subjects walked on curved paths to the target with their physical heading aimed toward the egocentric direction of the target.

The thick black lines show heading errors for the last five adaptation trials. Visual heading error remained approximately constant over the course of a trial. Compared to performance in the initial adaptation trials, visual heading errors during the final adaptation trials were smaller, corresponding to aiming their physical motion slightly away from target. The reduction in

a. Ground-flow

Textured ground

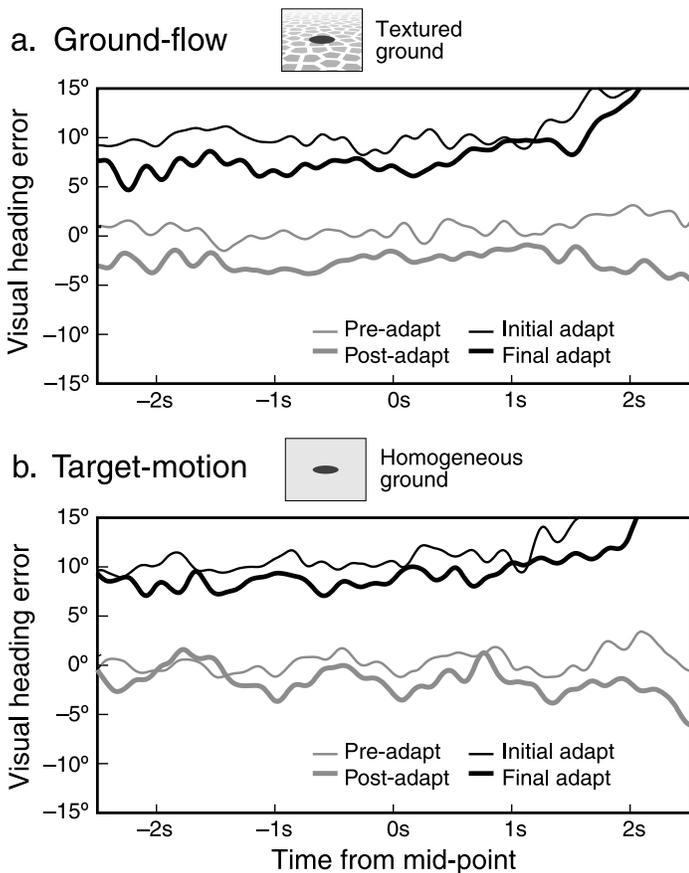## b. Target-motion

Homogeneous ground

Figure 3. Mean heading errors as a function of time for subsets of trials from different parts of the trial sequence. The thin gray lines show mean heading errors from the last 5 trials of the pre-adaptation phase with no conflicts (trials 6–10). Thin black lines show means for the initial 5 adaptation trials with 10° conflicts (trials 11–15). Thick black lines show means for the final 5 adaptation trials (trials 26–30). Thick gray lines show means for the first 5 post-adaptation trials (trials 31–35). Plots show mean data averaged across subjects and blocks. Trials were temporally aligned at the point where the subject was midway to the target. Top and bottom graphs correspond to the (a) ground-flow and (b) target-motion conditions. Adaptation can be seen as differences between initial and final adaptation trials and between pre-adaptation and post-adaptation trials.

heading error was consistent with compensation for the induced conflict (see Figure 2c) and resulted in less visual drift of the target and straighter paths.

The thick gray lines in Figure 3 show mean heading errors for the first five post-adaptation baseline trials. Compared to the pre-adaptation baseline trials, heading errors were biased in a negative direction, indicating that subjects' adjustments from the adaptation phase persisted after the conflicts were removed. The difference between pre-adaptation and post-adaptation baseline trials was consistent with negative aftereffect (see Figure 2d).

To analyze the time course of adaptation, we first obtained an estimate of the mean heading error for each

trial by pooled heading errors over a 3-s window of time, starting at 2 s before reaching the midpoint of the movement through 1 s after reaching midpoint. The individual trial measures were binned into sets of five trials to further reduce noise and then pooled across subjects. Figure 4 plots the resulting average heading errors as a function of trial sequence, for both ground-flow and target-motion conditions. Trials 11–30 are those with conflicting visual and physical headings. Adaptation can be observed as a decrease in visual heading error across trials.

For statistical analysis, we further combined data across the first and second blocks, normalizing for the direction of adaptation. The left graph in Figure 5 shows the change in mean heading error over the course of adaptation trials. For both ground-flow and target-motion conditions, mean heading errors significantly decreased from the first five adaptation trials to the second five trials (ground-flow: $t(11) = 9.3$, $p < 0.001$, target-motion: $t(11) = 23.5$, $p < 0.001$). Thus, for both conditions, subjects made detectable adjustments to their walking paths within the first 10 trials of experiencing the visual displacement. The initial decrease in heading error was greater for the textured condition ($t(11) = 2.68$, $p = 0.02$). However, the decrease in heading error at the end of the adaptation period was indistinguishable for textured and untextured conditions ($t(11) = 1.07$, $p = 0.31$ n.s.). For these final adaptation trials, subjects had adjusted their mean heading errors to compensate for 20–25% of the visual displacement.

The right graph in Figure 5 shows the post-adaptation aftereffects observed in our data. The graph plots the mean heading errors from the final five pre-adaptation trials (trials 6–10 in a block) and first five post-adaptation trials (trials 31–35 in a block). The post-adaptation heading errors were different for both ground-flow condition ($t(11) = 7.39$, $p < 0.001$) and the target-motion condition ($t(11) = 2.36$, $p = 0.037$). Thus, subjects' adjustments in response to visual displacement persisted after the displacement was removed, producing a negative aftereffect that is characteristic of adaptation. Comparing across optic flow conditions, we found that the magnitude of the aftereffect was larger for the ground-flow condition ($t(11) = 2.71$, $p = 0.02$). The aftereffects for the ground-flow and target-motion conditions corresponded to 29% and 14% of the adapted displacement, respectively, which were comparable to the amount of adaptation observed.

Discussion

Our results demonstrate that our visual–motor system can rapidly and automatically adapt in response to conflicting information about self-motion, even with minimal visual input. Adaptation to visual displacement was detectable within 10 trials of exposure for either ground-flow or target-
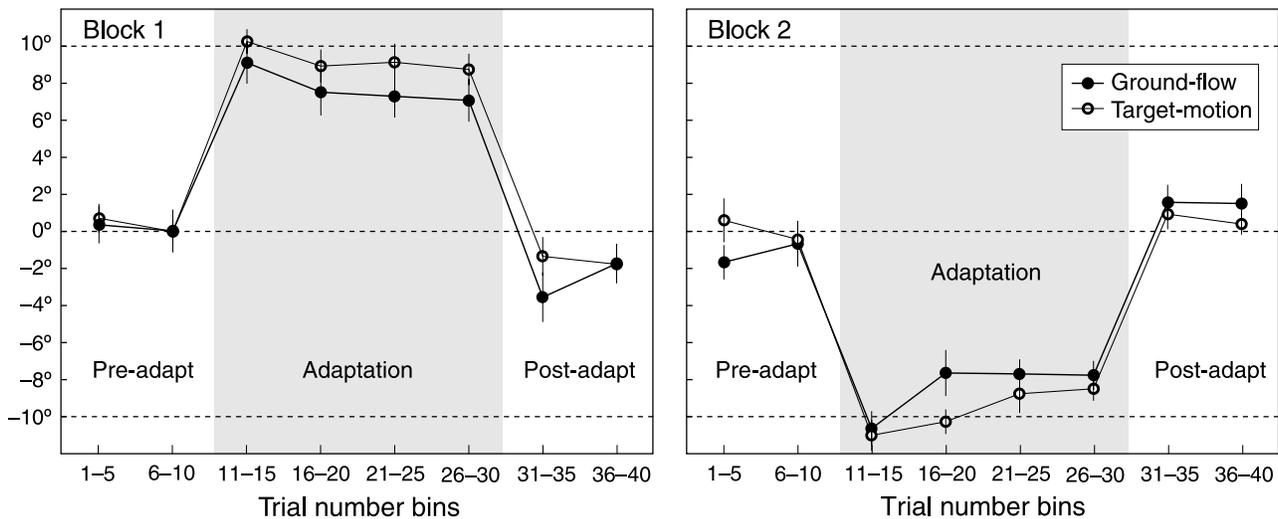
Figure 4. Change in mean heading error over the course of an experimental session. Mean heading error for a single trial was computed by averaging over 3-s windows (see Methods section). Trials were then binned into sets of five and averaged across subjects to obtain the results shown. The two plots on each graph show results for the ground-flow (solid circles) and target-motion (open circles) conditions. Shaded regions depict bins with adaptation trials. The left and right graphs show results of the two blocks performed in each session, which tested opposite directions of adaptation. The initial direction of adaptation was varied across subjects but was normalized to be positive in Block 1 to combine data for these plots. Error bars depict ±1 standard errors.

motion conditions, and this occurred even though subjects were unaware of the displacement and performed a secondary distracter task. The adaptation over the course of 20 trials corresponded to 20–25% of the visual displacement and produced a corresponding negative aftereffect when the cue conflict was subsequently removed.
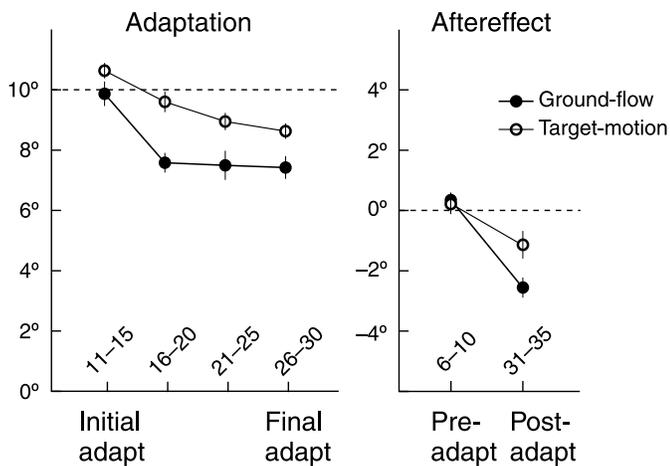

Figure 5. (Left) Mean amount of adaptation and (right) magnitude of aftereffect averaged across subjects and blocks. The left graph plots mean heading error for adaptation trials, collected into 5-trial bins. The right graph plots mean heading error for the last five pre-adaptation trials and the first five post-adaptation trials. The two plots on each graph show results for the ground-flow (solid) and target-motion (open) conditions. Error bars depict ±1 standard errors.

We compared performance in two simulated environments, with and without global optic flow, to test whether visual feedback from the target is sufficient for locomotor adaptation. The ground-flow condition, which provided optic flow throughout the display, was more effective at inducing adaptation than the condition with a homogeneous ground plane, which provided only target motion. This was evidenced by a faster rate of initial adaptation and the larger aftereffect. Global optic flow is known to be a strong visual cue to self-motion, so its absence in the target-motion condition could explain the difference in adaptation. On the other hand, the target-motion condition also produced significant adaptation, despite the fact that the only visual motion information was from the target. Moreover, the reduction in heading error from the initial to final adaptation trials—a measure of total adaptation—was statistically indistinguishable for the two conditions. This null result may be due to lack of sensitivity, given that there was a detectable difference in magnitude of aftereffects. Nevertheless, it is surprising that the amount of adaptation was so similar for the two conditions, given the large difference in the amount of optic flow available.

In our experiment, walking performance during initial adaptation trials was similar for the ground-flow and target-motion conditions, as intended, so this factor was not confounded with the presence of global optic flow. In both conditions, observers aligned their physical direction of motion with the target when the conflicting visual information was first introduced, resulting in curved paths. During all adaptation stages, observers walked on paths that maintained an approximately constant visual heading

error. The visual heading error reduced from initial to final adaptation trials, but there was no indication of a change of strategy, and no qualitative difference in performance for the ground-flow and target-motion conditions.

Although the target-motion condition provided minimal optic flow, it was sufficient for a subjective sense of moving toward a location in 3D space. Perception of self-motion might be the key factor for adaptation rather than how self-motion is specified by sensory information. This would be consistent with some evidence from adaptation of self-motion speed. Durgin, Fox, and Kim (2003) and Durgin et al. (2005) observed locomotor speed recalibration when blindfolded observers felt themselves to be stationary while walking or hopping on a treadmill (perhaps as a result of haptic contact with the handrails of the treadmill); this suggests that perceived speed of self-motion, rather than optic flow per se, was the controlling variable. Adaptation of self-motion direction might similarly depend primarily on perception of self-motion direction through space rather than on the presence and amount of optic flow. By this account, adaptation would be observed whenever sensory feedback provides a strong percept of self-motion that is in conflict with expectations, which could occur even without full-field optic flow.

Our results are generally consistent with those of Bruggeman et al. (2007). As in their study, we observed adaptation in both minimal and full-field optic flow conditions and found that adaptation and aftereffects were larger with full-field optic flow. There was also similarity in the time course of adaptation. In the rich optic flow condition tested by Bruggeman et al., adaptation was detectable within the first 3 trials and reached an asymptote within 10 trials. This is comparable to the time course of adaptation for our ground-flow condition (Figure 5). Adaptation was slower in our target-motion condition, which is also qualitatively consistent with the observations of Bruggeman et al.

We observed less difference between minimal and full-field optic flow conditions than Bruggeman et al. (2007) in terms of both magnitude and speed of adaptation. The differences in simulated environments could account for this discrepancy. In our target-motion condition, the target was a circle on the ground plane rather than an infinitely tall pole in space and, therefore, provided better information about egocentric target location and self-motion relative to the target. On the other hand, our ground-flow condition was comparatively minimal relative to the rich flow condition tested by Bruggeman et al. Thus, the minimal and rich flow conditions tested by Bruggeman et al. differed in a more extreme way, which could account for the larger differences in performance.

When global optic flow is available, subjects could potentially make online steering adjustments to reduce visual heading error, which would produce straighter paths even prior to adaptation. This was observed by Bruggeman et al. (2007) in their rich flow condition: heading error reduced over time during the first adaptation

trial. In contrast, we found no evidence for direct use of optic flow to control steering. Visual heading error was approximately constant over the course of movement in the ground-flow condition, and adaptation across trials took the form of a shift in average visual heading error. The discrepancy may also be due to the different simulated environments used in our study and in Bruggeman et al. Warren et al. (2001) tested both types of environments and observed larger visual heading errors for the ground-flow condition. However, Warren et al. observed some reduction in heading bias over time in their ground-flow condition, while our data were entirely consistent with a strategy of walking in the visual direction of the target.

We used a cover story and secondary task to disguise the purpose of our experiment, which may have attenuated the amount of adaptation. Redding, Clark, and Wallace (1985) tested the effect of a secondary cognitive task on prism adaptation from walking and found that adaptation was significantly reduced by a simultaneous mental arithmetic or mental imagery task. Based on these findings, one might expect reduced adaptation in our conditions relative to a situation with no secondary task. This makes the adaptation in the minimal flow condition all the more striking, while making it unlikely that our results can be attributed to experimental demand characteristics (see Durgin et al., 2009).

There are multiple possible sites of adaptation that could produce our observed changes in performance. Prior to adaptation, in both visual environments, observers appeared to be using a strategy of aiming their physical direction of motion toward the visual direction of the target. Reduction in heading error following repeated exposure could, therefore, be produced either by a general remapping of visual direction (Morton & Bastian, 2004; Rushton & Salvucci, 2001) or by locomotor-specific recalibration (Bruggeman & Warren, 2010), and this remapping could be either to optic flow or to perceived direction of walking (Rushton et al., 1998). The speed and magnitude of adaptation observed here argues against a general remapping. As pointed out by Bruggeman et al. (2007), studies of prism adaptation have observed very limited adaptation of perceived straight ahead (<10%) over a time course of minutes (Held & Bossom, 1961; Morton & Bastian, 2004; Redding & Wallace, 1985). This interpretation would also be consistent with the results of Bruggeman and Warren (2010), who found no transfer of adaptation to visually guided tasks that did not involve locomotion. Indeed, in adaptation of perceived self-motion speed, recalibration has been shown to be specific not only to locomotion (Rieser et al., 1995) but to the manner of locomotion (Durgin et al., 2005), and, for hopping, to the specific limb involved in that locomotion (Durgin et al., 2003).

The similar adaptation observed in ground-flow and target-motion conditions further constrains the locus of locomotor recalibration. In principle, global optic flow could be used for direct control of steering (Warren et al.,

2001), which would have the advantage of bypassing coordinate transformations between the eye, head, and body. We believe that this is unlikely to be the site of the adaptation observed here. Such a model would not be directly sensitive to a conflict between physical and visual headings; rather, adaptation would have to be driven by visual heading error. Recalibration of a direct visual control strategy would, therefore, be expected to strongly depend on the presence of global optic flow. We found that visual heading errors remained large and approximately constant after adaptation and that there was little difference between conditions with minimal and global optic flows. These results are more compatible with recalibration of a model that uses an integrated estimate of self-motion direction from visual and non-visual information. Global optic flow would then be advantageous but not essential, thereby accounting for the small observed difference between ground-flow and target-motion conditions.

In conclusion, our results demonstrate that the visual–motor system can rapidly adapt to discrepancies between physical and visual headings and that this adaptation can occur even with relatively minimal optic flow. Full-field optic flow increased the speed and magnitude of adaptation, but relative motion of the target was also sufficient to produce rapid adaptation of similar magnitude.

Acknowledgments

Commercial relationships: none.
Corresponding author: Jeffrey A. Saunders.
Email: jsaun@hku.hk.
Address: Department of Psychology, University of Hong Kong, Hong Kong.

References

Bedford, F. L. (1989). Constraints on learning new mappings between perceptual dimensions. *Journal of Experimental Psychology: Human Perception and Performance, 15,* 232–248.

Britten, K. H. (2008). Mechanisms of self-motion perception. *Annual Review of Neuroscience, 31,* 389–410.

Bruggeman, H., & Warren, W. H., Jr. (2010). The direction of walking—but not throwing or kicking—is adapted by optic flow. *Psychological Science, 21,* 1006–1013.

Bruggeman, H., Zosh, W., & Warren, W. H., Jr. (2007). Optic flow drives human visuo-locomotor adaptation. *Current Biology, 17,* 2035–2040.

Durgin, F. H., Baird, J. A., Greenburg, M., Russell, R., Shaughnessy, K., & Waymouth, S. (2009). Who is being deceived? The experimental demands of wearing a backpack. *Psychonomic Bulletin & Review, 16,* 964–969.

Durgin, F. H., Fox, L. F., & Kim, D. H. (2003). Not letting the left leg know what the right leg is doing: Limb-specific locomotor adaptation to sensory-cue conflict. *Psychological Science, 6,* 567–572.

Durgin, F. H., & Pelah, A. (1999). Visuomotor adaptation without vision? *Experimental Brain Research, 127,* 12–18.

Durgin, F. H., Pelah, A., Fox, L. F., Lewis, J. Y., Kane, R., & Walley, K. A. (2005). Self-motion perception during locomotor recalibration: More than meets the eye. *Journal of Experimental Psychology: Human Perception and Performance, 31,* 398–419.

Harris, J. M., & Bonas, W. (2002). Optic flow and scene structure do not always contribute to the control of human walking. *Vision Research, 42,* 1619–1626. [PubMed]

Harris, M. G., & Carre, G. (2001). Is optic flow used to guide walking while wearing a displacing prism? *Perception, 30,* 811–818. [PubMed]

Held, R., & Bossom, J. (1961). Neonatal deprivation and adult rearrangement: Complementary techniques for analyzing plastic sensory-motor coordinations. *Journal of Comparative and Physiological Psychology, 54,* 33–37.

Held, R., & Freedman, S. J. (1963). Plasticity in human sensorimotor control. *Science, 142,* 455–462.

Lappe, M. (Ed.) (2000). Neuronal processing of optic flow. In *International review of neurobiology* (vol. 44). San Diego, CA: Academic Press.

Loomis, J. M., da Silva, J. A., Fujita, N., & Fukusima, S. S. (1992). Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception & Performance, 18,* 906–921.

Mohler, B. J., Thompson, W. B., Creem-Regehr, S. H., Willemsen, P., Pick, H. L., & Rieser, J. J. (2007). Calibration of locomotion resulting from visual motion in a treadmill-based virtual environment. *ACM Transactions on Applied Perception, 4* 20–32.

Morton, S. M., & Bastian, A. J. (2004). Prism adaptation during walking generalizes to reaching and requires

a cerebellum. *Journal of Neurophysiology, 92,* 2497–2509.

Redding, G. M., Clark, S. E., & Wallace, B. (1985). Attention and prism adaptation. *Cognitive Psychology, 17,* 1–25.

Redding, G. M., & Wallace, B. (1985). Perceptual-motor coordination and adaptation during locomotion: Determinants of prism adaptation in hall exposure. *Perception & Psychophysics, 38,* 320–330.

Redding, G. M., & Wallace, B. (1987). Perceptual-motor coordination and prism adaptation during locomotion: A control for head posture contributions. *Perception & Psychophysics, 42,* 269–274.

Regan, D., & Gray, R. (2000). Visually guided collision avoidance and collision achievement. *Trends in Cognitive Sciences, 4,* 99–107.

Rieser, J. J., Pick, H. L., Jr., Ashmead, D. H., & Garing, A. E. (1995). Calibration of human locomotion and models of perceptual-motor organization. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 480–497.

Rock, I. (1966). *The nature of perceptual adaptation.* New York: Basic Books.

Rushton, S. K. (2008). Perceptually-guided action: A step in the right direction. *Current Biology, 18,* R36–R37.

Rushton, S. K., Harris, J. M., Lloyd, M. R., & Wann, J. P. (1998). Guidance of locomotion on foot uses perceived target location rather than optic flow. *Current Biology, 8,* 1191–1194. [PubMed]

Rushton, S. K., & Salvucci, D. D. (2001). An egocentric account of the visual guidance of locomotion. *Trends in Cognitive Sciences, 5,* 6–7.

Rushton, S. K., Wen, J., & Allison, R. S. (2002). Egocentric direction and the visual guidance of robot locomotion: Background, theory and implementation. In H. H. Bülthoff, S.-W. Lee, T. A. Poggio, & C. Wallraven (Eds.), *Biologically motivated computer vision: Lecture notes in computer science* (pp. 576–591). Berlin: Springer-Verlag.

Thomson, J. A. (1983). Is continuous visual monitoring necessary in visually guided locomotion? *Journal of Experimental Psychology: Human Perception and Performance, 9,* 427–443.

Warren, W. H., Jr., Blackwell, A. W., Kurtz, K. J., Hatsopoulos, N. G., & Kalish, M. L. (1991). On the sufficiency of the velocity field for perception of heading. *Biological Cybernetics, 65,* 311–320.

Warren, W. H., Jr., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature Neuroscience, 4,* 213–216. [PubMed]

Warren, W. H., Jr., Morris, M. W., & Kalish, M. (1988). Perception of translational heading from optic flow. *Journal of Experimental Psychology: Human Perception and Performance, 14,* 646–660.

Warren, W. H., Jr., & Saunders, J. A. (1995). Perceiving heading in the presence of moving objects. *Perception, 24,* 315–331.

Welchman, A. E., Tuck, V. L., & Harris, J. M. (2004). Human observers are biased in judging the angular approach of a projectile. *Vision Research, 44,* 2027–2042.