Changes in task parameters during walking prism adaptation influence the subsequent generalization pattern

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Alexander MS, Flodin BWG, Marigold DS. Changes in task parameters during walking prism adaptation influence the subsequent generalization pattern. J Neurophysiol 109: 2495–2504, 2013. First published February 27, 2013; doi:10.1152/jn.00810.2012.—An understanding of the transfer (or generalization) of motor adaptations between legs and across tasks during walking has remained elusive due to limited research and mixed results. Here, we asked whether stepping sequences or task constraints introduced during walking prism-adaptation tasks influence generalization patterns. Forty subjects adapted to prism glasses in precision-walking or obstacle-avoidance tasks that required a specific stepping sequence to the center of two/three targets or laterally over an obstacle. We then tested for generalization, reflected by aftereffects in the nonadapted task. Our previous study using these tasks found that only one leg generalized. Here, we reversed the stepping sequence and found that only the opposite leg generalized in the subject group that adapted in a precision-walking task. The combination of stepping sequence and direction of prism shift caused subjects in two groups to collide with the obstacle early during adaptation, thus making the step prior to going over the obstacle more important. Both legs subsequently generalized. A fourth subject group experienced a three-target, precision-walking task, resulting in a balanced, right-left, left-right stepping sequence, meant to induce bilateral generalization. While only one leg generalized, foot placement aftereffects before stepping over the obstacle would have caused subjects to collide with it. Together with our previous study, the results suggest a contribution of stepping sequence during the adapted task on generalization patterns, likely driven by proprioceptive feedback. The results also support the idea that negative consequences during adaptation and/or perceived threat can influence generalization.

Generalization, a key component of motor learning, refers to the ability to transfer what has been learned (e.g., through adaptation) in one context or task to another (Krakauer et al. 2006; Pearson et al. 2010; Poggio and Bizzi 2004; Shadmehr 2004). Importantly, the pattern of generalization provides insight into how the adaptation is encoded (by updating internal models) and thus facilitates our understanding of how the nervous system controls movement (Pearson et al. 2010; Shadmehr 2004; Shadmehr and Moussavi 2000). The ability to generalize adaptation is also of practical importance for developing training methods and rehabilitation techniques. For instance, it may be desirable to train an individual following neurological injury in such a manner as to induce benefits beyond the clinical setting and across a range of motor tasks.

Reaching studies have shown that generalization between tasks may be narrow or broad, based on different contexts, such as direction (Pearson et al. 2010), speed (Hwang et al. 2003), or limb position/posture (Shadmehr 2004; Shadmehr and Moussavi 2000), and depends on prior history of the movement (Krakauer et al. 2006) and the complexity of the perturbation during adaptation (Thoroughman and Taylor 2005). The robustness of the transfer also seems contingent on the similarity between the learned and unlearned task (Ghahramani et al. 1996; Shadmehr 2004). Whether the insight gained from studying goal-directed reaching is applicable to walking remains to be determined, given very different task constraints, such as balance.

Generalization during locomotion has been relatively understudied compared with reaching. Van Hedel et al. (2002) found that learning to step over an obstacle with reduced vision using one leg transfers to the other leg. However, hopping on a treadmill with one leg showed little transfer to the opposite leg (Anstis 1995). Furthermore, adapting on a split-belt treadmill with legs moving at different speeds (Prokop et al. 1995) or directions (Choi and Bastian 2007) leads to minimal transfer between legs. More recently, Houldin et al. (2012) have also shown that adaptation to a velocity-dependent force field, when treadmill walking is constrained to a unipedal gait, has minimal transfer to the contralateral leg.

Transfer of adaptation between different locomotor tasks has also shown mixed results. For instance, walking on a rotating disc generalized from forward walking to backward walking (Earhart et al. 2001), as did stepping in place to hopping (Earhart et al. 2002). Interestingly, three recent studies have shown that following prism adaptation, there is an asymmetric generalization pattern between the arm and the leg. One study found that walking broadly generalizes to reaching, but reaching does not generalize to walking (Morton and Bastian 2004).
In contrast, Savin and Morton (2008) and Michel et al. (2008) found an opposite generalization pattern, where arm-pointing generalized to leg-pointing or walking trajectory, respectively, but not vice versa. Asymmetric generalization is also evident in reaching to targets: Krakauer and colleagues (2006) found that reaching toward a target while wearing prism glasses generalized from arm to wrist motion but not wrist to arm motion. Taken together, the results suggest that generalization depends on the detailed nature of the tasks studied. However, there has been limited research on generalization between two visually guided walking tasks.

Recently, we found that individuals were able to adapt to a rightward prism shift while walking and stepping to targets (i.e., precision walking) or walking and stepping laterally over an obstacle (i.e., obstacle avoidance) (Alexander et al. 2011). Furthermore, we demonstrated that adaptation in one of the walking tasks generalized to the other and vice versa. Unexpectedly, we found that generalization between the tasks was unilateral, such that foot placement of only one leg transferred. We suggested that the nature of the stepping pattern may have resulted in the unilateral generalization. Specifically, the coordinated and repetitive right-left stepping sequence in both tasks (either to two targets or stepping laterally over an obstacle) reinforced the sensorimotor mapping during the adaptation, causing only the left leg to generalize. In both tasks, the visually guided step to either a second target or over an obstacle with the left leg depended on the right leg’s position and required a greater modification to gait.

The goal of this study was to determine whether generalization following prism-induced walking adaptation depends on elements of the adapted task. Specifically, we asked whether generalization is affected by different stepping sequences and/or obstacle collisions experienced during the adaptation phase. To test these ideas, we reversed the stepping sequence in the precision-walking and obstacle-avoidance tasks from our previous study in two separate groups of subjects. If the stepping sequence dictates the generalization pattern, then we should expect to see unilateral generalization but with the right leg rather than the left. Furthermore, we added a third target to the precision-walking task for another group of subjects to create a stepping sequence that required coordination of both legs. Since this required a right-left and left-right stepping sequence, we expected to observe bilateral generalization to the obstacle-avoidance task. We show that the stepping sequence dictated the generalization pattern in the precision-walking task. However, the nature of the stepping sequence and direction of prism shift caused subjects in the group adapting to the obstacle-avoidance task to collide with the obstacle. This task constraint may have masked the role of stepping sequence in this group. To explore whether obstacle collisions influence generalization patterns, we tested another group with a different combination of stepping sequence and direction of prism shift that also caused subjects to veer into the obstacle in the adaptation phase until they adapted. We reasoned that the negative consequences associated with obstacle collisions would result in greater generalization, likely due to a stronger motivational or fear-based mechanism for adaptation (Green et al. 2010). Indeed, we show bilateral generalization in these groups.

METHODS

Subjects. A total of 40 subjects (age = 21.8 ± 2.8 yr; 15 men and 25 women) from Simon Fraser University participated in this experiment. The subjects were assigned to one of four groups. **Group 1** consisted of one man and nine women (age = 24.0 ± 2.7 yr); **group 2** two men and eight women (age = 22.0 ± 2.3 yr); **group 3** six men and four women (age = 21.5 ± 2.7 yr); and **group 4** six men and four women (age = 19.7 ± 1.6 yr). There were no effects of gender on our measures, consistent with our previous study. Asking subjects which leg they would use to kick a soccer ball assessed leg dominance. Right-leg dominance was reported in nine of 10, nine of 10, eight of 10, and 10 of 10 subjects of groups 1–4, respectively. The Office of Research Ethics at Simon Fraser University approved the study, and all subjects gave informed consent before performing the experiment. Those with known musculoskeletal, neurological, or visual disorders were excluded.

Walking tasks. To address our goal, subjects adapted to 20-diopter wedge prisms (standard prism-training glasses; Bernell, Mishawaka, IN) while performing either a precision-walking or obstacle-avoidance task with a specific stepping pattern, depending on their assigned group. Subsequently, subjects were tested on a nonadapted task. The experimental setup for the walking tasks is shown in Fig. 1A. Tasks were modified from a previous study (Alexander et al. 2011).

There were three variations of the precision-walking task, which required subjects to step to the center of targets (35.5 × 19 cm) without stopping as they walked across the laboratory. One variation had subjects walk toward and step onto two consecutive targets in a left-right sequence (L-R Targets). Therefore, the first target was always stepped on with the left foot and the second target with the right foot. The second variation had subjects walk toward and step onto three consecutive targets in a right-left-right sequence (R-L-R Targets). The right foot always stepped first and the third target and the left foot to the second target. The third variation, which was only used as a nonadapted task (for **group 4**), had subjects walk toward and step onto two consecutive targets in a right-left sequence (R-L Targets).

There were two variations of the obstacle-avoidance task. Each variation required a lateral step over an obstacle (height = 36 cm; width = 9 cm; length = 130 cm) before continuing to walk for several more steps. In one variation, subjects walked toward the obstacle from the left side, planted the left foot (Step N-1) beside the obstacle before stepping over with the right foot first (Step N), and continued walking. We refer to this as the L-R Obstacle task. In the other variation, subjects walked toward the obstacle from the right side, planted the right foot (Step N-1) beside the obstacle before stepping over with the left foot first (Step N), and continued walking. We refer to this as the R-L Obstacle task. In both cases, the sequence started were required to have Step N-1 occur in line with (i.e., next to) the obstacle (as shown in Fig. 1). This occurred in ≥97% of trials.

Procedure. Subjects in each group underwent baseline, adaptation, generalization, and postadaptation phases. In all phases, subjects wore modified glass frames that forced them to look through one of two lenses: 0-diopter (control lenses) or 20-diopter wedge prisms. Subjects wore their normal corrective lenses under the goggles if necessary. The prisms induced an 11.3° shift of objects in the visual field. This shift was rightward for groups 1–3 and leftward for group 4. All trials were performed with the subjects’ eyes open.

The baseline phase consisted of 15 precision-walking trials and 15 obstacle-avoidance trials with the control lenses, the order of which depended on the group (see Fig. 1C). In the adaptation phase, subjects performed 60 trials of their assigned walking task while wearing the 20-diopter wedge prisms. Subjects were asked to keep their eyes closed before starting each trial. Subjects opened their eyes when they were told to start a walking trial. Subjects were instructed to walk at a brisk pace (as if they might be late for class) and were informed that they should look where necessary (including the targets/obstacle) to

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perform the tasks successfully. A random starting anterior-posterior position was selected by the laboratory assistant before each trial to prevent subjects from developing a learned stepping pattern and thus encouraged them to use vision to guide their movements. For both the precision-walking and obstacle-avoidance tasks, the first target or obstacle was approximately 2.5–4 m from the starting position. Upon completion of the trial, subjects turned around, closed their eyes, and were guided back to the starting location by a laboratory assistant. This ensured that adaptation to the visual shift did not occur while walking back to the starting position. In the generalization phase, the 20-diopter prism lenses were replaced with the control lenses. Subjects performed one trial of the nonadapted task. In the postadaptation phase, subjects performed 30 trials of their adapted walking task while continuing to wear the control lenses. Vision was controlled in the same way for the generalization and postadaptation phases as during the adaptation phase: the subjects’ eyes remained closed at the beginning of the trial, were opened on command to begin the trial, and then closed upon completion of the trial.

Figure 1C summarizes the protocol for each group. Subjects in group 1 wore rightward-shifting prisms while performing the precision-walking task, stepping in a left-right sequence (L-R Targets), and generalized stepping left-right over the obstacle (L-R Obstacle). Subjects in group 2 wore rightward-shifting prisms while performing the obstacle-avoidance task, stepping in a left-right sequence (L-R Obstacle), and generalized stepping to two targets in a left-right sequence (L-R Targets). The stepping sequence in these two groups was the exact opposite of the groups in our previous study (Alexander et al. 2011). Subjects in group 3 wore rightward-shifting prisms while performing the precision-walking task, stepping in a right-left-right sequence (L-R-R Targets), and generalized stepping right-left over the obstacle (R-L Obstacle).

The results of group 2 in the present study showed that both legs generalized to the nonadapted task rather than just one leg, which would have been expected, based on our previous study (Alexander et al. 2011). This might suggest that the stepping sequence during adaptation does not dictate the generalization pattern as hypothesized.
Alternatively, the results may arise from the consequence of colliding with the obstacle, which frequently occurred during early adaptation, since the prism shift caused subjects to veer toward it. To test this idea, subjects of group 4 wore leftward-shifting prisms while performing the obstacle-avoidance task in a right-left sequence (R-L Obstacle) and generalized stepping to two targets in a right-left sequence (R-L Targets). This combination of prism shift and stepping sequence was the exact opposite of group 2 and also caused subjects to veer into the obstacle during adaptation.

An Optotrak Certus motion-capture system camera (Northern Digital, Waterloo, Ontario, Canada) was positioned perpendicular to the walkway and used to record kinematic data (sampling frequency of 100 Hz). Infrared-emitting diodes (IREDs) were placed on the body, including the chest and bilaterally on the mid-feet (at the lateral cuneiforms) and toes (at the head of the fifth metatarsals). An additional IRED was used to calibrate target and obstacle locations. A Panasonic high-definition camcorder (model HDC-SD60) recorded videos of each walking trial.

Data and statistical analyses. All data were analyzed using custom-written LabVIEW (National Instruments, Austin, TX) programs. In the precision-walking tasks, performance was measured by calculating the medial-lateral end-point errors of foot placement (using the IRED marker at the mid-foot) relative to 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) and leading foot (i.e., Step N) from the mid-foot marker. For both Steps N-1 and N, increasing positive numbers represent a greater deviation away from the obstacle (see Fig. 1B). In addition, we calculated the leading-limb toe clearance (Lead TC), which represented the clearance of the lead foot over the obstacle and was defined as the distance between an IRED marker on the toe and the height of the obstacle at the point of crossing.

Adaptation is reflected by a decrease in performance error over time during exposure to altered visual input. Errors in the opposite direction (aftereffects) following removal of the prisms reflect whether this adaptation is stored internally after exposure to the novel effect of the prism glasses. Thus generalization would be evident by the presence of an aftereffect in a nonadapted task. To confirm that adaptation to the visually guided walking task occurred, we compared performance for each measure [i.e., foot-placement deviation (target 1 step, target 2 step, and if required, target 3 step), deviations from the obstacle (Steps N-1 and N), and TC (Lead TC)] among baseline (the average of the last five baseline trials of the adapted task), early-adaptation (the first adaptation trial), late-adaptation (the average of the last five adaptation trials), early-postadaptation (the first postadaptation trial), and late-postadaptation (the average of the last five postadaptation trials) phases using separate, one-factor repeated-measures ANOVAs. Bonferroni post hoc tests were performed when ANOVAs yielded significant results.

In groups 2 and 4, the majority of subjects hit the obstacle in the first adaptation trial. In these instances, lead TC was defined as zero, and there was no Step N (the obstacle being knocked over prevented this step, and subjects usually stopped). Thus for the statistical analysis described above, we used the first trial in which there was a proper Step N as the early-adaptation-phase value. This always coincided with trial 2 or 3 of the adaptation phase. Our rationale for this approach was that without an actual Step N, there was no deviation from the obstacle to use for adaptation of this step by the nervous system.

To determine the extent of generalization for the visually guided walking tasks within each group, we compared the baseline phase (the average of the last five baseline trials of the nonadapted task) with the generalization phase (the single generalization trial of the nonadapted task) using paired-samples t-tests. All statistical analyses were completed using SPSS software (Chicago, IL) with an α-level of 0.05.

RESULTS

Prism adaptation. Subjects in each group were able to perform the walking tasks and did so without making online corrections. The absence of online corrections was confirmed through video analysis and analyses of the displacement and velocity profiles of the toe markers. In the precision-walking tasks, subjects had an average speed of 1.46 ± 0.16 m/s (group 1) and 1.41 ± 0.17 m/s (group 3), which were significantly faster than the subjects in the obstacle-avoidance tasks, who had an average speed of 0.99 ± 0.25 m/s (group 2) and 0.97 ± 0.27 m/s (group 4; group 1 vs. 2 and 4 and group 3 vs. 2 and 4, t-tests, P < 0.0001). The slower gait speed in the obstacle-avoidance task may be related to the leg being elevated to clear the obstacle, which required the subjects to slow down to control the trajectory of the movement. There was no difference in gait speed across the different testing phases.

To determine whether adaptation to a rightward prismatic shift occurred during the precision-walking and obstacle-avoidance tasks, we compared lateral foot deviation across baseline, adaptation, and postadaptation phases. Figure 2 clearly shows prism adaptation and aftereffects in the two precision-walking tasks for groups 1 and 3. Upon initial exposure to the prisms, a large, rightward deviation in foot placement to each target was evident. Gradually, this error returned to baseline levels (Fig. 2, A and C). Removal of the prisms demonstrated a large, leftward (or negative) aftereffect, as subjects made large, leftward-stepping deviations. These too returned to baseline levels over multiple trials.

Group means for the lateral deviations of each foot in the various phases of each precision-walking task are shown in Fig. 2, B and D. There was a significant effect of phase for subjects in group 1 (ANOVA: target 1, F4,36 = 45.9, P < 0.001; target 2, F4,36 = 71.7, P < 0.001) and group 3 (ANOVA: target 1, F4,36 = 155.8, P < 0.001; target 2, F4,36 = 81.3, P < 0.001; target 3, F4,36 = 48.1, P = 0.002). Subjects in group 1 showed initial rightward deviations from the center of the targets relative to baseline for targets 1 and 2 with their left and right foot, respectively (baseline vs. early-adaptation phase, P < 0.001). However, the initial step to target 1 with the left foot was larger: left-foot deviations (with respect to baseline) were 311.4 ± 34.9 mm, and right-foot deviations (with respect to baseline) were 248.0 ± 28.8 mm. Group 3 showed similar results with large, initial rightward deviations from the center of each of the three targets with their right, left, and right foot, respectively (baseline vs. early-adaptation phase, P < 0.001). However, the left foot showed larger initial deviations from the target: left-foot deviation from target 2 (with respect to baseline) was 271.1 ± 64.8 mm, whereas average right-foot deviation from target 1 was 253.2 ± 29.8 mm and from target 3 was 221.0 ± 75.5 mm.

Over repeated trials, deviations decreased (early vs. late prism-adaptation phase: all targets, P < 0.001), and performance returned to near-baseline levels (baseline vs. late-adaptation phase, P > 0.05) for groups 1 and 3. After subjects removed the prisms in the postadaptation phase, there was a distinct negative aftereffect, reflected by stepping to the left of the targets (baseline vs. early-postadaptation phase, P < 0.0001). For both groups, performance of steps to all targets returned to baseline levels (baseline vs. late postadaptation, P > 0.05), except for target 2 of group 3 (P = 0.024).
The obstacle-avoidance task proved more challenging with exposure to the prisms. A total of seven of 10 subjects of group 2 and five of 10 subjects of group 4 hit the obstacle with their lead foot on their first adaptation-phase trial. Another one of 10 and two of 10 subjects in groups 2 and 4, respectively, hit the obstacle with their trail foot on the first adaptation trial. The rightward and leftward shift, depending on the group, directed subjects closer to the obstacle. Several subjects kicked, stepped on, or knocked over the obstacle on subsequent trials throughout the adaptation phase. During the adaptation (including the first trial) and postadaptation phases, subjects of group 2 hit the obstacle with their lead foot 22 and zero times, respectively, and in separate trials, hit the obstacle with their trail foot 17 and two times, respectively. Subjects of group 4 hit the obstacle with their lead foot 32 and six times during adaptation (including the first trial) and postadaptation phases, respectively, and in separate trials, hit the obstacle with their trail foot 18 and three times, respectively. All subjects in both groups hit the obstacle at least once during the adaptation phase.

Fig. 2. Mean ± SE deviation from targets for the 2 precision-walking groups. A: averaged trial-by-trial data for group 1 adapting in the L-R Target precision-walking task. A large rightward deviation (+ve) can be observed during the initial adaptation phase, while wearing the prisms, and a negative aftereffect is evident during the initial postadaptation phase when the prisms are removed. Black diamonds: deviation from target 1; white squares: deviation from target 2. Dashed, horizontal lines indicate the location of the target edges (0 deviation indicates center of target). The arrows denote the 1st trial in the adaptation or postadaptation phase for each measure. B: mean lateral deviation from the targets for group 1 across the different phases of the precision-walking task. C: averaged trial-by-trial data for group 3, adapting in the R-L-R Targets precision-walking task. A large, rightward deviation can be observed during the initial adaptation phase, while wearing the prisms, and a negative aftereffect is evident during the initial postadaptation phase when the prisms are removed. Gray diamonds: deviation from target 1; black squares: deviation from target 2; white triangles: deviation from target 3. Definitions of the dashed, horizontal lines and arrows are similar to A. D: mean lateral deviation from the targets for group 3 across the different phases of the precision-walking task. *Significant differences of P < 0.05 based on post hoc tests.

The obstacle-avoidance task proved more challenging with exposure to the prisms. A total of seven of 10 subjects of group 2 and five of 10 subjects of group 4 hit the obstacle with their lead foot on their first adaptation-phase trial. Another one of 10 and two of 10 subjects in groups 2 and 4, respectively, hit the obstacle with their trail foot on the first adaptation trial. The rightward and leftward shift, depending on the group, directed subjects closer to the obstacle. Several subjects kicked, stepped on, or knocked over the obstacle on subsequent trials throughout the adaptation phase. During the adaptation (including the first trial) and postadaptation phases, subjects of group 2 hit the obstacle with their lead foot 22 and zero times, respectively, and in separate trials, hit the obstacle with their trail foot 17 and two times, respectively. Subjects of group 4 hit the obstacle with their lead foot 32 and six times during adaptation (including the first trial) and postadaptation phases, respectively, and in separate trials, hit the obstacle with their trail foot 18 and three times, respectively. All subjects in both groups hit the obstacle at least once during the adaptation phase.

Figure 3 illustrates the mean lateral foot-deviation data for groups 2 and 4. In contrast to the precision-walking tasks, prism adaptation and aftereffects were less-clearly distinguishable. The Lead TC was reduced in the first prism-adaptation
late adaptation. Post hoc tests revealed that Lead TC was reduced in early vs. late adaptation trial, due to the fact that most subjects failed to clear the obstacle, and there was a significant one-factor repeated-measures ANOVA for group 2 across phases ($F_{4,32} = 8.6, P = 0.018$). Specifically, post hoc tests showed that there was a significant reduction in Lead TC from baseline to early adaptation ($P = 0.002$). Lead TC then increased over repeated trials (early vs. late adaptation, $P = 0.001$). There was also a significant phase effect for group 4 ($F_{4,36} = 7.3, P = 0.017$). Post hoc tests revealed that Lead TC was reduced in early vs. late adaptation ($P = 0.024$), and there was a trend toward significance between baseline and early postadaptation ($P = 0.052$), indicative of a negative aftereffect. The lack of significant difference between baseline and early adaptation was likely due to the large variability (as not all subjects hit the obstacle with their lead foot on the first adaptation trial).

There was a significant phase effect for Steps N-1 ($F_{4,36} = 20.2, P = 0.001$) and N ($F_{4,36} = 26.7, P = 0.001$) for subjects in group 2. Specifically, Steps N-1 and N exhibited a significant rightward shift from the obstacle in the initial prism-adaptation trial relative to baseline (Fig. 3B; baseline vs. early adaptation: Step N-1 and N, $P < 0.0001$). This was reflected by a smaller value for Step N-1 and a larger value for Step N, due to the method of calculating the foot deviations (see Fig. 1B). The rightward deviation by Step N-1 was an average of $199.3 \pm 23.5$ mm toward the obstacle (relative to baseline), and Step N showed an average deviation increase of $155.4 \pm 16.5$ mm away from the obstacle (relative to baseline). Upon multiple trials, Steps N-1 and N returned to baseline levels (early vs. late adaptation: Step N-1, $P = 0.005$, and Step N, $P = 0.021$; baseline vs. late-adaptation phase: Step N-1, $P = 0.018$).
We found a significant phase effect for Steps N-1 (F4,36 = 8.5, P = 0.012) and N (F4,36 = 27.9, P = 0.001) for subjects in group 4. Post hoc tests for Step N-1 demonstrated a significant leftward shift toward the obstacle in the first adaptation trial relative to baseline (Fig. 3D; baseline vs. early adaptation: Step N-1, P = 0.005), which was reduced over repeated adaptation trials (early vs. late adaptation: Step N-1, P = 0.035) but did not return to baseline levels (baseline vs. late adaptation: Step N-1, P = 0.028). There was no evidence of an aftereffect (baseline vs. early postadaptation; Step N-1, P = 0.183). However, Step N-1 was shifted away from the obstacle when comparing late adaptation with early postadaptation (P = 0.004). Post hoc tests for Step N revealed a significant leftward shift away from the obstacle in early adaptation (Fig. 3D; baseline vs. early adaptation: Step N, P = 0.0001). However, this shift was not reduced significantly over repeated adaptation trials (early vs. late adaptation: Step N, P = 0.313; baseline vs. late adaptation: Step N, P = 0.002). Whereas there was no indication of a negative aftereffect in the postadaptation phase relative to baseline (baseline vs. early postadaptation: Step N, P = 0.762), Step N was shifted toward the obstacle when comparing late adaptation with early postadaptation (P = 0.0001).

Generalization. We manipulated the stepping sequence to determine if that would alter the generalization pattern following prism-induced walking adaptation. Our previous study showed that stepping in a right-left sequence only generalized to the left lower limb or the second step in precision-walking and obstacle-avoidance tasks. To establish whether reversing the stepping sequences from our previous study would reverse the generalization pattern, we performed similar tasks but using a left-right sequence. Since group 1 adapted to rightward-shifting prisms during a precision-walking task in a left-right stepping sequence (L-R Targets), we would expect generalization to occur for the right foot based on our previous observations. This would be reflected by a decrease in the distance from the obstacle of the right foot (Step N) in the generalization phase. Indeed, we found that the right foot’s step over the obstacle generalized (Fig. 4A; Step N, P = 0.001) by stepping closer to the obstacle, whereas the step before the obstacle did not (Fig. 4A; Step N-1, P = 0.210). TC was not different compared with baseline (P = 0.813). Thus these results are consistent with Alexander et al. (2011).

Group 2 adapted to rightward-shifting prisms during an obstacle-avoidance task, stepping in a left-right sequence (L-R Obstacle). Based on our previous observations, we would expect to see subjects deviate foot placement to the left (or negative) when stepping to the target with the right foot (target 2) in the L-R Target task but no generalization with the left foot. In fact, we found that both legs generalized (Fig. 4B; target 1, P = 0.003; target 2, P = 0.041).

To determine whether frequent collisions with the obstacle during adaptation enhanced the generalization pattern of group 2, group 4 adapted to leftward-shifting prisms during an obstacle-avoidance task, stepping in a right-left sequence (R-L Obstacle). If the negative consequences associated with collisions enhanced generalization, then we would expect that both legs would generalize in this group as well. Indeed, this is what we observed (Fig. 4D; target 1, P = 0.008; target 2, P = 0.012).

For group 3, we added a third target to the precision-walking task, creating a right-left-right stepping sequence (R-L-R Targets). We expected that the equal right-left and left-right pattern would cause generalization of both Steps N-1 and N in the nonadapted, obstacle-avoidance task (R-L Obstacle). Specifically, we should see a decrease in the distance from the obstacle of Step N-1 and an increase in distance from the obstacle of Step N compared with baseline. However, we found that the step over the obstacle generalized (Step N, P = 0.022) but not the step before it (Step N-1, P = 0.536; Fig. 4C). Generalization was also not evident for Lead TC (P = 0.123).

**DISCUSSION**

The objective of our study was to determine whether generalization patterns would be altered following different task elements, including stepping sequences and obstacle collisions, introduced during prism-adaptation walking tasks. Our results demonstrated that subjects are capable of rapidly adapting to a visuomotor perturbation to step onto floor targets in a precision-walking task and to step laterally over an obstacle in another walking task. The results of group 1, in conjunction with our previous study, support the notion that the specific stepping sequence in the adapted task can influence generalization. However, the results of groups 2 and 4 and to some extent group 3 demonstrate that the negative consequences and induced, perceived threat from repetitive collisions with the obstacle during adaptation greatly affect generalization. In fact, the aversive experience with obstacle collisions facilitated generalization. Thus the nature of the task likely masked the contribution from the stepping sequence in these groups.

**Generalization patterns.** In Alexander et al. (2011), we found that adapting to a rightward prism shift with a R-L stepping sequence to targets in the precision-walking task resulted in generalization of the left-foot placement (their Step N) in the nonadapted, obstacle-avoidance task. This R-L sequence meant that the left step required greater visually guided coordination than stepping to the first target, and there was a repetitive R-L stepping pattern throughout adaptation. We suggested that these were contributing factors for the generalization pattern. In the present study, when we had subjects adapt with an opposite L-R sequence (group 1), the right-foot placement (Step N) generalized in the nonadapted, obstacle-avoidance task. In both cases, the right- and left-foot placements demonstrated adaptation over the course of repeated trials with the prisms and subsequent aftereffects when the prisms were removed. Thus the lack of generalization in Step N-1 cannot be attributed to the absence of adaptation. Consequently, these results strongly support a contribution of stepping sequence, likely driven by specific proprioceptive feedback obtained during the precise lower-limb movements. This may represent a form of use-dependent learning (Diedrichsen et al. 2010; Huang et al. 2011; Verstynen and Sabes 2011; Wang and Müllers 2012), where the repetitive stepping sequence strengthened the adaptation and generalization of that step (or leg).

An association between the stepping sequence in the adapted task and the generalization pattern of group 2 was less clear,
and the results appear influenced by the nature of the task. Subjects in group 2, who adapted in the obstacle-avoidance task, demonstrated bilateral generalization in that both the left and right steps to the targets in the nonadapted, precision-walking task were shifted to the left (Fig. 4B). This is in contrast to Alexander et al. (2011), where only one step (with the left foot) generalized. The difference between these results may stem from the importance of the step immediately prior to stepping over the obstacle (i.e., Step N-1) in the adaptation phase. Indeed, errors in foot placement of this step increase the
likelihood of obstacle contact (Chou and Draganich 1998; Lajoie and Drew 2007). The L-R sequence in our obstacle-avoidance task required subjects to step over the obstacle starting from the left-hand side (see Fig. 1A). Thus in the initial adaptation trials, the rightward prismatic shift had the tendency to steer subjects toward the obstacle as they approached. Prism glasses are known to cause deviations in walking trajectory (Morton and Bastian 2004). In fact, nearly all subjects hit the obstacle on their first adaptation trial, and many continued to collide sporadically throughout the early portion of the adaptation phase. Consequently, Step N-1 was critical for successful obstacle avoidance in conjunction with Step N (which represents the step over the obstacle). In Alexander et al. (2011), however, subjects adapting to prisms during the obstacle-avoidance task stepped over the obstacle starting from the right-hand side with the left leg leading; therefore, they were shifted away from the obstacle initially. Whereas the majority of subjects in that experiment also collided with the obstacle (by typically stepping onto it rather than running into it, as in the present study), Step N-1 was less important, provided Step N underwent a greater adjustment to compensate.

These results led us to hypothesize that the negative consequences of an inappropriate Step N-1 (i.e., colliding with the obstacle) and subsequent perceived threat of collision can enhance the adaptation and generalization of this step. To test this idea, we had subjects of group 4 adapt to a leftward prism shift during an obstacle-avoidance task with a right-left stepping sequence, such that they would also deviate into the obstacle. This scenario was the mirror image of the task of group 2. It was also a modification of a task in our previous study, where a rightward prism shift was used and did not cause subjects to veer into the obstacle. In support of our hypothesis, we found that similar to group 2, subjects generalized both legs, rather than one leg, as seen in Alexander et al. (2011).

Perceived threat (or fear) can have a powerful influence on motor behavior (Adkin et al. 2000). Interestingly, Green et al. (2010) argue that the locomotor aftereffect, seen when walking onto a floor that had been moving previously (also known as the “broken escalator phenomenon”), is affected by arousal levels, which reflect fear, risk, or the perception of task difficulty. A significant evolutionary advantage of an aversive stimulus generating stronger adaptation and generalization is that it presumably aids in survival. The role of reward, risk, and aversive stimuli in adaptation and generalization during walking requires further investigation to determine the benefit on motor learning and rehabilitation.

The addition of a third target in the precision-walking task for group 3 and hence, a R-L-R stepping sequence, led to the left leg (representing Step N), but not the right leg, generalizing to the obstacle-avoidance task (Fig. 4C). This is despite the fact that both legs adapted in the precision-walking task, and this adaptation was stored, as evident from the presence of aftereffects (Fig. 2D). In Alexander et al. (2011), subjects who adapted to a two-target, precision-walking task with a similar R-L stepping sequence also demonstrated generalization of only the left leg (i.e., Step N). Although not supported, we hypothesized that the balanced R-L/R sequence of our three-target, precision-walking task would result in complete, bilateral generalization to the obstacle-avoidance task. If only one leg were to generalize, it might be expected that it would be the right one, since the R-L-R stepping sequence during the adaptation phase for group 3 required two visually guided steps with the right foot compared with only one with the left foot in each trial, resulting in twice the number of adaptation steps relative to the left. Increasing the amount of adaptation trials can alter subsequent performance. For example, Krakauer et al. (2005) showed that increasing the amount of adaptation trials during a visuomotor rotation reaching paradigm led to stronger consolidation, reflected by greater resistance to intervening counter-rotations prior to delayed relearning test blocks. However, a leftward aftereffect of Step N-1 (with the right foot), which is indicative of generalization, would have shifted the subject into the obstacle. The perceived threat involved in colliding with the obstacle may have overridden any effect of the repetitive right step to a target and/or the balanced R-L-L-R stepping sequence of the adapted task. Taken together, generalization patterns seem to rely heavily on the specific task being performed, drawing on the adapted information as long as safety is not compromised.

**Neural mechanisms.** Sensory prediction errors created by prism glasses or visuomotor rotations drive adaptation, a process that depends on the cerebellum (Shadmehr and Krakauer 2008; Tseng et al. 2007). Evidence of a role for the cerebellum in locomotor adaptation comes from studies using a split-belt treadmill. Damage to the cerebellum results in smaller aftereffects and generalization (Morton and Bastian 2004). Conversely, anodal transcranial direct-current stimulation applied to the cerebellum to increase excitability enhances the adaptation of spatial gait elements during split-belt treadmill walking, with the two belts set at different speeds (Jayaram et al. 2012).

Together with our previous study, our results suggest that the stepping sequence during locomotor prism adaptation contributes to the pattern of generalization to some extent. This implies a possible role for proprioceptive feedback generated during the adaptation. Proprioceptive feedback regarding the lower-limb state reaches the cerebellum through the dorsal spino-cerebellar tracts (Bosco and Poppele 2001). In cats, the majority of dorsal spino-cerebellar tract neurons discharge during both passive ipsilateral and contralateral limb movements (Poppele et al. 2003). In addition, Bosco et al. (2006) have found that these neurons encode the orientation angle of the limb axis and limb loading during active treadmill walking. Furthermore, neurons in the lateral cerebellum of the cat are known to discharge during a task that requires precision stepping on a series of horizontally placed ladder rungs (Marple-Horvat and Criado 1999). Therefore, a potential contribution of lower-limb proprioceptive feedback to the prism adaptation and subsequent generalization in our study likely occurs via the cerebellum.

Our results also point toward a role of threat or negative consequence in influencing generalization. Collision with the obstacle (an aversive stimulus) could set off a cascade of events in distinct brain regions, including the ventral tegmental area, dorsal and ventral striatum of the basal ganglia, and the amygdala (Bromberg-Martin et al. 2010; Jensen et al. 2003; Taub and Mintz 2010). It is also becoming clear that the cerebellum, particularly the vermis, is involved in the regulation of emotional behavior, including fear learning, through its connections with the amygdala and nucleus accumbens (Sacchetti et al. 2005, 2009). Collectively, error- and reward-driven processes may work in concert during our locomotor prism-adaptation tasks.

**Conclusions.** Taken together, our results suggest that the nature of the task (e.g., detailed stepping sequence and the importance of a step or negative consequences/perceived threat
associated with obstacle collisions) contributes to the generalization pattern, a concept that is supported by other types of walking and reaching adaptation studies. Our results raise the intriguing possibility that threat (or some form of negative consequence) can enhance adaptation and/or generalization. The roles of proprioceptive feedback and negative consequences associated with the task requirements in adaptation and generalization have important implications for rehabilitation. The nature of the task selected to induce adaptation must be chosen carefully as to produce the optimal generalization. The nature of the task selected to induce adaptation must be chosen carefully as to produce the optimal generalization pattern based on the goal of the patient or therapist. Further research is warranted, given the complexity of available tasks to use in training and the range of neurological and/or visual conditions affecting the sensorimotor system.

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