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Immediate and Latent Interlimb Transfer of Gait Stability Adaptation Following Repeated Exposure to Slips

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Abstract

The authors trained 21 participants by using blocked-and-mixed exposure to right-side slips and then caused them to slip unexpectedly on the untrained left side. Authors retested participants with a right slip and a left slip at 1 week, 2 weeks, 1 month, and 4 months. The authors found that preslip stability on the first untrained left slip improved and was significantly greater than that on the first right slip, which probably contributed to the reduction in incidence of falls from ~30% to ~10%. Postslip stability and base of support (BOS) slip velocity were similar to those on the first right slip and much lower than those on the last right slip. Increases in pre- and postslip stabilities and BOS slip velocity during the left slip led to reductions in backward balance loss (BLOB) from ~95% on initial left slip to ~60% and to ~25% on the 1st and 3rd retest sessions, respectively. In contrast, BLOB remained at a constant ~40% level on the right slip of the same retest sessions. The results indicate a partial immediate transfer and a possible latent transfer.

Keywords

balance loss; fall prevention; memory; motor program; plasticity

The capability of transferring motion state adaptations to changing environmental and task constraints after they have been learned or acquired could be fundamental to individuals' simultaneously maintaining the upright posture and ongoing mobility that are characteristic of human beings. Researchers consider such transfer the last of the three essential components of motor learning, with acquisition and retention being the first two (Schmidt & Lee, 1999). However, compared with what is known for skilled voluntary movements, few researchers have examined such transfer effects within the locomotor-posture control system that operates in the prevention of falls (Abeele & Bock, 2003; Bagesteiro & Sainburg, 2005; Dizio & Lackner, 1995; Morton, Lang, & Bastian, 2001; Shadmehr & Moussavi, 2000).

Researchers have often measured transfer or generalization as a percentage indicating the proportion of possible practice-related improvements in a context—for example, tasks (Earhart et al., 2002b) or effectors (limbs; Morton et al., 2001)—that is different from that in which these improvements were originally acquired (Schmidt & Lee, 1999). Studies of generalization of training effects within the posture and locomotor control system have provided evidence both for and against such transfer (Anstis, 1995; Earhart et al., 2001; Earhart et al., 2002b; Prokop, Berger, Zijlstra, & Dietz, 1995; Reynolds & Bronstein, 2004; van Hedel, Biedermann, Erni, & Dietz, 2002). Such mixed findings may have been related to the nature of the task, depending on whether (a) the task required skill acquisition, which involved establishing a new

motor program or modifying an existing motor program, or (b) the task merely required a sensory or perceptual adaptation, involving recalibration of specific sensory channels (Reynolds & Bronstein). For example, no interlimb transfer has been observed for the acquired adaptation of walking on either a split-belt treadmill or a rotating treadmill (Anstis, 1995; Prokop et al., 1995). Researchers have shown the observed after-effect of stepping onto a moving sled with the training limb to persist in only a few participants when they stepped on the sled with the transfer limb (Reynolds & Bronstein, 2004). In contrast, researchers have demonstrated inter-limb transfer for an obstacle avoidance task, where participants showed no difference in optimal foot clearance between the last training trial and the first transfer trial. In addition, participants also showed similar angle trajectories of the lower limb joints on both the training limb and the transfer limb during these trials (van Hedel et al., 2002).

Definite empirical evidence of interlimb transfer of adaptive training from exposure to support-surface perturbation during gait is still limited. Furthermore, researchers have not yet studied the effects of transfer of adaptive motor improvements resulting from repeated real-life slip-like perturbations. However, our recent studies have revealed that improvements in the control of postslip stability are essential to recovery (Bhatt, Wang, & Pai, 2006; Bhatt, Wening, & Pai, 2006). These improvements resulted mainly from the reactive control of the base of support (BOS) velocity under the training (slipping) limb after the onset of a slip. On the other hand, such control was closely associated with, and thus influenced by, feed-forward control-related proactive adjustments in stability and slipping-limb-landing kinematics measurable immediately before slip onset (Bhatt, Wening, et al., 2006). Pai, Wening, Runtz, Iqbal, and Pavol (2003) proposed that updating the internal representation of stability limits for preventing BLOB led to improved performance even under unpredictable environmental conditions (i.e., slip or no-slip). There is evidence that such learned or acquired control of stability during locomotion will be retained at least up to a period of several months (Bhatt, Wang, et al., 2006). Although as a group participants showed deterioration in performance in comparison to that at the end of the training session, possibly because of decay in motor memory, they nevertheless showed a significantly greater performance than that measured on the first slip of the training session on each retest over a 4-month period. It remains to be determined whether these training-related improvements can be transferred onto the contralateral untrained limb when it is exposed to an unexpected slip for the first time and whether such a generalization can be retained on longer term. Evidence either for or against such a transfer will undoubtedly increase our understanding of whether the central nervous system (CNS) uses and updates a single—therefore generalized—internal representation of stability limits or whether it has limb-specific representation (Morton et al., 2001; Sainburg & Wang, 2002; Wang & Sainburg, 2003). Furthermore, such understanding will also necessarily have practical implications in providing a rationale for designing new fall-prevention paradigms.

Our primary purpose in the present study was to determine whether participants could immediately transfer to the untrained left side the gait stability improvements that they acquired through repeated slip exposure on the training right side. We also wanted to investigate the potential long-term effect of such transfer by determining whether the immediate transfer could be retained as previously observed for the training side (Bhatt, Wang, et al., 2006). We wanted alternatively to discover whether motor training in combination with priming (single slip exposure on untrained side) could induce performance improvements on the untrained side over the long term. We trained participants by using a combination of initial blocked practice and subsequent random practice, consisting of 24 slips and 13 nonslips (total = 37), as previously reported (Bhatt, Wang, et al., 2006). Once our participants had become well adapted to the training conditions, a slip was introduced unexpectedly on the untrained left limb. The participants were retested subsequently at 1-week (1wk), 2-week (2wk), 1-month (1mo), and 4-month (4mo) intervals.

We expected that participants would not only exhibit a significant immediate interlimb transfer of the training effect but also retain such effects during the 4-month period. Specifically, we first hypothesized that participants would demonstrate better performance (greater pre- and postslip stabilities and lower incidence of falls and balance loss) on the first unexpected slip on the left side (L-1) than that which they demonstrated on the first right slip (R-1). In addition, we expected that participants would exhibit a *complete* transfer, demonstrated by a similar performance on the first untrained left slip, exactly equivalent to that of the preceding last slip exposure on the trained right side (R-24). Second, we hypothesized that the immediate interlimb transfer of the training effect would persist throughout the retest sessions. Therefore, we expected that performance on the left slips of the retest sessions would be significantly better than performance on R-1 although it could be inferior to that on L-1, and we would attribute this to the motor-memory decay. Furthermore, we expected that on the left slips of the retest sessions, participants would exhibit a performance similar to that demonstrated on the preceding right side slip of that session, which would remain constant over the retests (Bhatt, Wang, et al., 2006). Alternatively, we hypothesized that even if participants demonstrated an absence of an immediate transfer, motor training in combination with priming from the initial left slip would facilitate a latent transfer in performance on the untrained left side during the 4-month period. Specifically, in contrast to the performance on the right training side that remained constant during the retests (Bhatt, Wang, et al., 2006), we expected an improvement on the untrained side with each retest session, with performance on each retest being significantly better than performances measured on both R-1 and L-1. In addition, we expected that with such improvement on the untrained side, the difference in measured performance between the trained and untrained sides would diminish during the retests.

Method

Participants

The participants were 21 healthy young adults (age = 25.4 ± 5.9 years; 12 men, 9 women) whom we screened for exclusionary factors such as neurological, musculoskeletal, cardiopulmonary, and other systemic disorders; and selected drug use. All participants completed the three retest sessions with one slip on each of the training side (right, R-1wk, R-2wk, and R-1mo) and the untrained, transfer side (left, L-1wk, L-2wk, and L-1mo), but only 16 participants completed the last retest session (R-4mo and L-4mo). The most common reason for a participant's drop-out was simply moving to another city. The test of leg dominance that we conducted by using a set of four simple tasks (Beling, Wolfe, Allen, & Boyle, 1998), revealed all participants to be right dominant. Prior to participation, all participants gave informed consent as approved by the Institutional Review Board.

Experimental Setup

We placed two sliding devices side by side to enable the inducing of the bilateral slips. Each was capable of inducing a slip with a low-friction, nonmotorized movable top plate (65×30 cm, 2.7 kg) mounted on a frame with linear bearings that were 2.5 m long, which was then bolted onto two force platforms (OR6-5-1000, AMTI, Newton, MA; Bhatt, Wening, & Pai, 2005; Yang & Pai, 2007). These devices were locked and embedded in a 7-m walkway with stationary decoy platforms around the walkway (Figure 1). The actual coefficient of friction that we obtained from measurements of the ground reaction forces (GRF) was less than 0.05.

We induced slips by a computer-controlled release mechanism that unlocked one of the movable platforms at the beginning of each trial without the knowledge of the participant. Once released, the movable platforms were free to slide on the linear bearings for up to a maximum travel distance of 150 cm on the right and 90 cm on the left before locking into the end position. A computer program written in LabView (National Instruments Inc., Austin, TX) was used for

online monitoring of the GRF and generation of the lock-release signal. The participants wore their own athletic shoes and a full-body safety harness attached at the shoulders by a pair of shock-absorbing dynamic ropes to a manually driven trolley on a ceiling-mounted I beam (Figure 1). We adjusted the rope lengths so that the participants' knees could not touch the surface of the floor on suspension.

Motor Skill Acquisition

In the initial session, we told the participants that they would be walking a block of trials at their preferred regular speed and in their ordinary manner and that they “might or might not be slipped.” They were also told that in case of a slip, they should try to recover their balance and continue walking. At the beginning of the experiment, the participants performed 10 regular walking trials at their self-selected speeds. Without revealing the purpose, the experimenter would adjust each participant's starting position so that his future slipping (right) foot would land entirely on the movable plate at touchdown. All participants were able to take at least 3 steps before stepping onto the movable platform. Similarly, the participants were able to take at least 6 steps after passing the device. Thus, the participants walked at least 10 steps for each trial. On the 11th trial, a slip was induced without prior warning or practice. The participants were not aware of which trial or where on the walkway the slip would occur. After exposure to the first unexpected slip, the participants were told to continue walking at the same speed as that of the previous trial and that they “might or might not be exposed to slipping again.” The training paradigm included 37 trials, each consisting of a block of eight repeated slips, a block of 3 nonslip trials, another block of eight slips, followed by the second block of 3 nonslip trials and a final block of 15 mixed (8 slip and 7 nonslip) trials. The randomly selected sequence of the mixed block was consistent for each participant (Bhatt, Wang, et al., 2006).

Transfer

After the motor skill acquisition, we gave the participants a rest break for about 5–10 min while the experimenter changed the positions of the movable plates. The participants faced away from the walkway and were engaged in conversation with another experimenter while the change was made without their knowledge. This adjustment was made to ensure that the heel-strike landing of the untrained limb (left) was on the left plate to induce the transfer-side slip. The participants were then told that they were resuming the experiment. They walked for five to eight regular walking trials followed by an unexpected slip induced on the untrained left side. Only one left slip was induced on the first session, because we did not want to generate any motor training effect on the left side that could influence the transfer effect on the retest sessions more profoundly than any that might result merely from the single trial.

This single initial session preceded four retest sessions at intervals of 1 week, 2 weeks, 1 month, and 4 months. The exact return date was within 1 or 2 days beyond or short of a week in the first two retest sessions and 3–5 days beyond or short of a month in the latter two retest sessions. For each retest session, the setup and instructions were identical to those of the initial session. The protocol consisted of only one unannounced slip on the untrained right side induced after 8–13 regular walking trials. After this, the participants were given a short break to enable our adjustment of the plates, followed by another five to eight unperturbed walking trials with the left limb landing on the left movable plate and one unannounced slip induced on the untrained left side at the end. We adopted the random number of walking trials to prevent the participants from predicting the trial during which a slip would occur.

Data Collection and Reduction

We attached a set of 24 full-body light-reflective markers to the bilateral upper and lower extremities and the torso, and we attached 1 marker to each movable platform. Marker coordinates were recorded at 120 Hz by using a six-camera motion capture system (Motion

Analysis Corporation, Santa Rosa, CA). Marker displacement data were low-pass filtered at marker-specific optimal cut-off frequencies (range = 4.5–9 Hz) by using a recursive second-order Butterworth Filter (Winter, 2005). Force plate, harness load cell data, and trigger-release onset signal were collected at 600 Hz by using a 64-channel, 16-bit analog-to-digital (A/D) converter. The ground reaction force and motion data were time synchronized at the time of data collection.

Analysis of Gait Stability

We computed the center of mass (COM) position and its velocity from the kinematic data by using known gender-dependent segmental parameter information in a 13-segment representation of the body (de Leva, 1996). The position of the COM in the anteroposterior direction was expressed relative to the rear of the BOS ($\dot{X}_{COM/BOS}$) of the foot most recent to touchdown (i.e., the heel of the sliding foot for slip onset) and normalized to foot length. The COM velocity in the anteroposterior direction was expressed relative to the velocity of the BOS ($\dot{X}_{COM/BOS}$) and normalized as a dimensionless fraction of $\sqrt{g \times h}$ (McMahon, 1984), where g is the acceleration due to gravity and h is the height of the participant.

We assessed stability through comparison of the COM state with the previously published threshold values for BLOB under slip conditions (Pai & Iqbal, 1999). *Stability* was defined as the shortest distance between this predicted boundary for BLOB and that of the instantaneous COM state (Bhatt et al., 2005; Pai et al., 2003). The model simulation predicts that BLOB must occur for COM states below the threshold (i.e., stability < 0). BLOB should not occur when the stability measure is above the predicted value (i.e., stability > 0). Thus, more positive values indicate greater stability against BLOB. Conversely, a COM state farther below the threshold represents an increased likelihood of BLOB under slipping conditions (Bhatt et al., 2005; Pai et al.).

We restricted analysis to the anteroposterior direction. The instances of step liftoff and touchdown were identified from the vertical ground reaction forces. These values were identified from foot kinematic data, if the touchdown occurred outside of the force plates or if both feet were on the same force plate at an instance. Preslip stability was measured and noted at touchdown of the slipping limb. Postslip stability was recorded at liftoff of the contralateral limb. To further understand the contributing factors for adaptive changes in the COM stability, on the basis of the findings from the previous studies (Bhatt & Pai, 2005; Bhatt, Wening, et al., 2006), we analyzed the correlative changes in the BOS velocity and preslip foot angle. The BOS velocity was obtained from the heel marker of the slipping limb at the liftoff of the contralateral limb following the slip. Because there was no relative movement between the foot and the movable plate once it landed on the plate, the movable plate and heel (BOS) velocity profiles were identical up to the point when the foot was in contact with the plate. *Foot angle* was obtained as the angle between the foot segment (line joining the heel and fifth metatarsal) and the horizontal plane immediately prior to touchdown of the slipping limb.

The outcome of slip was classified as a *fall* if the average force on the safety harness exceeded 4.5% of body weight over any 1-s period after the slip onset or if the hip midpoint descended below 15% of minimum body height during normal walking trials. Otherwise, we classified the trial as a *recovery*. Each fall was verified with harness load-cell and video recordings of performance. When the contralateral limb landed posterior to the sliding heel with negative values in postslip step length during the slip, the recovery trials were classified as *loss of balance* trials with protective stepping. Conversely, trials with the contralateral limb landing anterior to the sliding heel and positive postslip step length were classified as *no loss of balance* trials, in which protective stepping was unnecessary, and forward progression was not disrupted (Bhatt et al., 2005).

Statistics

To test our first hypothesis, we performed the Cochran's Q test and follow-up Wilcoxon Signed Ranks tests on three trials from the initial session: the first and last right slips (R-1 and R-24) and the first left slip (L-1). The outcome for each participant on each trial was determined and categorized as either a fall (value = 0) or a recovery (value = 1). Each recovery trial was further categorized as a balance loss (value = 0) or as no loss of balance (value = 1) and analyzed as above. Similarly, one-way repeated measures analyses of variance (ANOVAs) followed by planned paired *t* tests were performed on these trials with stability (pre- and postslip) and BOS control (foot angle at preslip touchdown of the slipping limb and BOS velocity at postslip liftoff of the contralateral limb) as dependent measures.

We defined *complete transfer* as a lack of demonstrated statistical difference between the first left slip and the last right slip. *Partial transfer* was defined as the detection of a significantly greater value between the first right slip and the first left slip, in the measured variable; however, lower values on first left slip in comparison with those for the last right slip indicated an absence of complete transfer. To rule out any baseline differences, a paired *t* test was performed on preslip stability on the right and left limbs from the regular walking trial collected prior to the first unexpected slip on the right side. Similarly, to detect a transfer effect, paired *t* tests were performed on preslip stability at left-limb touchdown on the regular walking trial before and after motor training on the right side.

For the second hypothesis, we performed the Cochran's Q test with planned Wilcoxon Signed Ranks tests to test for changes in incidence of balance loss and falls across the first left slip trial (L-1) of the initial session and the four left slip trials of the retest sessions (L-1wk, L-2wk, L-1mo, L-4mo). To test changes in stability and BOS control across these trials, the one-way repeated measures ANOVAs with planned comparisons (between consecutive trials) were performed. Planned comparisons were made between R-1 and each of the retest slips on the untrained side. The Wilcoxon Signed Ranks test and paired *t* tests were respectively performed on incidence of balance loss and on stability and BOS control, between the left and right slips on each of the retest sessions (1wk, 2wk, 1mo, and 4mo). Similar analyses were performed to verify the previously established changes across right side slips on the retest sessions and included the first slip of the initial session and the four right slips of the retests (R-1wk, R-2wk, R-1mo, R-4mo).

We report absolute *p* values between .05 and .001 for the planned comparisons. A significance level of .05 was used for all the analyses. Analyses were performed by using SPSS (Chicago, IL).

Results

Immediate Transfer

All participants were able to adapt to the repeated slip exposure and prevent incidence of falls and BLOB. The results indicated a main effect of fall incidence, $Q(2, 21) = 13.00, p < .002$, with participants being able to successfully and significantly reduce incidence of falls on the untrained side from 28.5% on the first right slip to 0% on the last right slip, $p < .001$. Further, the participants who fell on the first right slip were successful in significantly reducing the incidence of falls on the untrained side to 9.5%, $p = .046$, between the first right slip and the left slip, $p > .05$ between first left slip and the last right slip. The results also indicated a significant main effect of balance loss incidence, $Q(2, 21) = 40.91, p < .001$. The participants reduced their incidence of BLOB from 100% on the first right slip to 0% on the last right slip, $p < .001$; however, all but 1 participant experienced a BLOB when first exposed to the

unexpected left slip, $p > .05$ between first right and left slips, $p < .001$ between last right and first left slips (Figure 2—Initial Session, Hypothesis 1 [H_1]).

Examination of preslip stability clearly indicated a partial transfer effect. There was a significant main effect of trial on both preslip stability, $F(2, 40) = 15.84$, $p < .001$, and postslip stability, $F(2, 40) = 86.77$, $p < .001$. All participants were able to improve control of stability with the repeated slip exposure, with both pre- and postslip stability being significantly greater on the last slip trial in comparison with the first slip trial, $p < .001$ for both. These improvements in preslip stability partially transferred to the untrained side. Preslip stability on the first left slip improved and was significantly greater than that on the first right slip, $p = .001$. However, it remained lower than that of the last, training, right slip, $p = .045$ (Figure 3A—Initial Session, H_1). However, postslip stability showed a slight trend of improvement on the first left slip: It was not significantly different from that on the first right slip, $p > .05$, and it was significantly lower than that of the last right slip, $p < .001$ (Figure 3B—Initial Session, H_1). There was no baseline difference in preslip stability in the regular walking trials between the right limb and the left limb before motor training, $p > .01$ (Figure 1, Reg-1). However, after motor training, preslip stabilities at left-limb touchdown on the first left slip and on the preceding regular walking trial (Reg-2) were significantly higher than stability at the same instant on the regular walking trial before motor training (Figure 2). There was no difference in preslip stability at left-limb touchdown between the first left slip and its preceding regular walking trial (Figure 2, $p > .05$).

The changes in postslip stability were mostly attributable to changes in the control of BOS slipping velocity, main-effect $F(2, 40) = 74.52$, $p < .001$, which in turn was influenced by preslip control of limb landing, main-effect foot-angle $F(2, 40) = 10.32$, $p < .001$. The BOS velocity at liftoff of the trailing limb showed a notable adaptive improvement; it diminished significantly from the first right slips to the last right slips, $p < .001$. Such improvement did not significantly transfer to the untrained side. The BOS velocity on first left slip was not considerably different from that on the first right slip, $p > .05$, and was significantly greater than that on the last right slip, $p < .001$ (Figure 4A—Initial Session, H_1). As a result of the adaptive training, the slipping limb control at preslip touchdown was associated with a significantly lower foot angle (more flat-footed landing) from the first right slip to the last right slip, $p < .001$. However, the preslip foot landing angle on the first left slip was not strikingly different from that on the first right slip, $p > .05$ for both comparisons, and it was significantly higher (less flat-footed) than that on the last right slip, $p < .001$ (Figure 4B—Initial Session, H_1).

Transfer on Retest Sessions

There was a significant reduction in fall incidence in the retest sessions with none of the participants exhibiting a fall during any of the retest sessions. This reduction was the case on both the right and left slips. Overall, there was an improvement in incidence of BLOB on the left slips of the retest sessions in comparison with that on the initial session, main-effect $Q(4, 16) = 24.63$, $p < .001$. In contrast, participants showed significant persistence of the acquired training effects on the right slips of the retests, main-effect $Q(4, 16) = 23.24$, $p < .001$. Approximately 40% of the participants experienced a balance loss on the right slips during the first through fourth sessions in comparison with 100% balance loss on the first right slip, $p < .001$ for all comparisons. Yet, there was no notable change in the incidence of balance loss among the four retest sessions, $p > .05$. However, the incidence of balance loss on the left slip reduced from 95% on the first left slip of the initial session to 57% on the first retest session at the 1-week interval, $p < .01$. This was significantly lower than that measured on the first right slip of the initial session as well, $p < .01$. However, the balance loss incidence still remained higher than that on the corresponding right slip of the same retest session (41%), p

= .05. Balance loss incidence on the left retest slips at 2 weeks, 1 month, and 4 months remained lower than that on both the first left slip and first right slip of the initial session, $p < .01$. There was a slight further reduction in balance loss incidence on the left slips from the first retest session to the second retest session, $p > .05$, which was sufficient to affect the overall trend by which the difference between the left and right retest slips diminished on this second retest session at the 2-week interval, $p > .05$. A significant reduction in balance loss incidence was accomplished in the third retest session, $p = .04$ between 2 weeks and 1 month, to such an extent that the balance loss incidence was slightly lower on the left slip than on the preceding right slip of that session, $p = .05$. Incidence of balance loss on the left slip showed a sharp rise during the fourth retest session at the 4-month interval in comparison with the previous 1-month retest session, $p = .04$, with no significant difference between the left and right retest slips in this session, $p > .05$ (Figure 2—Hypothesis 2 [H_2]).

As with the incidence of loss of balance, there were improvements in preslip stability on the untrained left side in the period from the initial training session slip through that of the third retest slip, main-effect $F(4, 60) = 6.725$, $p < .001$. In contrast, participants showed significant persistence of training effects on the right slips of the retests, with no notable change in preslip stability among the four retest sessions, $p < .05$ for all comparisons. However, the significantly greater stability on all four retests in comparison with that for the first right slip ($p < .01$ for all comparisons) explains the significant main-effect, $F(4, 60) = 11.33$, $p < .001$. Preslip stability improved on the left slip of the first retest at the 1-week interval; it was significantly greater than that on the first left and first right slips of the initial session, $p = .01$ and $p < .01$, respectively, but it did not differ from the preceding right slip of that session. Preslip stability remained greater at the 2-week, 1-month, and 4-month retests in comparison with both the first left slip and the first right slip of the initial session, $p < .05$ for all comparisons. There was no significant change from the first retest session to the second retest session, $p > .05$ between 1 week and 2 weeks, and no difference between the left and right slips of the second retest session. However, preslip stability on the left side increased in the third retest session, $p = 0.02$ between 2 weeks and 1 month, so that stability on the left slip exceeded that of the preceding right slip of that session. There were no further changes on the fourth retest at the 4-month interval, $p > .05$ between 1 month and 4 months, with no difference between the left and right slips on this session (Figure 3A— H_2).

The postslip stability during the left slip also notably improved on the retest sessions, main-effect $F(4, 60) = 25.55$, $p < .001$. In contrast, participants showed significant persistence of training effects on the right slip of the retests, main-effect $F(4, 60) = 11.33$, $p < .001$, with significantly greater stability on all four retests in comparison with the first right slip, $p < .01$ for all comparisons; and no notable change among the four retest sessions, $p > .05$ for all comparisons. Postslip stability was significantly higher on the first retest session at the 1-week interval in comparison with that on both the left slip and the first right slip of the initial session, $p < .001$ for both. Nevertheless, it was significantly lower than the preceding right slip of the same retest session, $p < .01$. Postslip stability on the retests at 2 weeks, 1 month, and 4 months remained lower than that on both the first left slip and first right slip of the initial session, $p < .001$. The postslip stability on the left slips continued to improve between the first and second retest sessions, $p < .01$ between 1 week and 2 weeks, so that the difference between the right and left slips on the same retest session at the 2-week interval diminished, $p > .05$. This improvement in postslip stability on the left slips reached a plateau on the third retest session at the 1-month interval, $p > .05$ between 2 weeks and 1 month. Similarly, the measured results between the right and left slips at the 1-month interval remained indistinguishable, $p > .05$. The postslip stability on the left slip showed a decrease on the fourth retest session at the 4-month interval, $p = .02$ between 1 month and 4 months, being slightly lower than that measured on the preceding right slip of this session, $p = .03$ (Figure 3B— H_2).

In a manner similar to that of the aforementioned results for postslip stability, the postslip BOS velocity improved on the retest sessions, main-effect $F(4, 60) = 22.64, p < .001$. In contrast, the training effect persisted on the right side retests, main-effect $F(4, 60) = 22.75, p < .001$, with a significantly lower BOS velocity on all four retests in comparison with the first right slip, $p < .01$ for all comparisons, and no significant change among the four retest sessions, $p > .05$ for all comparisons. Although the postslip BOS velocity was considerably lower on all four retest sessions in comparison with that on both the first left slip and first right slips of the initial session, $p < .01$ for all comparisons, it continued to show a change over the retest sessions. The BOS velocity improved from the first retest session to the second retest session, $p = .02$ between 1 and 2 weeks, and improved slightly on the third retest session, $p > .05$ between 2 weeks and 1 month; but it deteriorated by the fourth retest, $p < .01$ between 1 and 4 months. The BOS velocity remained higher on the left slip of the first retest session in comparison with the preceding right slip of that session, $p < .05$; however, this difference diminished with no significant variation between the right and left slips on any of the other retest sessions, $p > .05$ for all comparisons (Figure 4A— H_2). The observed decreases in the BOS slipping velocity came with improvements in preslip foot landing angle on the left slips of the retest sessions, main-effect-foot $F(4, 60) = 2.59, p < .01$. The changes on the training side were constant, main-effect-foot $F(4, 60) = 5.31, p < .05$, with significantly lower foot angles on all the retest right slips in comparison with the first right slip, $p < .05$, and there were no session-to-session differences, $p > .05$ for all comparisons. The landing of the slipping foot was more flat-footed on the left slips of the retest sessions in comparison with both the first left slip and the first right slip of the initial session, $p < .05$ for all comparisons. Although the foot angle showed a trend of improvement on the left slips of the retest sessions, no significant differences were detected between consecutive retest sessions, $p > 0.05$ for all. The foot angle on left slip of the first retest was significantly greater (less flat-footed) than that on the preceding right slip of that session, $p < .05$. This difference disappeared on the second and third retests, $p > .05$, but reappeared on the fourth retest session at the 4-month interval, $p < .05$ (Figure 4B— H_2).

Discussion

Our results indicated that the CNS was able to transfer, at least partially, the increased control in stability acquired through blocked-and-mixed motor training to the opposite limb immediately. Such partial transfer was evident in the improvement of the preslip stability. Our results also clearly indicated that although such interlimb transfer was insufficient to significantly reduce the participant's need to take a backward recovery step, it was adequate to reduce the incidence of actual falls when we unexpectedly induced slipping on the untrained, contralateral side. Notably, the blocked-and-mixed motor training may also have yielded a latent transfer effect that was readily detectable on the retest sessions. Continuous improvements were evident on the untrained side during these sessions and peaked 1 month later. However, these improvements were unmatched on the training side, where the overall incidence of balance loss was mostly unchanged from session to session. This apparent partial transfer that was immediately evident in preslip stability and the longer-term graded improvements together suggest that the CNS may rely on a generalized motor program that requires adequate updating of limb-specific somatosensory for the control of BOS slip velocity. This program in turn determines to a great extent the COM state stability and hence the balance recovery after a slip during gait.

Immediate Transfer

Our results supported only partially the first hypothesis of complete and immediate interlimb transfer of improvements in stability and incidence of balance loss. Participants showed a greater preslip stability on the untrained, transfer (left) side in comparison with that on the first slip of the training (right) side, and in comparison with that on the same untrained side on the

baseline walking trial before the blocked-and-mixed motor training. However, there was no significant difference in postslip stability and incidence of balance loss between the first left and right slips, and we noted a much lower postslip stability and higher losses of balance on the untrained side slip in comparison with the last training slip. The preslip stability analyses appeared to have a greater effect on fall incidence than the outcome measurement of BLOB. The improvement in preslip stability could have been sufficient to enable participants to prevent a fall but not sufficient to reach the threshold to prevent BLOB.

Results from our previous studies (Bhatt & Pai, 2005; Bhatt, Wening, et al., 2006) have indicated that participants better retained the feed-forward acquired improvements in preslip stability in comparison with postslip stability. The transfer of the feed-forward controlled improvement in preslip stability was planned, and it was by itself probably insufficient to improve, ad hoc, the reactive postslip stability by exceeding the threshold against BLOB. Nevertheless, such improvement in stability with feed-forward control could have enabled participants to exhibit successful backward stepping to avert actual falls (Pai et al., 2003), and that possibility was indicated by a reduced incidence of falls on the first left slip in comparison with the first right slip. Feed-forward adjustments can also influence landing characteristics of the gait pattern (i.e., limb control), which would then affect postslip reactive control of the BOS velocity and hence postslip stability (Bhatt, Wening, et al., 2006). However, our results indicated a significant improvement in preslip foot angle and the BOS velocity from the first training trial to the last training trial; this improvement did not significantly transfer to the contralateral side during the first unexpected slip, unlike that in preslip stability. Overall improvement in stability (pre- and postslip) failed to reach a threshold level that could completely eliminate the need to take a backward step. Therefore the number of participants who experienced BLOB in the first left slip was nearly equal to the number of participants who experienced BLOB in the first right slip.

Researchers examining limb-specific transfer within the posture and locomotor control system have produced mixed findings (Lam & Dietz, 2004; Reynolds & Bronstein, 2004; van Hedel et al., 2002). It is always difficult to make direct comparisons between findings of different studies, partly because of the differences in the task being trained and the skills being acquired. We discuss the probable factors that explain differences between those studies that showed positive interlimb transfer within the locomotor-posture control system and our own. First, it is likely that the outcome on a given trial depends on individuals' expectation of an upcoming event, which in turn might depend on their most recent experience. The left slip in our study was indeed unexpected, with participants not knowing that they would be slipped on the left side after the intensive training on the right. For example, van Hedel et al. (2002) noted positive interlimb transfer during an obstacle avoidance task, in which participants exhibited limb trajectories on the transfer side that were similar to those on the trained side. In the aforementioned study, participants were made aware of the upcoming obstacle with a warning signal, so they knew that the leading leg had been changed. Thus, although the participants could not see the obstacle, they had accurate knowledge of the change in condition. Reynolds and Bronstein demonstrated a transfer of the aftereffect of the acquired adaptation to a moving platform perturbation, when the participants stepped on the platform with the contralateral untrained limb. Participants in that study were also consciously aware of the change in the limb used to step on the platform to induce perturbation. Therefore, the transfer effects could most likely have been differently influenced by expectation of the upcoming slip (i.e., participants expecting a right slip instead of a left slip). Thus, the possibility that there would be a greater likelihood of transfer to the untrained side if participants in our study had accurate knowledge of the upcoming left slip cannot be ruled out. However, the effect of such cognitive awareness, although it could conceivably facilitate transfer, may not be able to substitute for the motor training effect.

The other factor contributing to a positive interlimb transfer effect may relate to the explicit acoustic feedback that indicates knowledge of performance during the training (van Hedel et al., 2002). In contrast, our training was dependent only on error of implicit stimulus-related sensory feedback. We postulated that participants could use such perturbation-related sensory feedback information during the initial acquisition period to update the internal representation of stability limits (Bhatt & Pai, 2005; Bhatt, Wening, et al., 2006). This factor would be particularly noteworthy because the two limbs adapt in different ways depending on the limb-specific proprioceptive information received regarding the dynamics of the movement (Anstis, 1995; Earhart et al., 2002a). Successful recovery is directly related to reducing the perturbation intensity by reducing the need for the braking impulse and providing vertical limb support during slip (Bhatt, Wening, et al., 2006; Pavol & Pai, 2007), whereas the contralateral limb is responsible for controlling the propulsive impulse prior to its liftoff after slip onset (Bhatt et al., 2005). Because the two limbs must adapt to serve different, potentially competing goals and functions of increasing propulsion while reducing braking impulse, without any explicit information about upcoming perturbation or lacking actual proprioceptive experience, the CNS may not be able to achieve a complete interlimb transfer of the acquired sensory information.

The presence of only a partial interlimb transfer of training effect in the present study supports the postulate that limited interhemispheric communication (Sainburg & Wang, 2002) could have prevented the contralateral controllers in the CNS from accessing the acquired limb-specific information for reactive control of the BOS slip velocity promptly after an unexpected slip. The limited communication probably results from the bias induced by the cognitive centers predicting the probability of upcoming slip. Because the absolute COM motion undergoes little change from that of regular gait following a slip (Bhatt, Wening, et al., 2006), the control of the BOS velocity would largely dictate the outcome of the slip-induced change in the relative motion between the COM and BOS, which is a key to the control of the COM state stability and hence to overall recovery from a slip. This prospect may have been especially useful when the participants did not have preexisting awareness or any precedent of using such information, as in the present study. Likewise, we postulate that such limitations may also result from the inability of the individuals' CNS to apply the acquired sensory information to a different (contralateral) effector system (Sainburg & Wang), again with no prior knowledge of the need to use that effector system.

Transfer on Retest Sessions

Our results supported our second hypothesis of a latent transfer on the untrained side during the retest sessions. We saw significant improvements in both pre- and postslip stabilities and incidence of falls and balance loss on the left slip (untrained side) of the first retest session in comparison with the first right slip (training side) and the left slip of the initial session. Despite this improvement, postslip stability on the left slip of the first retest was lower, and incidence of balance loss was higher, in comparison with the preceding right slip of that session. The trend of continuous improvements on the retest sessions, which peaked on the third retest, was similar to that previously observed on the training side in the first slipping block of the motor training sessions (Bhatt, Wang, et al., 2006; Bhatt, Wening, et al., 2006). We must note that such a gain could not be held over the long term, resulting in deterioration of performance on the fourth retest at the 4-month interval.

Our previous studies have suggested that individuals achieve improvements in stability and incidence of balance loss as results of a shift from reliance on sensory feedback information to a more dominant feed-forward control-related change in gait pattern and limb control, influencing reactive control of BOS perturbation intensity (Bhatt, Wening, et al., 2006; Bhatt, Wang, et al., 2006). Accordingly, in the present study, a reduction in preslip foot angle and postslip BOS velocity on the retest sessions paralleled the improvements in stability on the

retest sessions. We must note that although foot angle at touchdown of the slipping limb, which can significantly influence the BOS control (Bhatt, Wening, et al., 2006; Cham & Redfern, 2002), did not show strong session-to-session changes such as those of BOS velocity, other factors such as knee angle or heel velocity at touchdown could have contributed to improvements in the reactive control of the BOS velocity (Bhatt, Wening, et al., 2006; Lockhart, Woldstad, & Smith, 2003).

We postulate that the likelihood of transfer is higher if the task requires the particular sensorimotor systems involved to share memory sources rather than developing independent limb-specific memory resources (Wang & Sainburg, 2003). The partial transfer in the present study suggests that the CNS has the ability to apply the acquired information to a new effector system (Sainburg & Wang, 2002) to such an extent that incidence of falls can in fact be effectively reduced. The latent transfer in the first through third retests also supports the notion of downloading and updating information from the training side and applying it to the contralateral effector system. Such information probably enabled the generalized motor program for the control of the BOS velocity to be updated for dealing with exposure to the potential slippery environment in future. We must note that the updated internal representation of stability control, downloaded with the relatively few repetitions, was probably in a labile state and not as strongly consolidated (Shadmehr & Holcomb, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003) as that of the untrained side, which was formed with extensive training using principles of block and random practice and overlearning. Consequently, it was prone to interference and fading (Walker et al.), which explains the deterioration in performance over the longer 3-month interval from the 1-month retests to the 4-month retests. The implicit learning of an order effect of the left slip's always occurring after the training side right slip could have further aided the transfer effect, allowing participants to better anticipate the occurrence of a slip on the untrained side by the third retest session, thus better explaining the peaking of performance on this session.

As an alternative to the aforementioned postulate suggesting a download of information from the untrained side, we postulate that an add-on effect that was created with each single slip exposure on the left side enabled the untrained limb to independently update its internal representation for BOS velocity and stability control through the process of sensorimotor adaptation. Such a process could have improved stability beyond the threshold for BLOB, resulting in significantly improved performance. Our previous results on adaptation to repeated slips have indicated that most adaptive changes occurred in merely one or two trials with a reduction in loss of balance incidence from 100% to 20% by about the third slip in a repeated slip block (Bhatt, Wang, et al., 2006, Bhatt, Wening, et al., 2006). In other words, a single slip by itself may indeed yield noticeable training effect. Such a reduction is similar to that in the retest sessions, each with only a single slip in the present study. This possibility needs further investigation, because if subsequent research proves it to be as we postulate, the intermittently added single-slip exposure yielding such significant long-term effects would be of great practical importance. However, the fact that the single slip exposure on identical retest sessions failed to generate any add-on effect (in terms of increments in performance on the training side) strongly supports the possibility of a latent transfer effect on the untrained left side.

In summary, the present findings indicated that the nervous system was able to partially transfer immediately and more completely transfer later the acquired training-related skills that reduced the incidence of falls and BLOB on the contralateral untrained side. Our results also indicated the ability of the CNS to generalize acquired information to the contralateral side, enabling acquisition and retention of skill-related information for an extended period of time. We suggest that clinical intervention could use the properties of interlimb transfer to reduce the need for or the intensity of bilateral training to improve its efficiency.

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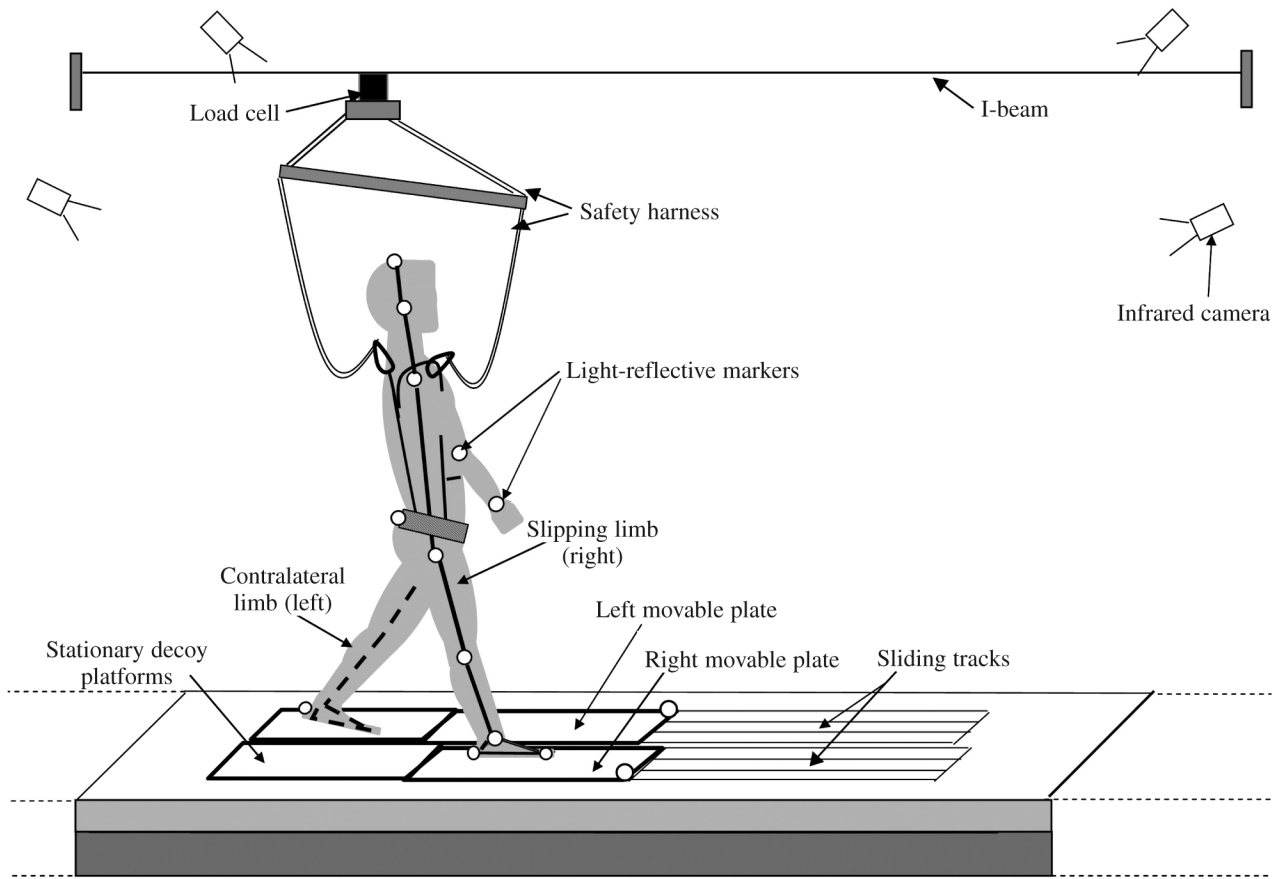


FIGURE 1.

Schematic diagram of the experimental setup with approximate position of the participant at touchdown of the training (right limb). Unfilled circles indicate positions of passive-reflective markers on the body segments and movable platform. Solid and dotted lines joining the markers represent the body-segment links used to calculate the whole-body center of mass. The I-beam and safety harness system were much higher than shown (9 m above the ground). The I-beam extended the length of the 7-m walkway. The two sliding devices were placed side by side to enable inducing the bilateral slips. The low-friction, nonmotorized movable top plates were mounted on a frame with linear bearings. Once released, the movable platforms were free to slide along the track on the linear bearings. These devices were locked and embedded in a 7-m walkway and made less apparent by the stationary decoy platforms.

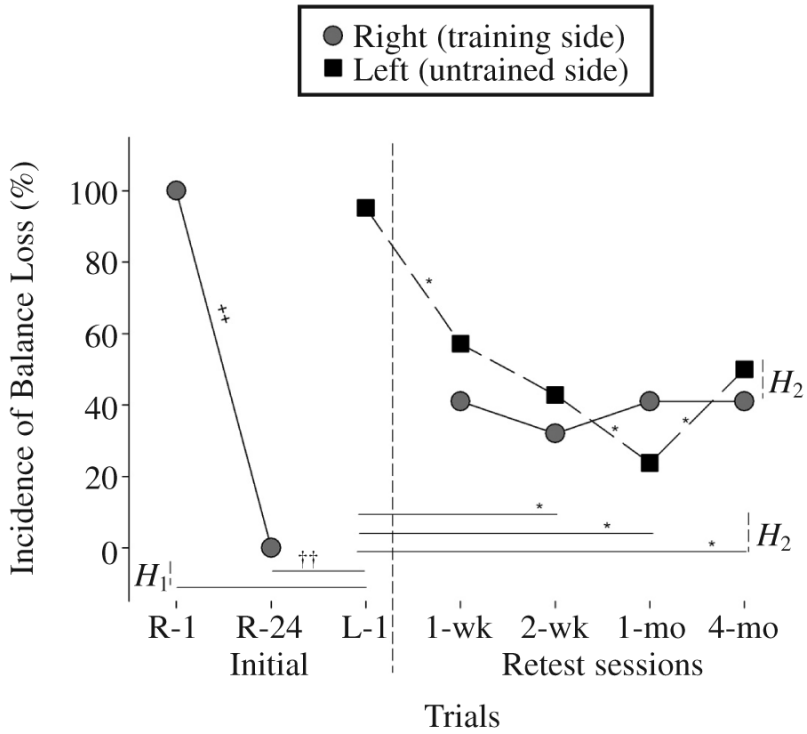


FIGURE 2. Incidence of balance loss for the first and last training (right) side slips (R-1 and R-24, respectively) and the slip on the untrained (left) side slip (L-1) from the initial session (Hypothesis 1– H_1). Also shown are the slip trials from the right and left sides for the 4 retest sessions conducted about 1 week, 2 weeks, 1 month, and 4 months after the initial training session (Hypothesis 2– H_2). * indicates $p < .05$ for left side comparisons; ++ and †† indicate, $p < .001$ for right and interlimb comparisons, respectively. A solid line connecting 2 data points without symbols or an asterisk indicates $p > .05$.

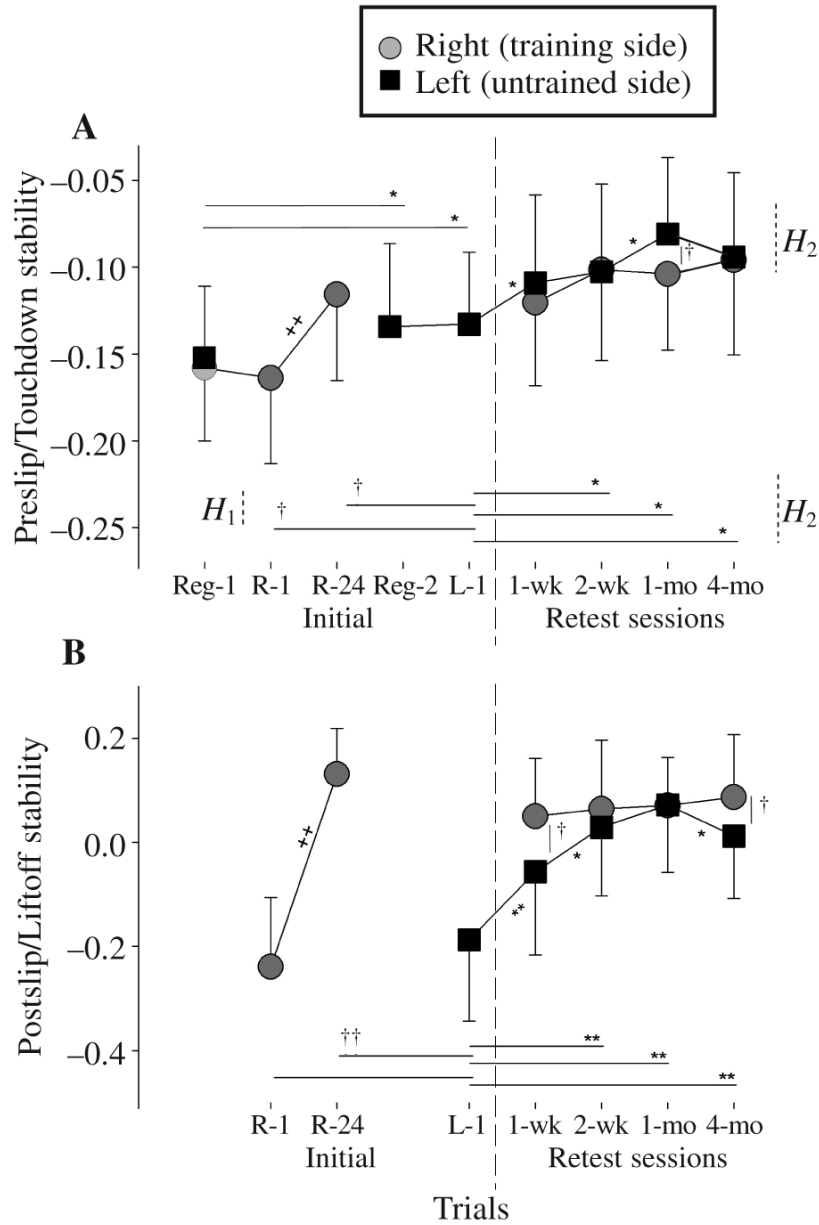


FIGURE 3. Group means (± 1 SD) of (A) pre- and (B) postslip stability for the first and last training (right) side slips (R-1 and R-24, respectively) and the slip on the untrained (left) side (L-1) from the initial session (Hypothesis 1- H_1). Also shown are the slip trials from the right and left sides for the 4 retest sessions conducted about 1 week, 2 weeks, 1 month, and 4 months after the initial training session (Hypothesis 2- H_2). The preslip stability is also demonstrated for the right and left limbs (at touchdown) during a regular (Reg-1) walking trial prior to the first right slip and prior to the first left slip (Reg-2). * and † indicate $p < .05$ for left and interlimb comparisons, respectively; ++, ** and †† indicate for right, left, and interlimb comparisons, $p < .001$. Less negative values of stability indicate higher stability. A solid line connecting 2 data points without symbols indicates $p > .05$.

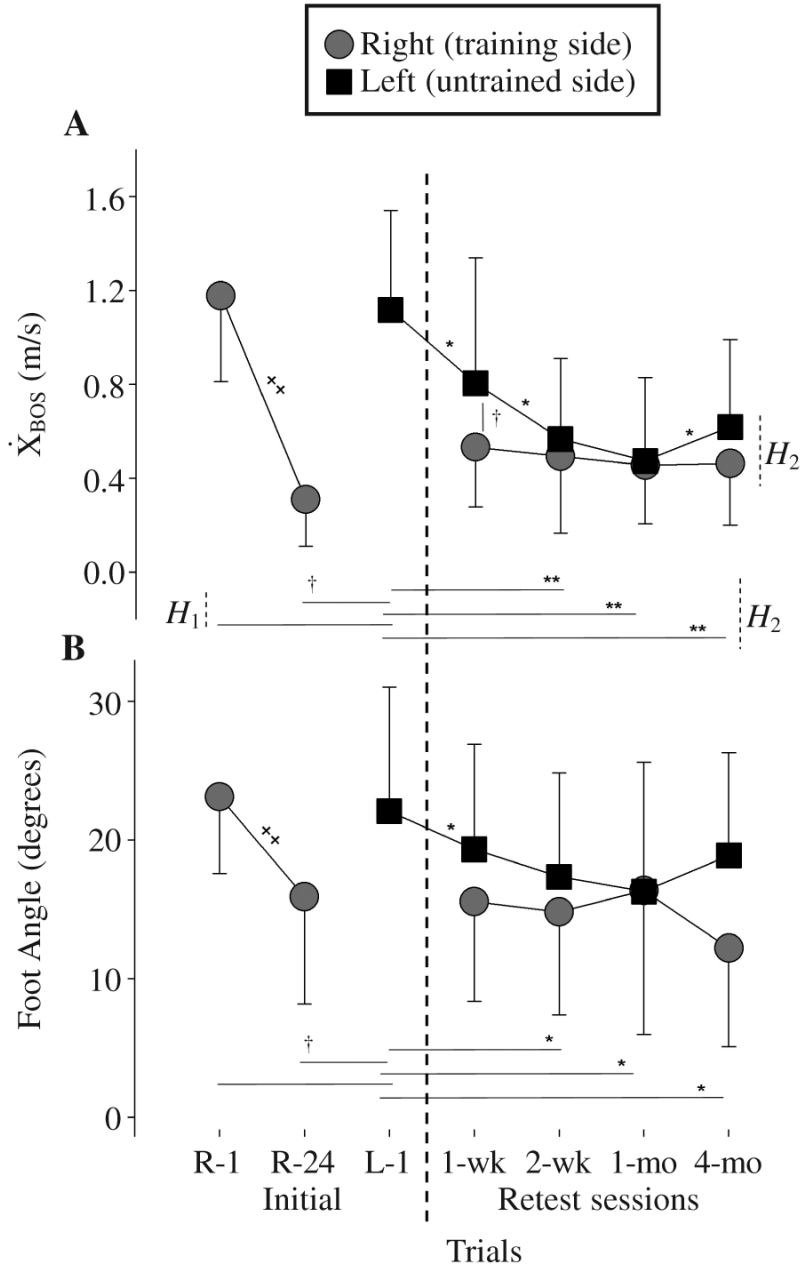


FIGURE 4. Group means (± 1 SD) of (A) BOS velocity (\dot{X}_{BOS}) and (B) foot angle for the first and last training (right) side slips (R-1 and R-24, respectively) and the slip on the untrained (left) side (L-1) from the initial session (Hypothesis 1- H_1). Also shown are the slip trials from the right and left sides for the 4 retest sessions conducted about 1 week, 2 weeks, 1 month, and 4 months after the initial training session (Hypothesis 2- H_2). Foot angle was obtained at pre-slip touchdown of the slipping limb and BOS was obtained at postslip liftoff of the contralateral, trailing limb. * and † indicate $p < .05$ for left and interlimb comparisons, respectively; ++ and ** indicate for right and left comparisons, respectively, $p < .001$. A solid line connecting 2 data points without any symbols indicates $p > .05$.