Prism adaptation and generalization during visually guided locomotor tasks

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Prism adaptation and generalization during visually guided locomotor tasks. J Neurophysiol 106: 860–871, 2011. First published May 25, 2011; doi:10.1152/jn.01040.2010.—The ability of individuals to adapt locomotion to constraints associated with the complex environments normally encountered in everyday life is paramount for survival. Here, we tested the ability of 24 healthy young adults to adapt to a rightward prism shift (~11.3°) while either walking and stepping to targets (i.e., precision stepping task) or stepping over an obstacle (i.e., obstacle avoidance task). We subsequently tested for generalization to the other locomotor task. In the precision stepping task, we determined the lateral end-point error of foot placement from the targets. In the obstacle avoidance task, we determined toe clearance and lateral foot placement distance from the obstacle before and after stepping over the obstacle. We found large, rightward deviations in foot placement on initial exposure to prisms in both tasks. The majority of measures demonstrated adaptation over repeated trials, and adaptation rates were dependent mainly on the task. On removal of the prisms, we observed negative aftereffects for measures of both tasks. Additionally, we found a unilateral symmetric generalization pattern in that the left, but not the right, lower limb indicated generalization across the 2 locomotor tasks. These results indicate that the nervous system is capable of rapidly adapting to a visuomotor mismatch during visually demanding locomotor tasks and that the prism-induced adaptation can, at least partially, generalize across these tasks. The results also support the notion that the nervous system utilizes an internal model for the control of visually guided locomotion.

A hallmark of the nervous system is its ability to adapt to changing situations. Whether through reorganization caused by disease or injury or adaptation to meet the current task demands, the brain is remarkably capable of change. Prisms can be used to disrupt the normal relationship between visuomotor and proprioceptive-motor reference frames, thereby enabling the study of how and to what extent the nervous system can adapt across different contexts (Redding et al. 2005). Prism glasses work by displacing the visual perception of an object to one side of its actual location. The degree of displacement depends on the orientation and strength of the prisms. Importantly, this visual shift results in a mismatch between the initial motor command generated for a limb movement to the object and the predicted sensory consequences estimated by a so-called forward internal model such that the limb is not where it is expected to be. These sensory prediction errors are thought to drive adaptation (Shadmehr et al. 2010; Tseng et al. 2007).

Prism adaptation during reaching or throwing has been extensively studied (Harris 1965; Martin et al. 1996a,b; Morton and Bastian 2004; reviewed in Redding and Wallace 2002 and Redding et al. 2005; Savin and Morton 2008). Initial exposure to prisms during reaching to a target results in a large end-point error in the direction of the prismatic visual shift. This error is reduced over time following repeated attempts; but when the prisms are removed, there is a large end-point error in the opposite direction, referred to as the negative aftereffect. It has been argued that prism adaptation during reaching involves at least two adaptive processes that work on different time scales: a short-term, fast adaptive process called strategic control (specifically recalibration) and a slower, adaptive process called spatial realignment (Redding and Wallace 2002; Redding et al. 2005). Strategic control encompasses recalibration, which in the case of prismatic distortion occurs through resetting of feedforward motor plans with knowledge of results (or feedback) from previous attempts and leads to the direct effects of prism exposure (i.e., reduction in error). On the other hand, spatial realignment adjusts for constant differences in spatial coordinates between sensorimotor systems (i.e., realigns visual and proprioceptive spatial coordinates through updating of internal models) and is reflected in the presence of aftereffects.

In comparison, prism adaptation during walking has received relatively little attention. Prisms cause locomotor trajectory to deviate in the direction of the prism shift, which adapts over repeated attempts (Kennedy et al. 2003; Michel et al. 2008; Morton and Bastian 2004). In addition to prism adaptation, studies have shown that the nervous system can adapt to imposed constraints on the walking pattern through the use of a split-belt treadmill to decouple the two limb speeds (Choi and Bastian 2007) or a force applied to the foot or leg during treadmill walking (Blanchette and Bouyer 2009; Fortin et al. 2009; Savin et al. 2010). Taken together, these results support the notion that the nervous system is capable of adapting to altered constraints during locomotion.

The ability to step to specific locations (i.e., precision target stepping) and to avoid obstacles (i.e., obstacle avoidance) is paramount for safe locomotion. We often find ourselves in a position to step up onto a curb or position our feet on a particular ground location to prevent a loss of balance due to a particular unstable surface. Locomotion in this context relies heavily on visual information (Marigold et al. 2011; Marigold 2008). In contrast to reaching and simple walking, precision stepping and obstacle avoidance are considerably more complex. This complexity is manifested in several different ways. First, balance constraints associated with these tasks are increased. Unlike reaching or simple walking, improper foot placement, particularly in the case of obstacle avoidance, may result in a loss of balance and a subsequent fall. Second, the two lower limbs must be coordinated vs. a single (upper) limb during reaching. For example, precision stepping to targets may require changes in step width and length of both lower limbs. Obstacle avoidance also requires coordination of both

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lower limbs but has the added requirement of overcoming the height of the obstacle. Thus obstacle avoidance during locomotion requires the limb to traverse multiple planes as opposed to most reaching paradigms. The extent to which the nervous system can adapt to conflicting expected and actual sensory consequences of leg movements during these common locomotor tasks is largely unknown.

Knowledge of generalization patterns allows us to gain insight into how adaptation is encoded (e.g., limb and/or task specific, direction dependent) by the nervous system (Pearson et al. 2010). Many arm movement paradigms have demonstrated narrow generalization patterns. For example, prism adaptation generalizes poorly to different throwing trajectories and between arms (Martin et al. 1996b). The capacity for generalization may be expanded for locomotor tasks due to the fact that multiple segments of the body must be coordinated, requiring more complex sensorimotor recalibration or realignment. Learning to perform an obstacle avoidance task via acoustic feedback of obstacle clearance (and without vision of the obstacle or leg) has been shown to transfer between limbs and across similar obstacle avoidance tasks (Lam and Dietz 2004; van Hedel et al. 2002). Recently, Morton and Bastian (2004) found that prism adaptation generalizes broadly from walking to reaching but not from reaching to walking. In contrast, Savin and Morton (2008) found generalization of prism-adapted single limb pointing movements is asymmetric in that arm pointing generalizes to the leg but not vice versa. The difference in these findings may reside in the fact that in the latter experiment, the task was to step to a target from a seated or standing posture, but in the former experiment, the task was to walk within a path marked by boundary lines. However, generalization between different visually demanding locomotor tasks after adaptation to prisms has not been explored yet is important for understanding how locomotor tasks generalize and may facilitate the planning of rehabilitation strategies (Bastian 2008; Krakauer 2006). Therefore, the purpose of this study was to determine 1) the extent of prism adaptation for two visually guided locomotion tasks (i.e., precision target stepping and obstacle avoidance), and 2) the generalizability between precision target stepping vs. obstacle avoidance prism adaptation. We hypothesized that the nervous system would adapt to the mismatch between the expected and actual sensory consequences created by the prisms consistent with the notion that the nervous system uses an internal model to guide lower limb movements. Additionally, we hypothesized that adaptation to one task would generalize to the other.

METHOD

Subjects. A total of 24 subjects (age = 25.2 ± 3.3 yr; height = 174.6 ± 8.6 cm; mass = 69.9 ± 13.6 kg; 13 males and 11 females) from Simon Fraser University participated in this study. The subjects were pseudorandomly assigned to 1 of 2 groups. Group 1 (Stepping) consisted of 6 males and 6 females (age = 25.9 ± 3.4 yr), whereas group 2 (Obstacle) consisted of 7 males and 5 females (age = 24.4 ± 3.2 yr). The Office of Research Ethics at Simon Fraser University approved the study, and all subjects gave informed consent before performing the experiments. Those with known musculoskeletal, neurological, or visual disorders were excluded. If a subject required glasses, they were allowed to wear contact lenses, as frames interfered with the prism glasses. Asking subjects which leg they would use to kick a soccer ball assessed leg dominance. In groups 1 and 2, right leg dominance was reported in 11/12 and 10/12 subjects, respectively.

Procedure. All subjects performed two different visually guided walking tasks to varying degrees depending on which task they were chosen to adapt to while wearing prism glasses. An Optotrak Certus (Northern Digital, Waterloo, Ontario, Canada) camera was positioned perpendicular to the walkway and used to record kinematic data (sampling frequency of 100 Hz). We placed infrared-emitting diodes on the body including the head and chest and bilaterally on the knees, ankles, and feet.

Figure 1A shows the experimental setup for both walking tasks. For the precision stepping task, subjects stood at one end of the laboratory facing the walkway. On command, subjects were asked to walk to the other end of the laboratory and step onto the center of two targets (35.5 × 19 cm), without stopping, as they passed. The right foot
always stepped on the first target, and the left foot always stepped on the second target. For the obstacle avoidance task, subjects were asked, on command, to walk to the right side of the obstacle (height = 36 cm; width = 9 cm; length = 130 cm) and step over the middle of it laterally, first with the left foot and then with the right foot before continuing to walk for several more steps. In both tasks, subjects were positioned between approximately 2.5 and 4 m from the targets or obstacle (requiring approximately 2-4 steps before the 1st target or obstacle) and asked to walk at a relatively fast but comfortable pace.

Subjects of group 1 (Stepping) performed the precision stepping task while wearing the prism glasses during the adaptation phase, and group 2 (Obstacle) subjects performed the obstacle avoidance task while wearing the prism glasses during the adaptation phase. Table 1 illustrates the experimental protocol (including the order of testing) for both groups. Specifically, subjects were tested in baseline, adaptation, generalization, and postadaptation phases. In the baseline phase, subjects wore control glasses that did not distort vision (0-diopter shift). Subjects performed these trials with their eyes open. The baseline phase consisted of 15 precision stepping trials and 15 obstacle avoidance trials, the order of which depended on the group (see Table 1). In the adaptation phase, subjects wore 20-diopter wedge prism glasses (Standard Prism Training Glasses; Bernell, Mishawaka, IN), inducing a visual field shift of ~11.3° to the right. These prism glasses frames were equipped with black cloth to block the underside of the frame and thus partially obscured the lower visual field so that subjects were forced to look through only the prisms. A similar technique was also used with the control glasses. Subjects were asked to have their eyes closed before the start of each trial. On command, subjects opened their eyes and began to walk for 1 of the 2 tasks. Once they reached the end of their forward movement, subjects turned around, closed their eyes, and raised an arm while a laboratory assistant guided them back to the starting location. This was to ensure that the subjects could not adapt during the walk back. The laboratory assistant randomly altered the starting location for each trial to prevent subjects from developing a learned stepping pattern to complete their task from memory and thereby forcing them to use vision to guide their movements. During this adaptation phase, subjects performed 60 trials of 1 of the 2 walking tasks (either precision stepping or obstacle avoidance based on their group number; see Table 1). In the generalization phase, subjects removed the prism glasses and replaced them with the control glasses. With their eyes still closed at the beginning of the trial, subjects were asked to perform 1 trial of the condition opposite to the adaptation phase opening their eyes on command and closing them again once completed. In the postadaptation phase, subjects performed 30 trials of the adapted task with their eyes open during the task, closing their eyes while being escorted back to the start.

In addition to the walking tasks, each subject underwent visual shift and proprioceptive shift tests (adapted from Morton and Bastian 2004; Redding and Wallace 1988, 1994). Specifically, subjects underwent five trials of both the visual and proprioceptive shift tests before the baseline phase and then a single trial of each test after the adaptation phase but before the generalization phase. The visual shift test looked at the degree to which prism adaptation affected the felt position of the eyes relative to the head or the perceived “straight-ahead” direction (Morton and Bastian 2004). In total darkness, subjects stood ~1 m from a projection screen with their feet, hips, and head aligned and oriented straight-ahead. At the start of a trial, subjects opened their eyes and indicated when they perceived the dot of a laser pointer that was shone on the screen to be directly in front of them. They were allowed to verbally ask for adjustments (by telling the investigator to move the laser slightly left or right) until they believed it was in the correct location. If prisms stimulate a visual shift, we would expect to see subjects identify straight-ahead as being to the right of midline during the visual test after prism exposure (Morton and Bastian 2004; Redding and Wallace 1988, 1994).

The proprioceptive shift test looked at the degree to which prism adaptation caused a shift in the felt position of the lower limbs relative to the head/body. Subjects stood with their feet shoulder-width apart in the middle of a room with their eyes closed. On command, they were asked to step with their left foot toward the projected midline of their body (keeping their eyes closed throughout the movement). If prisms stimulated a proprioceptive shift, subjects would step to the left of their midline relative to their head during the proprioceptive shift test after prism exposure (Morton and Bastian 2004; Redding and Wallace 1988, 1994).

Data and statistical analyses. In the precision stepping task, performance was measured by calculating the lateral (left-right) endpoint errors of foot placement (using a position marker at the level of the midfoot) from the center of the target location. A positive number represents error to the right of the target and a negative number represents error to the left of the target (see Fig. 1B). In the obstacle avoidance task, performance was measured by calculating the distance from the obstacle of both the trailing foot (i.e., step N-1, the right foot) and leading foot (i.e., step N, the left foot) from a midfoot marker. For both step N and N-1, increasing positive numbers represent a greater deviation away from the obstacle (see Fig. 1B). In addition, we calculated the left toe clearance (LTC), which represented the clearance of the lead foot over the obstacle. The LTC was measured at the level of a position marker on the toe.

We compared the performance of each walking task at several time periods: baseline (the average of the last 5 baseline trials, calculated separately for each movement); early adaptation (the 1st adaptation trial); late adaptation (the average of the last 5 adaptation trials); generalization (the single generalization trial); early postadaptation (the 1st postadaptation trial); and late postadaptation (the average of the last 5 postadaptation trials) phases. For the precision stepping task, right and left feet were analyzed separately.

The rate of adaptation (i.e., adaptation phase) for each measure that demonstrated adaptation was determined on a subject-to-subject basis. We fit different functions (e.g., exponential, cubic, power, and log) to the data and chose the function with the largest $r^2$ value in the majority of subjects to use in the analysis. Thus we fit exponential functions to plots of deviation from target/obstacle vs. trial number for target 1 (stepping task), target 2 (stepping task), and step N (obstacle task). The exponential time constant was used as an approximation of the adaptation rate (Martin et al. 1996a; Morton and Bastian 2004).

We also compared the magnitudes of visual and proprioceptive shifts before and after prism exposure. For the visual shifts, a laboratory assistant marked the locations on the screen that subjects

| Table 1. Testing protocol |

<table>
<thead>
<tr>
<th>Phase</th>
<th>Baseline</th>
<th>Adaptation</th>
<th>Generalization</th>
<th>Postadaptation</th>
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<td>5</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>Prisms</td>
<td>Vision Dark</td>
<td>Prisms OFF</td>
<td>Prisms ON</td>
<td>Prisms OFF</td>
</tr>
</tbody>
</table>

Group 1: Vision Prop Obstacle Stepping Vision Prop Obstacle Stepping

Group 2: Vision Prop Vision Prop Obstacle Obstacle

Dark, room dark; EC, eyes closed; EO, eyes open; Prop, proprioceptive shift test; Vision, visual shift test.

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indicated as straight-ahead with an “extra” infrared-emitting diode. We calculated the distance between the head marker and the identified straight-ahead location on the screen in the medial-lateral dimension and the anterior-posterior dimension. For the proprioceptive shifts, we calculated the distance between the head marker before stepping and the toe marker after stepping in both the medial-lateral dimension and the anterior-posterior dimension. For both tests, we calculated the angle of the shift as the inverse tangent of the ratio of the medial-lateral to anterior-posterior distances. Positive and negative angles were assigned to indicate rightward and leftward deviations, respectively. We compared performance on the shifts tests at the baseline phase (the average of all 5 trials) and just after the adaptation phase (single trial).

All data were collected and analyzed using custom-written LabVIEW (National Instruments, Austin, TX) programs. Statistical analysis was completed using SPSS (Chicago, IL) software with an α-level of 0.05. Performance (i.e., baseline, early adaptation, late adaptation, early postadaptation, and late postadaptation phases) for each measure (i.e., foot placement deviation [target 1 step and target 2 step], distance to obstacle [step N-1], distance after obstacle [step N], and toe clearance [LTC]) was compared using one-way repeated-measures ANOVAs. Bonferroni post hoc tests were performed when ANOVAs yielded significant results. Generalization (i.e., baseline vs. generalization phases) and shift test (i.e., baseline vs. postadaptation) performance were compared using paired-samples t-tests.

RESULTS

Adaptation to precision target stepping and obstacle avoidance. In these experiments, our first goal was to determine whether healthy adults were able to adapt to a rightward prismatic shift during a precision target stepping or obstacle avoidance task. Average gait speed pooled across the testing phases during the precision stepping task was 1.44 ± 0.15 m/s, which was significantly faster (paired t-test, \( P < 0.0001 \)) than the gait speed during the obstacle avoidance task (1.01 ± 0.23 m/s). There was no difference in gait speed across the different testing phases. The slower gait speed in the obstacle avoidance task was due to the limb being elevated to clear the obstacle, which required subjects to slow down to control the trajectory of the movement. There was no evidence of online corrections during the step to targets or obstacle as evident from video analysis and kinematic profiles.

Figure 2A clearly demonstrates a classical prism adaptation pattern for an example subject performing the precision stepping task (group 1). On initial exposure to prisms while performing the task, there was a large rightward deviation in foot placement with respect to both targets, as denoted by the arrows in the adaptation phase. The subject represented in the figure completely missed the two targets and required multiple attempts before they were successful. This was commonly observed for all subjects. The rightward deviation was reduced after repeated trials with the prisms and returned to baseline levels. After removal of the prisms, the subject demonstrated a large negative aftereffect. This was reflected by a large leftward deviation, as denoted by the arrows in the postadaptation phase.

Figure 3A displays the group means for the lateral deviation from target 1 by the right foot and from target 2 by the left foot for the various phases during the precision stepping task. As is evident from the figure, group data also support the notion of prism adaptation for this task (1-way repeated-measures ANOVA, \( P < 0.0001 \) for both target steps). The results were similar for both steps. In the adaptation phase, all subjects showed an initial rightward deviation from the targets compared with baseline for both target 1 and 2 for the right and left feet, respectively (baseline vs. early adaptation phase, post hoc \( P < 0.0001 \)). The initial deviation was larger for target 2 with the left foot: left foot deviations (with respect to baseline) were 357.2 ± 77.5 mm, and right foot deviations (with respect to baseline) were 308.7 ± 59.8 mm to the right of both targets.

Over repeated trials, performance gradually improved to near-baseline levels (early vs. late prism adaptation phase, post hoc \( P < 0.0001 \); baseline vs. late adaptation phase, post hoc \( P > 0.05 \)). After the prisms were removed for the postadaptation phase, all subjects showed a distinct negative aftereffect (targets 1 and 2: baseline vs. early postadaptation phase, \( P < 0.0001 \)) with initial deviations (with respect to baseline) of \(-100.7 ± 45.9 \) mm for the right foot and \(-124.4 ± 31.4 \) mm for the left foot to the left of the target. Whereas the step to target 1 with the right foot late postadaptation lateral deviation values returned to baseline levels (baseline vs. late postadaptation, post hoc \( P > 0.05 \)), the step to target 2 with the left foot late postadaptation values were reduced compared with the early postadaptation phase (post hoc \( P < 0.001 \)) but were still different from baseline values (baseline vs. late postadaptation phase, post hoc \( P < 0.0001 \)).

The obstacle avoidance task proved to be substantially challenging when subjects were 1st exposed to the prisms. A total of 9/12 subjects hit the obstacle on the 1st adaptation trial in the obstacle group (i.e., group 2). Despite repeated attempts, many subjects still knocked over, stepped on, or kicked the obstacle throughout the adaptation phase. During the adaptation and postadaptation phases, the obstacle was hit 44 and 3 times, respectively.

Data from an individual subject performing the obstacle avoidance task are shown in Fig. 4. When exposed to the prisms, this subject hit the obstacle on the 1st attempt during the adaptation phase. The arrows indicate this trial for each of the three measures (see Fig. 4A). Toe clearance (diamonds) was near 0. Note that this value does not reach 0 as the marker on the toe was placed on the top of the foot. This unsuccessful attempt was presumably due to the large rightward shift in step N-1 (squares). After repeated attempts at the task with the prisms, the deviations in step N-1 and step N were reduced. However, step N-1 deviations never returned to baseline. Toe clearance also did not return to baseline values. In fact, after the initial obstacle contact, the subject overcompensated with a large toe clearance. On removal of the prisms, a negative aftereffect was only seen for step N (see large shift during postadaptation phase in distance from the obstacle in the opposite direction to the early adaptation phase: triangles).

Figure 3B illustrates the group data for the obstacle avoidance task (group 2) at key points among the different phases. Whereas all three measures characterizing performance on the obstacle avoidance task exhibited significant one-way repeated-measures ANOVAs (LTC: \( P = 0.039 \); step N: \( P < 0.0001 \); step N-1: \( P < 0.0001 \)), adaptation during prism exposure and aftereffects were less obvious than for the precision stepping task. For instance, step N-1 (Fig. 3B, middle) was shifted significantly away to the right of the obstacle for the early adaptation phase compared with the baseline phase (post hoc \( P < 0.0001 \)). This rightward deviation was an average of 233.4 ± 108.6 mm from the average baseline phase values. However,
the decrease in rightward deviation away from the obstacle over repeated trials during the adaptation phase did not reach significance (post hoc $P > 0.05$, early vs. late adaptation phases). In addition, there was no evidence of an aftereffect (post hoc $P > 0.05$) as can be seen comparing the baseline and early postadaptation phases in Fig. 3B.

The LTC measure failed to show any difference in the early adaptation phase (baseline vs. early adaptation phase, post hoc $P > 0.05$) or any evidence of an aftereffect (baseline vs. early postadaptation phase, post hoc $P > 0.05$) for group 2 (Fig. 3B, left). This is not necessarily surprising given that the prisms act to displace visual information in the medial-lateral direction and not the vertical direction per se. Interestingly, of those nine subjects that hit the obstacle on the first adaptation trial, we noticed that this resulted in a large overcompensation in subsequent trials (i.e., larger toe clearance compared with baseline phase), which often did not stabilize throughout the adaptation phase.
However, similar to the precision stepping task, step $N$ of the obstacle avoidance task demonstrated adaptation (Fig. 3B, right). There was a clear initial rightward shift in distance from the obstacle for step $N$ (i.e., closer to obstacle; post hoc $P = 0.006$) in the early adaptation phase, which returned to baseline after repeated trials (baseline vs. late adaptation phase, post hoc $P > 0.05$). Furthermore, there was evidence of an aftereffect for this step (post hoc $P = 0.008$) in the early postadaptation phase.

**Adaptation rates.** Subjects adapted to the precision stepping task or obstacle avoidance task at different rates. Figure 5 shows the adaptation curves (fit by an exponential function) of representative subjects for the measures of the two locomotor tasks that demonstrated adaptation. As can be seen for the precision stepping task (Fig. 5, A and B), both steps to the two targets adapted at similar rates (mean rates of adaptation: target 1 = 6.2 ± 5.8 trials, $r^2 = 0.80$; target 2 = 5.5 ± 5.0 trials, $r^2 = 0.83$). The same subject displayed in Fig. 2 for the precision stepping task is shown in the right column of Fig. 5, A and B.

Adaptation curves for step $N$ of the obstacle avoidance task are displayed in Fig. 5C. The mean adaptation rate for this measure was 1.7 ± 1.1 trials ($r^2 = 0.47$). This rate was significantly faster (independent $t$-test: $P = 0.032$) compared with the rates for target 2 (same limb for each measure) in the precision stepping task. The adaptation curve of the subject displayed in Fig. 4 for the obstacle avoidance task is shown in...
the right column of Fig. 5C. Adaptation rate and $r^2$ values for the curve fits for all subjects are reported in Table 2. Taken together, the results of the adaptation rates indicate that subjects adapted quickly for the precision stepping task and step $N$ of the obstacle avoidance task.

Generalization between prism-adapted precision stepping and obstacle avoidance tasks. A further objective of our experiments was to determine whether prism adaptation in healthy adults would generalize across two different, and visually demanding, locomotor tasks. Specifically, we asked whether group 1 (Stepping) subjects, who adapted to prisms during a precision stepping task, demonstrated generalization to the obstacle avoidance task. Furthermore, we asked whether subjects in group 2 (Obstacle), who adapted to prisms during an obstacle avoidance task, demonstrated generalization to the precision stepping task.

For generalization from precision stepping to obstacle avoidance to be evident, we would expect to see subjects of group 1 (Stepping) biased to the left when stepping over the obstacle (i.e., similar to the negative aftereffect in the early postadaptation phase, for example, with step $N$ of group 2 subjects). Thus we should observe a decrease in distance from the obstacle of step $N-1$ and an increase in distance from the obstacle of step $N$. The latter result is evident in the single subject example in Fig. 2B. Subjects of group 2 (Obstacle), who adapted to prisms during the obstacle avoidance task, were exposed to a precision stepping task without the prisms during the generalization phase. For generalization from obstacle avoidance to precision stepping to be evident, a large rightward deviation can be observed during the initial adaptation phase while wearing the prisms for steps $N-1$ and $N$ (see Fig. 1B for an illustration of the meaning of the deviation values for these 2 steps). Subsequently, a negative aftereffect is evident during the initial postadaptation phase when the prisms are removed. The small toe clearance and deviation in step $N$ in the initial adaptation phase trial are indicative of the subject hitting the obstacle. The toe clearance is positive due to the location of the position marker on the toe (i.e., top of toe). Diamonds, deviation from obstacle for step $N-1$; triangles, deviation from obstacle for step $N$. The arrows denote the 1st trial in the adaptation or postadaptation phase for each measure. $B$: results of the generalization task are shown comparing the single precision stepping trial (i.e., generalization trial) after removal of the prisms following the obstacle avoidance adaptation phase compared with baseline precision stepping trials. Lateral deviation from the targets is shown. Diamonds, deviation from target 1; squares, deviation from target 2. Dashed horizontal lines indicate the location of the target edges (0 deviation indicates center of target). Note that the deviations are biased to the negative (i.e., left of target) due to the location of the position marker on the foot (i.e., lateral side of left foot and medial side of right foot).
stacle avoidance to precision stepping to be evident, we would expect to see subjects of group 2 (Obstacle) biased to the left when stepping to the two targets (i.e., similar to the negative aftereffect in the early postadaptation phase, for example, with target 1 and 2 steps of group 1 subjects). This would be reflected in a more negative lateral deviation from the targets. This is shown in Fig. 4B for a single subject, particularly for the step to target 2 with the left foot.

As illustrated by the group means in Fig. 6, both groups exhibited partial generalization. The average data are similar to the single subject examples shown in Figs. 2B and 4B. Only steps that required the left foot, and not the right foot, demonstrated generalization. In other words, foot placement of the left foot onto target 2 (i.e., step N; $P = 0.009$) in the obstacle avoidance task generalized. However, the step onto target 1 with the right foot and the step with the right foot before clearing the obstacle (i.e., step N-1) showed no generalization ($P > 0.05$). Toe clearance also did not show any generalization ($P > 0.05$).

**Fig. 5.** Adaptation curves of 3 representative subjects (pa04, pa05, pa18) performing the precision stepping task with the prism glasses are shown in A and B. A: lateral deviation of the right foot from target 1. B: lateral deviation of the left foot from target 2. Adaptation curves of 3 representative subjects (pa09, pa14, pa20) performing the obstacle avoidance task with the prism glasses are shown in C. In this panel, the deviation from the obstacle for step N is shown. Data in all panels were fit with an exponential function. The adaptation rate (exponential time constant) and $r^2$ of the fit are listed for each subject. The data of the example subjects in Figs. 2 and 4 are displayed in the right columns.
Table 2. Adaptation rates

<table>
<thead>
<tr>
<th>Group 1</th>
<th>Target 1: Right Foot</th>
<th>Target 2: Left Foot</th>
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<th>Step N</th>
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<tbody>
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<td>$r^2$</td>
<td>Rate</td>
<td>$r^2$</td>
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<td>0.84</td>
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<tr>
<td>pa22</td>
<td>3.6</td>
<td>0.83</td>
<td>1.5</td>
<td>0.82</td>
</tr>
<tr>
<td>pa24</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Mean</td>
<td>6.2</td>
<td>0.80</td>
<td>5.5</td>
<td>0.83</td>
</tr>
<tr>
<td>SD</td>
<td>5.8</td>
<td>0.05</td>
<td>5.0</td>
<td>0.07</td>
</tr>
</tbody>
</table>

- Unable to significantly fit curve due to trial-to-trial variability. †Unable to fit curve due to missing data from technical difficulties. Step N, leading left foot.

**Visual and proprioceptive shift tests.** Overall, there was a large amount of variability between subjects for both the proprioceptive and visual shift tests. Subjects from group 1 (Stepping) demonstrated an average proprioceptive shift of $-2.3 \pm 10.9^\circ$ and an average visual shift of $-2.5 \pm 3.2^\circ$. Subjects from group 2 (Obstacle) showed an average proprioceptive shift of $-0.7 \pm 8.1^\circ$ and an average visual shift of $0.5 \pm 4.6^\circ$. The only significant difference was for the visual shift in subjects from group 1 (Stepping; $P = 0.025$). A few subjects reported that after removing the prisms, they felt like their head was rotated in reference to their trunk. Thus we quantified head-on-trunk orientation based on position markers on the head and chest regions. We found a trend for a leftward shift ($-2.0 \pm 3.4^\circ$, $P = 0.083$) for subjects from group 1 (Stepping) and a highly variable and insignificant shift ($1.0 \pm 8.7^\circ$, $P > 0.05$) for subjects from group 2 (Obstacle). This may partially explain the leftward visual perceptual shift in subjects from group 1 (Stepping).

**DISCUSSION**

In this study, we demonstrated that the nervous system is capable of adapting to a novel prism-induced visuo-motor mismatch during complex, visually guided locomotor tasks. The rate of this adaptation depended on the task. The presence of aftereffects observed in several measures following the removal of the prisms support the notion of an internal model for the control of visually guided locomotion. Furthermore, we found a unilaterally symmetric generalization pattern in that only the left foot placement generalized across both tasks. This finding extends recent research into generalization patterns during reaching and locomotion. To our knowledge, this is the first study to examine prism adaptation and generalization during complex, visually guided locomotor tasks and thus adds important knowledge to the understanding of how the nervous system integrates sensory and motor information to perform essential everyday skills.

**Characteristics of prism-induced adaptation during precision stepping and obstacle avoidance.** In our experiments, prisms induced a rightward shift of visual information ($\sim 11.3^\circ$). This provided a mismatch between the seen position and the proprioceptive (or felt) position of the lower limbs. Consequently, a sensory prediction error resulted from the difference between expected sensory feedback estimated from the motor command to the lower limbs and actual sensory feedback generated during the limb movements (Shadmehr et al. 2010). Despite this mismatch, subjects were able to adapt to step to targets successfully or step over an obstacle while walking after the initial end-point error on the first prism exposure trial. Several of our measures subsequently demonstrated negative aftereffects on removal of the prisms, albeit smaller than the initial error during the adaptation phase. The smaller aftereffects may be partially explained by the fact that visual feedback was available during the generalization trial, which was performed before the first postadaptation trial, and thus subjects could have begun to readapt. Regardless, the implication for the presence of aftereffects is that the nervous system updates an internal model to account for the error and adapts the motor commands appropriately. When prisms are removed, the updated model is invalid, and aftereffects are present. Our results, therefore, provide evidence of the use of an internal model for visually guided locomotion.

In recent years, the notion of an internal model has been studied extensively for reaching and throwing actions using manipulations of vision and/or limb dynamics (Martin et al. 1996a,b; Midall et al. 2007; Shadmehr et al. 2010; Shadmehr and Mussa-Ivaldi 1994), whereas a limited focus on locomotion has concentrated primarily on manipulations of limb dynamics (Blanchette and Bouyer 2009; Choi and Bastian 2007; Fortin et al. 2009; Lam et al. 2006; Lam and Dietz 2004; Savin et al. 2010). For instance, Blanchette and Bouyer (2009) reported that subjects can adapt to an elastic force field applied to the foot during treadmill walking and show negative aftereffects in foot velocity and hamstrings muscle activity following its removal. Consequently, our results bridge the gap between the use of an internal model to control reaching to targets (a visually demanding task) and the use of an internal model to control locomotion (inferred from manipulations to lower limb dynamics).

Interestingly, not all of our measures demonstrated adaptation during prism exposure. The absence of aftereffects in these same measures is likely due to this lack of adaptation. The fact that step N-1 did not adapt during the obstacle task was surprising given that foot placement before the obstacle is critical for obstacle clearance since it is largely responsible for...
the success of the movement (Patla and Greig 2006; Lajoie and Drew 2007). However, there was no specific target to step to, and so there was less certainty of any error in foot placement to drive a subsequent adaptation. Alternatively, this step might have required a greater number of trials for the nervous system to adapt. Although step $N-1$ with the right foot did not adapt to the prisms, step $N$ with the left foot demonstrated both adaptation and the presence of aftereffects. This indicates that the nervous system can adapt the 2 lower limbs independently to meet the task demand. In support, Choi and Bastian (2007) recently found that aftereffects were specific to the limb after subjects underwent hybrid walking on a split-belt treadmill (stepping on 1 belt moving forward and 1 belt moving backward), suggesting that walking adaptations are stored independently for each leg.

Toe clearance of the lead limb over the obstacle is also essential, and that it, too, failed to adapt was unexpected. This lack of adaptation might be attributed to the use of a safety margin. Given that the majority of subjects collided with the obstacle on the first trial, a default strategy of maintaining a particular toe elevation to ensure that they did not hit the obstacle was likely chosen. This is evident from the example subject displayed in Fig. 4, although other subjects showed a larger overcompensation on the second trial. After a perturbation during locomotion, subjects typically adopt a cautious gait strategy on subsequent trials; foot placement onto a slippery surface is drastically altered following the first exposure (Marigold and Patla 2002).

Unilateral, symmetric generalization across the visually guided locomotor tasks. Our results demonstrated unilateral, symmetric generalization. Generalization was symmetric in that there was a bidirectional transfer between prism-adapted precision stepping and obstacle avoidance. Recent studies of prism adaptation between reaching and walking (Morton and Bastian 2004; Savin and Morton 2008) have found an asymmetric generalization pattern (1 task generalizes to the other but not vice versa). A potential reason for the symmetry of our results is the fact that both tasks were performed during
walking. Symmetric generalization between different external environments (obstacle avoidance during level walking vs. downhill walking) has been found with subjects performing an obstacle avoidance task via acoustic feedback (rather than vision of the obstacle and limbs) regardless of obstacle clearance (Lam and Dietz 2004). Taken together, generalization appears to be largely dependent on the task under investigation. This suggests that further study is warranted to determine which tasks may generalize using different manipulations and thus have the potential to facilitate targeted rehabilitation for those after neurological injury.

The unilateral aspect of the generalization was reflected by the fact that only measures associated with the left lower limb generalized across tasks. Although a lack of adaptation might account for the right lower limb of group 2 (Obstacle) subjects, it does not explain why the right lower limb of group 1 (Stepping) subjects failed to demonstrate generalization. Rather, a form of proprioceptive learning may explain these results. In both locomotor tasks, subjects had to make a visually guided and coordinated step with their left foot either to a second target or over an obstacle. This step required a greater modification than stepping to the first target or before the obstacle with the right foot. Furthermore, in the case of the precision stepping task, the second target remained a constant distance from the right target. Therefore, once subjects had adapted, they continually made the same active gait modification. The repetitive movement might have enhanced the development of a new spatial relationship between visual and left lower limb proprioceptive input over one for the right lower limb. The normal muscle spindle and Golgi tendon organ sensory feedback known to regulate stepping (Rossignol et al. 2006) may have facilitated this development through signaling of the cerebellum via spinocerebellar tracts. It would be interesting to determine in future work whether adding a third target or a second obstacle to force a left-right motion adaptation would lead to a complete symmetric pattern of, or wash out any, generalization.

Although the vertical trajectory is different between the right-left lower limb motion for the precision stepping and obstacle avoidance tasks, the final end point of the limb (i.e., foot placement onto the second target or on the other side of the obstacle) is critical in both cases. Thus proprioceptive learning is likely not the sole explanation for our generalization pattern as the proprioceptive feedback and necessary muscle activation patterns to achieve the desired trajectories between the two tasks are sufficiently different. This suggests that the nervous system might encode the adaptation in a nonspecific muscle activation pattern. That the nervous system controls the end position of the foot supports the idea that it represents limb location in terms of the end-point position (Bosco et al. 2000; Ivanenko et al. 2002; Lam and Dietz 2004). The shift tests provided insufficient evidence to explain entirely the adaptation or generalization results, which is similar to the recent findings of Morton and Bastian (2004). Thus the prism-induced adaptation likely was due to a motor recalibration involving a higher-level visuomotor transformation process due to the spatial remapping of visual and proprioceptive information used to plan and execute the motor command for the lower limbs (Baraduc and Wolpert 2002; Morton and Bastian 2004). Such higher-level encoding is reminiscent of posterior parietal cortex (PPC) or cerebellum function.

Possible neural structures associated with locomotor prism adaptation. Although several brain regions are most likely at work during prism adaptation, two structures in particular have emerged as playing a dominant role: the PPC and the cerebellum. Recent neuroimaging studies found that the anterior intraparietal sulcus (AIP) is active in the early phase of prism exposure when reaching error is high (Chapman et al. 2010; Clower et al. 1996; Danckert et al. 2008; Luauté et al. 2009). Luauté et al. (2009) suggest that AIP is involved in error detection since its activity is related to the trial-by-trial size of reaching error. A role for the PPC during reaching prism adaptation tasks is also supported by lesion studies (Pisella et al. 2004). Activity in the cerebellum has been shown to increase during the early phase of prism exposure such that it is elevated in late prism adaptation compared with early adaptation and remains higher for longer durations compared with the PPC (Chapman et al. 2010; Luauté et al. 2009). Results in patients with cerebellar lesions also support this idea, as they lack the ability to adapt to prismatic displacement during a throwing task (Martin et al. 1996a). It is likely that the PPC and cerebellum form a network, given known neuroanatomical connections, which work together so that errors detected by regions within the PPC inform and facilitate the updating of internal models in the cerebellum (Chapman et al. 2010; Clower et al. 2005; Shadmehr and Krakauer 2008).

We propose that similar to reaching prism adaptation, the cerebellum is heavily involved in both precision target stepping and obstacle avoidance prism adaptation. Indeed, lateral cerebellar neurons are known to discharge during locomotion in the cat (Marple-Horvat et al. 1998; Marple-Horvat and Criado 1999). Furthermore, the cerebellum appears to be important for prism-induced adaptation of walking trajectory; cerebellar subjects are slower and less able to adapt their walking trajectories to prisms to the same extent as controls and show less negative aftereffects and generalization (Morton and Bastian 2004). Neurons in the PPC have been found to discharge during locomotion in the cat (Andujar et al. 2010; Beloozerova and Sirota 2003; Drew and Marigold 2008). It has been argued that their function is in the motor planning and execution of gait modifications (Marigold et al. 2011), particularly related to placement of the limb (Beloozerova and Sirota 2003; Lajoie and Drew 2007) and to online corrections (Drew and Marigold 2008) similar to reaching (Pisella et al. 2000).

In conclusion, we demonstrated, for the first time, the capability of the nervous system to adapt to prisms during two visually guided locomotor tasks. Our findings of a unilateral, symmetric generalization pattern support growing literature suggesting that generalization is highly task-dependent, and further research is warranted to better understand the patterns to facilitate locomotor rehabilitation paradigms.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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