GENERALIZATION OF MOTOR ADAPTATION TO REPEATED-SLIP PERTURBATION ACROSS TASKS

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ABSTRACT

Similar adaptations improve both proactive and reactive control of center-of-mass (COM) stability and limb support against gravity during different daily tasks (*e.g.*, sit-to-stand and walking) as a consequence of perturbation training for resisting falls. Yet it is unclear whether – or to what extent – such similarities actually promote inter-task generalization. The purpose of this study was therefore to determine whether young adults could indeed transfer their adaptive control, acquired from sit-to-stand-slip, to improve their likelihood of a recovery from an unannounced novel slip in walking. Subjects underwent either repeated slips during sit-to-stand before experiencing an unannounced, novel slip during walking (training group, N=20), or they received no prior training before the same gait-slip (control group, N=23). The subjects demonstrated training-induced generalization of their improved proactive control of stability in post-training (unperturbed) gait pattern that was more stable against backward balance loss than was that of their own pre-training pattern as well the gait pattern of the subjects in the control group. Upon the unannounced novel gait-slip, the training group showed significantly lower incidence of both falls and balance loss than that shown by the control, resulting from the improvements in the reactive control of limb support and slip velocity, which directly influenced the control of their COM stability**.** Such transfer could occur when the subjects' central nervous system recalibrates the non-task-specific, generalized representation of stability limits during the initial training to guide both their feed-forward adjustments and their feedback responses. The findings of the inter-task generalization suggests that behavioral changes induced via the perturbation training paradigm have the potential to prevent falls across the spectrum of cyclic and non-cyclic activities.

Keywords: perturbation training, sit-to-stand, gait, stability, limb support, fall.

A vital functional plasticity of the central nervous system (CNS) is its ability to take motor adaptations obtained from one situation and apply it appropriately to different "contexts." Such context can mean different effectors (*e.g.*, interlimb generalization) (Bhatt and Pai, 2008a; Morton et al., 2001; Sainburg and Wang, 2002), different environmental constraints (*e.g.*, moveable-platform-to-slippery-floor generalization) (Bhatt and Pai, 2009), or different task objectives (*i.e.*, inter-task generalization) (Abeele and Bock, 2003; Conditt et al., 1997; Lam and Dietz, 2004; Morton and Bastian, 2004; Seidler, 2004). The latter, namely the inter-task generalization, conventionally defined by the improvement of performance in one task resulting from adaptive skills acquired from training in a different task (Schmidt and Lee, 2005), is especially important to clinical interventions that can focus only on a limited small subset of daily activities.

Previous findings have illustrated the CNS's ability to generalize its learned experience and response to similar perturbations occurring in untrained tasks (Lam and Dietz, 2004; Morton and Bastian, 2004; Seidler, 2004). As a prerequisite to generalization, motor adaptation requires a recalibration of motor control to meet novel and changing sensory demands (Bastian, 2008). During this process, the CNS builds and updates its corresponding representation (*i.e.*, a neural representation of the relation between motor commands and movements) where the altered task variables are transformed into intrinsic (*e.g.*, individual joint angle) or extrinsic (*e.g.*, endpoint motion) variables, to more accurately predict the actual outcome using feed-forward mechanisms (Imamizu et al., 1998; Wolpert and Ghahramani, 2000). Few studies have suggested that the CNS is able to code and generalize motor adaptation to changing task objectives by utilizing such an internal representation resulting from motor practice (Conditt et al., 1997; Shadmehr and Mussa-Ivaldi, 1994). When an acquired internal representation is more generalized and not specific to certain effectors, environments, or tasks, a greater degree of motor transfer is likely to be measurable (Morton et al., 2001).

In the context of posture and locomotor control, successful proactive adaptation (*i.e.*, action before onset of perturbation) would include a combination of change within the feed-forward mechanism and its influence on feedback loops. Adaptation can also occur reactively (after onset of perturbation) within "feedback-error based" mechanisms (Atkeson, 1989), as is apparent from the attenuation of both muscle activation and degree of postural sway with repeated support-surface translations (Horak et al., 1989; Nashner, 1976). An appropriate feed-forward mechanism can produce movements that accurately match the predicted sensory consequences and involve little need for real-time feedback adjustment in error correction.

Similarly, both young and older adults were able to adapt to prevent falls and balance loss after repeated exposure to slips induced during sit-to-stand and in walking (Bhatt et al., 2006a; Pai et al., 2010; Pavol and Pai, 2002; Pavol et al., 2004a). For both tasks, such adaptive control was achieved by improving proactive and reactive control of horizontal stability and vertical limb support against gravity (through both feed-forward and feedback mechanisms) (Pai et al., 2010). It is unclear, however, whether such similarities actually promote inter-task generalization.

The purpose of this study was therefore to determine whether young adults could transfer their adaptive control acquired from a single-session of repeated-slip exposure during sit-to-stand to increase the likelihood of recovery from a novel slip in walking. We hypothesized that these subjects were able to generalize motor adaptation to yield better proactive and reactive control of gait stability and limb support (resulting in their reduced incidence of falls and balance loss in novel gait-slip) than we found in the control group, who received no such training.

EXPERIMENTAL PROCEDURES

Subjects. Forty-three young adults (26 women; 17 men; age 26±5 years; height 168±9 cm; mass 64±11 kg) participated in either the training or control group (training: N=20; control: N=23). Although 46 subjects were recruited initially, only these 43 subjects who completed the protocol and had a full data set were included for analyses. The remaining three subjects were excluded because of incomplete training or missing data (see *Perturbation training during sit-to-stand*). All subjects gave informed consent and were given full and careful explanation of the purposes and procedures in the study. The study was approved by the Institutional Review Board. None of the subjects had histories of neurological, musculoskeletal, or other systemic disorders that would have affected their postural control. All were right-leg dominant (as determined by self-report of a preference to kick a ball with the right leg).

Experimental setup. The experimental setup was similar to that of our previous studies (Bhatt et al., 2005; Pavol et al., 2002) (Fig. 1). The stool with adjustable seat level (50 ~ 62 cm) was bolted to a transducer (MC3A-6-250, AMTI, Newton, MA) and was supported by a specially-built platform. A slip was induced by a side-by-side pair of low-friction movable platforms (65 × 30 × 0.6 cm, coefficient of friction < 0.05), each of which was mounted on a frame with two rows of linear bearings. The frame was bolted onto two force plates (OR6-7-1000, AMTI, Newton, MA) to measure the ground reaction force. The platforms were free to slide 150 cm and 90 cm forward for the right and left, respectively, when unlocked by a computer-controlled release mechanism. During sit-to-stand, the slip was induced shortly after seat-off by simultaneously unlocking both platforms when the stool supported less than 10% body weight and the forward velocity of the person's body center-of-mass (COM) exceeded 20 cm/s, to standardize the training conditions. Platform release data were computed in real-time from force plates and the transducer beneath the stool, using a computer program written in LabView (National Instruments Inc., Austin, TX). During walking, the slip was induced by computer-controlled unlocking of the moveable platforms at touchdown of the slipping foot. The subjects wore a full-body safety harness and their own athletic shoes. The length of the rope that connected the harness to the overhead low-friction trolley was adjusted so the body parts above the ankles could not touch the ground. A load cell measured the force exerted on the harness.

Perturbation training during sit-to-stand. The training group first underwent a regular walking protocol the same as the controls for baseline measure before any slip or their formal training (Fig. 2). After a 5-minute rest break, with one foot placed on each platform, they sat on the stool in a standard position with trunk straight, ankles dorsiflexed at 10°, knees flexed at 100°, and elbows flexed at 90° (Pavol and Pai, 2002). They were asked to stand up "as fast as possible" upon an auditory cue, without using their arms, and to maintain the standing position. They only knew that a slip would occur later on. After 5 nonslip (*i.e.,* regular sit-to-stand) trials, a slip was induced without warning.

After that first slip, the subjects were informed that they "may or may not" experience more slips during the subsequent trials. They were also told that they should "try not to fall" upon a slip and remain standing still. The training protocol included a block of 5 consecutive slip trials (including the first slip). This was followed by a block of 3 nonslip trials; another block of 5 consecutive slip trials; the second block of 3 nonslip trials, and a mixed block of slip and nonslip trials (consisted of 4 slip and 3 nonslip trials interspersed: see Fig. 2b). The initial block of repeated slips was for the CNS to have the opportunity to establish a prediction-error-based baseline, whereby the second block of slips was to strengthen the adaptive effects and reduce the washout effect (Bhatt et al., 2006b; Pavol and Pai, 2002). The mixed block given at the end was to introduce uncertainty, and thus the CNS had to take into account for different conditions in order to optimize the performance (Izawa et al., 2008).

Because successful adaptation is a prerequisite for generalization just as it is for retention, all subjects were expected to have successful recovery (no falls) from slips in the mixed block. Two subjects failed to meet this criterion. Previous findings have established that subjects can adapt to sit-to-stand-slips in 5 slips (Pavol and Pai, 2002) and that those persons who did not adapt well will have poor retention (Bhatt et al., 2006b). It is conceivable these two subjects might have benefited from additional practice to acquire proper motor adaptation, but that is beyond the scope of the current design. Because of the small sample size, on the other hand, it is impossible to investigate any transfer effect that remained with them. These two subjects, therefore, were excluded from further testing and analysis. One subject in the training group with a misplaced hip marker was also excluded from data analysis.

The control and the generalization test in gait-slip. The control group was instructed to walk a block of 8 trials at their self-selected pace and told that they might experience a slip later on. They were told to try not to fall and continue walking in the case of a slip. On the 9th trial, a slip was induced on the right side without warning (Fig. 2a). After the sit-to-stand-slip, the subjects in the training took a 5~10 min rest break. They were then asked to perform unperturbed walking trials, and were told that they might experience a slip later on without warning. They should "try not to fall," and continue walking in the case of a slip. A slip was induced on the right side on the 6th trial (Fig. 2b).

COM state stability and limb support. The data of 28 light-reflective markers placed on bilateral upper and lower extremities, torso, and platforms, was recorded at 120 Hz using an 8-camera motion capture system (Motion Analysis Corporation, Santa Rosa, CA). Marker displacement data was lowpass filtered at marker-specific cut-off frequencies (range 4.5~9 Hz) using fourth-order Butterworth filters. Force plate data, harness-load cell data, and trigger-release onset signals were collected at 600 Hz and synchronized with motion data at the time of data collection.

The COM position and velocity in the sagittal plane were calculated using a 13-segment rigid body model (de Leva, 1996). The COM position ($X_{COM/BOS}$) was defined as the absolute COM position in anteroposterior direction relative to the rear of base-of-support (BOS). The COM velocity ($V_{COM/BOS}$) was calculated from differentiation of COM position and normalized to $\sqrt{g \times bh}$, where g was the acceleration due to gravity and bh was height of the subject (McMahon, 1984).

Stability was quantified by measuring the shortest distance between the instantaneous COM motion state (*i.e.*, the COM position and velocity relative to the BOS) and the predicted feasible stability region (FSR) limits for backward balance loss under slip conditions (Pai and Iqbal, 1999; Yang et al., 2007, 2008). Greater values indicate greater stability against backward balance loss and falls (Bhatt et al., 2005; Espy et al., 2010; Pai et al., 2003). Limb support was measured by the instantaneous vertical height of the midpoint between a person's two hips and normalized by subjects' height (Pai et al., 2006; Pavol and Pai, 2007).

A lower hip height indicates poorer limb support against gravity, which is the primary causative factor for falls (Yang et al., 2009).

In both sit-to-stand and gait, several variables were obtained at pre- and postslip instants to document changes in proactive and reactive control, respectively (*i.e*. actions that occur respectively before and after the perturbation). During sit-to-stand-slip, proactive adaptation was examined by measuring preslip stability, the horizontal COM velocity at seat-off, and hip height, which were obtained at the instant seat-off (20 ms before onset of slip perturbation). Seat-off was defined as the time at which the vertical force on the stool dropped below 10% body weight. Reactive adaptation was examined by measuring postslip stability and hip height at 300 ms after slip onset, an instance determining outcomes of fall vs. recoveries at up to 70% accuracy (Pai et al., 2010). During walking, proactive adaptation was examined by measuring preslip stability, gait speed (*i.e.*, the absolute COM velocity in anteroposterior direction), and hip height at touchdown of the slipping limb (*i.e.*, the right limb, RTD), which occurred 30 ms before slip onset. Reactive adaptation during gait was examined by measuring postslip stability and hip height at recovery (left) foot liftoff (LLO) and touchdown (LTD). The instance of the recovery-foot touchdown was close to 300 ms after slip onset, the time instant chosen for examining reactive changes during sit-to-stand-slip. The instance of 300 ms after slip onset was chosen for the sit-to-stand-slip instead of the recovery foot touchdown because some subjects did not take a recovery step to regain their balance during reslips in the sit-to-stand-slip.

Kinematic measures. The following variables were analyzed to increase our understanding of the factors contributing to the adaptive changes in stability control (Bhatt et al., 2006a): step length, foot angle, and the slip (BOS) velocity. Step length affected the

COM location at RTD and was measured as the distance between heel markers of the leading foot and the contralateral foot (normalized to subjects' body height). The foot angle at RTD influenced subsequent braking impulses and was measured as the angle between foot segment (line joining the heel and fifth metatarsal) and the horizontal. The BOS velocity directly affected the relative velocity between the COM and BOS; it was obtained from the velocity of the sliding platform marker. During the sit-to-stand-slip, the greater of the two maximum velocities attained by the markers on the two sliding platforms represented the peak BOS velocity. During gait-slip, the BOS velocity was obtained from the velocity of the right sliding platform marker at LLO and LTD after slip onset.

Outcome of the slip trials. For sit-to-stand-slip, falls occurred when the midpoint between the hips descended to within 5% body height of its initial seated height. Outcomes were classified as recoveries if the mean force on the safety harness did not exceed 4.5% of body weight over any one-second period (Pavol and Pai, 2002). Backward balance loss occurred when the subject took a backward recovery step. Forward balance loss occurred when the subject took a forward recovery step. The remainder of the trials (*i.e.*, subjects recovered but did not step to regain balance) were classified as "no loss of balance."

For gait-slip, the outcome of slip was classified as a fall if the peak load cell force during the slip trial exceeded 30% body weight (Yang and Pai, 2011). A full recovery occurred when the average load cell force on the harness did not exceed 4.5% of body weight over any 1-second period after slip onset (Yang and Pai, 2011). Backward loss of balance occurred when subjects place their contralateral limb posterior to the slipping heel upon landing. The trials during which subjects landed their contralateral limb anterior to the slipping heel were classified as "no loss of balance" (Bhatt et al., 2006a). To guarantee the rigor of the study, the subjects would have been considered as "harness-assisted" and excluded from further analysis if their load cell force exceeded the 4.5% criteria in both activities.

Statistics. To examine training effects during sit-to-stand, slip outcomes, and adaptive changes in pre- and postslip stability, the horizontal COM velocity at seat-off, peak BOS velocity, and hip height of the first (S1) and last (S14) slips were compared by Wilcoxon signed rank test and paired-t tests respectively. To further evaluate feed-forward adjustments in COM state stability, a one-way repeated-measure ANOVA with *post-hoc* paired-t test with Bonferroni corrections was conducted to compare stability at seat-off among the following trials: S1; S5 (the last slip trial of the first slip block); N1 (the first nonslip trial of the first nonslip block); and S14. To determine whether the training group and the controls behaved the same way at the baseline, seven variables taken at RTD of the baseline measures were compared: the COM position and velocity, stability, gait speed, hip height, step length, and foot angle. To examine the generalization of the training effect on post-training unperturbed gait, the same seven variables were compared to those from the pre-training with paired t-tests, and to those from the control with t-tests (Fig. 2).

To examine the generalization of the training effect on responses to a novel, unannounced gait-slip (Fig. 2), the outcomes of the training group were compared to those of the controls by Chi-square test. A 2-by-2 mixed model ANOVA, with group (training and control) as between factor and event (LLO and LTD) as the repeated factor, was conducted to compare the difference in postslip stability, BOS velocity, and hip height. *Post-hoc* independent t-tests and paired t-tests were performed to compare between-group and within-group differences followed by significant main effect or interaction. All analyses were performed using SPSS (V.15.0, SPSS Inc, IL).

RESULTS

Adaptation to sit-to-stand-slip. All subjects experienced backward balance loss when the slip was first induced during sit-to-stand. Thirty-five percent of the subjects in the training group fell on the first slip trial (S1) during sit-to-stand. They were able to adapt rapidly and thus to reduce falls to 0% on the 3rd slip (S3*)* and thereafter (*P*<0.01). This was initially achieved by overcompensation, that all subjects experience a forward balance loss when the slip stopped abruptly (N1 in Fig. 3). However, they were able to significantly reduce the incidence of backward balance loss to 25% (*P*<0.05) and forward balance to 0% on the last slip (Fig. 3).

The decrease in the incidence of falls and balance loss resulted from improvements in stability and limb support. Both pre- and postslip stability significantly increased from the first (S1) to the last slip (S14) (*P*<0.001 and *P*<0.01, respectively: see Fig. 4a). The horizontal COM velocity at seat-off also increased significantly, from S1 to S14 (*P*<0.001). The improvement in pre- and postslip stability was paralleled by decreased peak BOS velocity after slip onset (*P*<0.001) (Fig. 4b). Notably, preslip stability against backward balance loss significantly increased, from S1 to S5 and to N1 (*P*<0.001), and also increased the risk for forward balance loss (Fig. 3). The re-adjustments came immediately thereafter (*i.e.*, preslip stability significantly decreased from N1 to S14, *P*<0.01) such that the COM state was located within the shaded area – an area that has been predicted to be stable under both slip and nonslip conditions (Fig. 5). In the end, preslip stability on S14 was still greater than that of S1 (*P*<0.001). In contrast to the stability findings, *only* postslip hip height showed significant increase from the first to the last slip (*P*<0.05) (Fig. 4c).

Regular walking and unperturbed gait. There were no significant between-group differences in the baseline measurements [the COM position (*P*=0.786), the COM velocity (*P*=0.573), stability (*P*=0.540), gait speed (*P*=0.633), hip height (*P*=0.965), step length (*P*=0.631), and foot angle (*P*=0.607)]. The subjects in the training group demonstrated noticeable generalization evidenced by increased stability at RTD and changes of gait pattern during unperturbed gait. More forward COM position (*P*<0.01), greater stability (*P*<0.001), shorter step (*P*<0.05), smaller foot angle (*i.e.*, landing more flat-footed) (*P*<0.001) were found in post-training unperturbed gait in comparison to those in pre-training regular walking (Fig. 6a, 6c, 6e, and 6f), yet no difference was found in COM velocity (*P*=0.086) and hip height (*P*=0.069) during post-training unperturbed gait (Fig. 6b and 6d). However, there was no difference in the gait speed between the pre-training regular walking and post-training unperturbed gait (*P*=0.091). The generalization effect was also evidenced by more forward COM position (*P*<0.05), greater stability (*P*<0.01), and smaller foot angle (*P*<0.01) at RTD (Fig. 6a, 6c, and 6f) demonstrated on post-training unperturbed gait of the training group in comparison to those on regular walking of the control group. No difference was found in the gait speed on post-training unperturbed gait of the training group in comparison to that recorded during regular walking of the control group (*P*=0.306).

Generalization in gait-slip. The training group demonstrated a measurable generalization effect in responding to a novel gait-slip, as evidenced by better slip outcomes and improved reactive control of stability and limb support. The training group showed a significant decrease in both the incidence of falls and backward balance loss after perturbation training during sit-to-stand. Significant improvement was found in the incidence of backward balance loss; only 75% of the subjects in the training group lost their balance in gait-slip as compared to 100% balance loss in the control group (*P*<0.05). The five people from the training group did *exceptionally* well by not even losing their balance in gait-slip. While 26% of the subjects in the control group fell during gait-slip, none of the subjects in the training group fell (*P*<0.05).

The postslip stability had a significant group-by-event interaction (*F*(1,41)=4.828, *P*<0.05), and a significant group main effect (*F*(1,41)=19.159, *P*<0.001). The training group demonstrated greater stability at both LLO (*P*<0.001) and LTD (*P*<0.01) as compared to the control group (Fig. 7a). Postslip stability remained constant from LLO to LTD for the training group (*P*=0.247), but decreased significantly from LLO to LTD for the control group (*P*<0.001) (Fig. 7a). The BOS velocity demonstrated significant group and event main effects (*F*(1,41)=13.977, *P*<0.01 and *F*(1,41)=23.603, *P*<0.001, respectively) but no group-by-event interaction (*F*(1,41)=0.350, *P*=0.557). The training group had lower BOS velocity than did the control group at both LLO (*P*<0.001) and LTD (*P*<0.01) (Fig. 7b). The postslip hip height demonstrated significant group-by-event interaction (*F*(1,41)=10.12, *P*<0.01). The training group's postslip hip height was still not different from that of the control at LLO (*P*=0.232), but it became significantly higher later at LTD (*P*<0.05) (Fig. 7c).

Elimination of those five *exceptional* subjects did not affect preslip stability; thus the remaining subjects still demonstrated greater preslip stability as compared to the control subjects (*P*<0.05). Their elimination would have affected postslip stability (Fig. 7a) and BOS velocity (Fig. 7b), but not limb support (Fig. 7c). Both training and control groups would have showed a significant decrease in stability and an increase in BOS velocity from LLO to LTD (all *P*<0.05); however, the training group still had greater stability at both LLO and LTD (*P*<0.001 and *P*<0.05, (respectively) and lower BOS velocity at LLO (*P*<0.01) as compared to the control (Fig. 7a and 7b). Finally, none of the outcomes was eliminated due to harness-assisted.

DISCUSSION

The findings demonstrated that young adults were able to transfer the acquired motor adaptation from sit-to-stand-slip to gait-slip; this was made evident by their lower incidence of balance loss and falls than that measured in the control group on the gait-slip. It is clear that this finding is a consequence of training-induced improvements in both proactive and reactive control of stability and in reactive control of limb support against gravity.

Adaptation and generalization in proactive control. Our previous work has shown that 3 to 5 slips were sufficient (Pavol and Pai, 2002) to achieve the objective of perturbation cancellation, an essential process of motor adaptation. Depending on the type of task, initial acquisition may take as few as 1-3 trials (Bhatt et al., 2006a; Bunday et al., 2006; Lang and Bastian, 1999; Morton and Bastian, 2004; Pavol and Pai, 2002), yet it can require trials numbering in the hundreds (Conditt et al., 1997; Shadmehr and Mussa-Ivaldi, 1994). Motor adaptations to artificial force fields and prism glasses do not occur in everyday living. Thus, the adaptation process and subsequent learning takes longer, as motor commands are relatively new (Baraduc and Wolpert, 2002; Conditt et al., 1997; Shadmehr and Mussa-Ivaldi, 1994). In contrast, the process of adaptation to familiar but potentially life-threatening perturbations is usually very swift; in some instances, it may require only 1-3 trials (Bunday et al., 2006). Such a rapid rate of adaptation in locomotion may result from factors such as past real-life experience, large initial task errors, and a penalty-driven mechanism (*i.e.*, a potential of fall and subsequent deadly injury) (Bunday et al., 2006).

The rapidness of the adaptive process could occur if the CNS needs only to recalibrate an existing internal representation of feasible stability region (FSR) rather than to acquire an entirely new motor program. The adaptation to the sit-to-stand-slip is not only a simple perturbation-cancellation process; the CNS also learns to reduce the prediction error via a trial-and-error practice under uncertain conditions (Bastian, 2008; Izawa et al., 2008). Indeed, at beginning of the perturbation training, the subjects' COM motion state at (preslip) *seat-off* was very stable under the nonslip condition (near Area 1 in Fig. 5 and at the center of the theoretically predicted FSR for the nonslip condition) but was very unstable against a slip (near the stability limits of the FSR for the slip condition). All subjects experienced a backward balance loss on the first sit-to-stand-slip (S1 in Fig. 3), but they were able to *rapidly* readjust their COM state by the end of first block from Area 1 to Area 2 (Fig. 5). Area 2 was rather unstable against forward balance loss under nonslip conditions. All subjects experienced forward balance loss precisely as predicted when slips stopped abruptly (N1 in Fig. 3), indicating an overcompensated *aftereffect* from the first block training. The final readjustments of the COM motion state were near Area 3 of Fig. 5. It is important to note that this adaptive process dictated by the CNS perfectly matched the theoretical prediction (demonstrated by the shaded area of FSR in Fig. 5), in which the adapted movements became optimally stable under both slip and nonslip conditions, thus minimizing any reliance on the prediction of their occurrence probability.

Nevertheless, to account for the rapidness of adaptation, one might argue that such a motor strategy (*i.e.*, movements that were stable in both slip and nonslip conditions) *already exists* prior to training, and thus it could be easily retrieved by the mere expectation of a slip or after a single mixed block of slip and nonslip trials (rather than after such an extensive training protocol). This might not be the case, however. First, context prediction is necessary for the CNS to develop accurate representations of stability limits. Without such predictability, first established through block design in the present study, a mixed-block-only approach may lead the CNS to rely more on reactive control (Horak et al., 1997) and could present greater difficulty in the calculation of prediction error that is necessary for calibration of the internal representation. Second, a sit-to-stand-slip is a less common experience than a gait-slip, suggesting that the change in behavior resulted from adaptation to a “relatively new” circumstance. The latter would require at the very least the reprogramming of motor commands consistent with the recalibrated internal representation of the stability limits, rather than a simple retrieval of an *existing* skill. Third, the *aftereffect* of forward balance loss shown on the first nonslip trial would in turn require further modification; this further refutes the suggestion that this error-driven process can be “pre-existing.”

Finally, although rapid adaptation demonstrated in the sit-to-stand-slip may also have a cognitive or motivational component in addition to the sensorimotor process involved, strong empirical evidence indicates that awareness or even cognitive learning *alone* cannot be a substitute for such motor adaptation (Bhatt and Pai, 2008b). Indeed, mere awareness of slippery conditions, even when combined with cognitive training induced via observational learning (Bhatt and Pai, 2008b) (although it did induce a “cautious” gait pattern) was insufficient to reduce slip intensity (BOS kinematics) and prevent a balance loss or fall (Bhatt and Pai, 2008b; Heiden et al., 2006). It is possible, although unlikely based on the aforementioned rationale, that the observed generalization could be reduced in it effects if subjects were unaware of the possibility of gait-slip.

The predicted FSR is very similar between sit-to-stand and gait (Yang et al., 2007, 2008). This provides the theoretical basis for the generalization of the training effect from the sit-to-stand-slip to the task of gait. Evidently, the improved control of the COM stability resulted mainly from feed-forward adjustments in COM position (anterior shift relative to heel partially from shortened step length) together with a more flat-footed landing and more knee flexion (Bhatt et al., 2006a). It also resulted in a reduced requirement for braking impulse in a slip (Bhatt et al., 2006a; Marigold and Patla, 2002). Notably, such generalization in the feed-forward mechanism was sufficient to prevent a backward balance loss in 5 subjects during the novel gait-slip.

According to general perception, the higher the degree of similarity between tasks, the greater the amount of generalization (Schmidt and Young, 1987). There are obvious differences between sit-to-stand and walking. For instance, balance control during walking involves integrating postural adjustments into the ongoing motor program for stepping in a predictable and cyclic braking-and-propulsion fashion. In contrast, the initial propulsion and the subsequent braking of the COM momentum is non-cyclic in sit-to-stand (Pai and Rogers, 1990). Most noteworthy is the difference in which the same subjects adapted by readjusting *both* the COM velocity and its position in sit-to-stand, but merely readjusted their COM position during subsequent unperturbed walking. In spite of these task-specific differences, however, the similarity in the FSR (Yang et al., 2007, 2008) must have the dominant effect, dictating the overall similarity in adaptive changes in stability (Pai et al., 2010) (Fig. 6).

*Adaptation and generalization in reactive control***.** Adaptation in reaction to slip occurring within the feedback mechanism plays an important role shaping the motor response (McIlroy and Maki, 1995; Owings et al., 2001; Pavol et al., 2004a). When feed-forward mechanism by itself is insufficient to eliminate the perturbation generated error, reactive feedback corrections must be critical in restoring and improving postslip stability during the first few slip exposures (Figs 3 and 4). In the later trials, these subjects improved their preslip stability and eliminated or reduced their need for any reactive stepping response. Adaptive changes in *reaction* following a slip induced during sit-to-stand not only reduced the need for a recovery step in gait-slip but also improved inter-task limb support, which would otherwise result in a fall (Pavol et al., 2004b). Notably, adaptive control in limb support mainly relies on the feedback mechanism — a clear difference from the control of the COM stability.

Task-specific differences also exist following slip onset: a greater forward COM momentum during gait than sit-to-stand results in a doubling of the slip (BOS) velocity (Yang et al., 2009). Even during a recovery step, gait-slip requires a mere modification of the ongoing motor program in which the foot still travels forward, whereas the subjects must initiate an additional motor program that moves the recovery foot backward during a novel response to the first sit-to-stand-slip, taking twice as long (Yang et al., 2009). Regardless of such differences, the global similarities in the reactive control of stability and limb support were evident on the first novel gait-slip; moreover, they were task-independent (Pai et al., 2010). In the present study, although 15 subjects still lost balance in gait-slip, they were able to improve postslip stability significantly better than the controls (Fig. 7), primarily through the reduction in their peak slip velocity (Yang and Pai, 2010).

*Neuromechanisms of generalization***.** Generalization is more likely to occur when the CNS develops global task objectives by coding extrinsic factors such as slip velocity during adaptation, in a manner similar to that of the endpoint control (Lam and Dietz, 2004). The cerebellum plays a critical role in the storage of such sensorimotor adaptation (Imamizu et al., 2000; Kawato and Gomi, 1992; Miall and Wolpert, 1996). Cerebellar activation near the posterior superior fissure was apparent during the generalization of acquired motor adaptation, suggesting that such generalization would require the retrieval of prior learned motor skills (Seidler, 2010; Seidler and Noll, 2008). Furthermore, people with cerebellar impairments have difficulties in acquiring locomotor adaptation and generalization to a changing context (Morton and Bastian, 2004, 2006). Based on such evidence, the locus of this generalized coding could be in the cerebellum.

In summary, the results from this study demonstrated the generalization of adaptation to perturbation training across two very different tasks. Although the subjects in the present study were young, similar adaptive mechanisms also develop among older adults during both sit-to-stand-slip and gait-slip (Pai et al., 2010). Thus, similar generalization will likely occur in the older adults, who are often more vulnerable to falls. Such understanding could have profound clinical implications pertaining to generalization and fall prevention.

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FIGURE LEGENDS

Figure 1: The diagrammatic representation of the experimental setup for a) sit-to-stand-slip and b) gait-slip. a) The diagram shows the average body position at seat-off. The force exerted on the stool was recorded by the force transducer bolted beneath the stool. b) The diagram shows average body position at leading/slipping foot touchdown (*i.e.*, right foot). A slip was induced by releasing two low-friction movable platforms shortly after seat-off for sit-to-stand-slip and at the instant of leading/slipping foot touchdown for gait-slip. Each of the two platforms was mounted on a frame with two rows of linear bearings, and the frame was bolted on to two force plates to measure the ground reaction force. During both sit-to-stand-slip and gait-slip, the movable platforms were free to slide 150 cm and 90 cm forward for the right and left, respectively. The movable platforms were embedded in a 7-m walkway and made less noticeable to the subject by surrounding stationary decoy platforms. A set of 28 light-reflective markers were placed on bilateral upper and lower extremities, torso, and platforms. The subjects were required to wear a safety harness which was individually adjusted to prevent a fall to the ground. A load cell was used to measure the force exerted on the harness. Note that the safety harness system was much higher than that shown.

Figure 2: Testing protocols for the a) control group and b) training group. The protocol for the control group consists of 8 regular walking trials (Gait) followed by a slip trial (Gait-Slip). The protocol for the training group consists of 8 regular walking trials (Pre-Training (Regular) Gait), followed by perturbation training during sit-to-stand, another block of 5 nonslip walking trials (Post-Training Unperturbed Gait), followed by a slip trial (Gait-Slip). The protocol for perturbation training during sit-to-stand consists of 5 regular sit-to-stand trials (STS), followed by a block of 5 slips (S1-S5), a block of 3 nonslip trials (N1-N3), a

second block of 5 slips (S6-S10), a second block of 3 nonslip trials (N4-N6), then a mixed block of 4 slips (S11-S14) and 3 nonslips (N7-N9).

Figure 3: Slip outcomes of total 14 slips and 3 nonslips in the first nonslip block during perturbation training during sit-to-stand (N=20). A decrease in the percentage of falls (filled bar) and backward balance loss (BLOB, hatched lines) from the first through the fourteenth slip trials (S1 to S14), and a decrease in percentage of forward balance loss (FLOB, cross lines) from the first nonslip to the last slip trials (N1 to S14) were associated with an increase in the percentage of "no loss of balance" instances recorded (NLOB).

Figure 4: Comparison of group means (± SD) for a) pre- and postslip stability, b) peak base-of-support (BOS) velocity after slip onset, and c) pre- and postslip hip height between the first slip (S1) and the last slip (S14) during sit-to-stand. Preslip was measured at seat-off; postslip was measured at 300 ms after slip onset. Stability was defined as the shortest distance between the instantaneous COM state and the predicted boundary for backward balance loss under slip conditions; greater values indicate greater stability against backward balance loss. The peak BOS velocity was obtained from the greater of the two maximum velocities attained by the markers on the two sliding platforms. Hip height was quantified as vertical distance from the ground to midpoint of bilateral hips and normalized by subjects' height (bh); a lower hip height indicates poorer limb support. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Figure 5: The group means (± SD) of COM motion state (position and velocity) at seat-off for the first sit-to-stand slip (S1, area 1), the first nonslip trial during the first nonslip block

(N1, area 2), and the last sit-to-stand slip (S14, area 3). The predicted feasible stability region (FSR) for slipping is represented by the area enclosed by solid line, and nonslipping conditions are shown in the area enclosed by dash-line. The COM position ($X_{COM/BOS}$) was defined as the absolute COM position in the anteroposterior direction relative to the rear of BOS and normalized by foot length. The COM velocity ($V_{COM/BOS}$) was calculated from the differentiation of COM position and normalized by body height. The shaded area represented the common feasible stability region, where balance loss could be prevented for both slipping and nonslipping conditions. On the first sit-to-stand slip, subjects' COM state at seat-off was around area 1, which was closer to the boundary of backward balance loss (BLOB) for slipping. Thus, all subjects experienced backward balance loss on the first unannounced slip. After repeated exposures to slipping, subjects' COM state at seat-off shifted from area 1 to area 2, which was further inside the stability region for slipping but near the forward balance loss (FLOB) for nonslipping conditions. Therefore, nearly all subjects experienced a forward balance loss on the nonslip trial when the slips stopped. However, by the end of training, subjects readjusted their COM state from area 2 to area 3, which was in the middle of the shaded area, where balance could be maintained regardless of whether a slip occurred or not.

Figure 6: Comparisons of group means (± SD) for a) COM position, b) COM velocity, c) stability, d) hip height, e) step length, and f) foot angle at touchdown of the leading/slipping limb for pre-training (regular) gait of the training group (black), post-training unperturbed gait of the training group (unfilled), and regular walking of the control group (hatched line). All variables were obtained from the last regular/unperturbed walking trial prior to the slip and averaged from all subjects in the designated group. The COM position ($X_{COM/BOS}$) was defined as the absolute COM position in anteroposterior direction relative to the rear BOS and normalized by foot length. The COM velocity ($V_{COM/BOS}$) was calculated from

differentiation of COM position and normalized by body height. Stability was defined as the shortest distance between the instantaneous COM state and predicted boundary for backward balance loss under slip conditions. Hip height was quantified as vertical distance from the ground to midpoint of bilateral hips and normalized by subjects' height (bh). Step length was the distance between heel markers of the leading foot and the contralateral foot at touchdown of the leading/slipping limb and normalized to subjects' height (bh). Foot angle was defined as the angle between foot segment and the horizontal; a more acute angle indicates a more flat-footed landing.

Figure 7. Comparison of group means (± SD) for postslip a) stability, b) BOS velocity, and c) hip height at liftoff (LLO) and touchdown (LTD) of the contralateral/recovery foot between the training (N=20) and control (N=23) groups. Stability was defined as the shortest distance between the COM motion state and the predicted boundary for backward balance loss under slip conditions. The BOS velocity was obtained from the velocity of the right sliding platform marker at LLO and LTD after slip onset. Hip height was quantified as vertical distance from the ground to midpoint of bilateral hips and normalized by subjects' height (bh). The filled diamond indicates the group mean for all of the subjects in the training group (All, N=20); the open diamond indicates the group mean for subjects in the training group who had backward loss of balance (LOB, N=15). * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Figure 1
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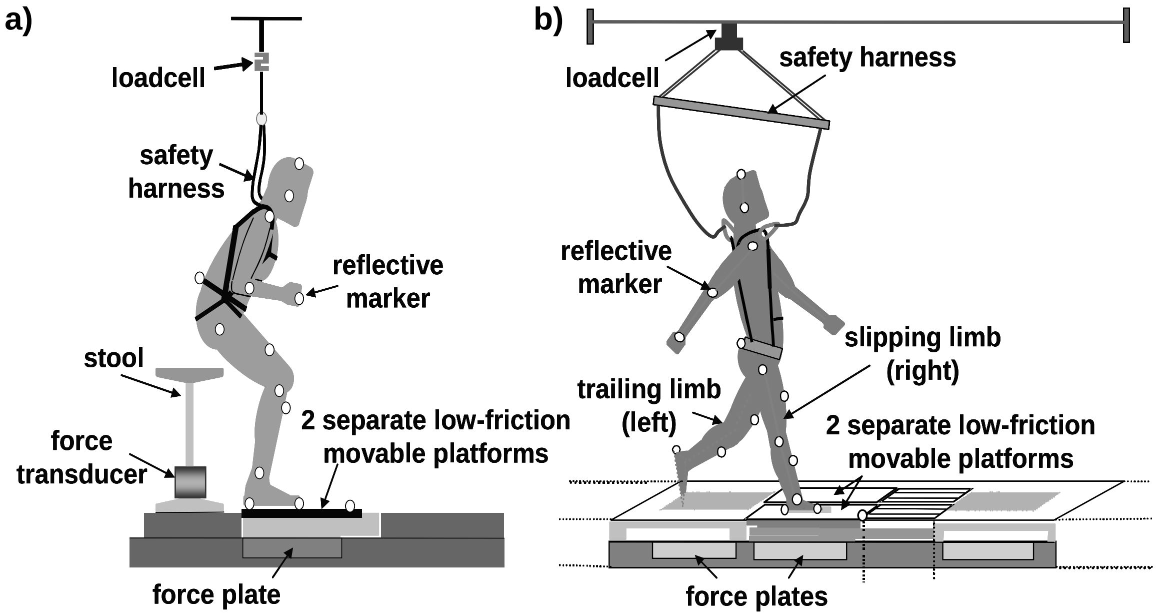

Figure 1

Figure 2
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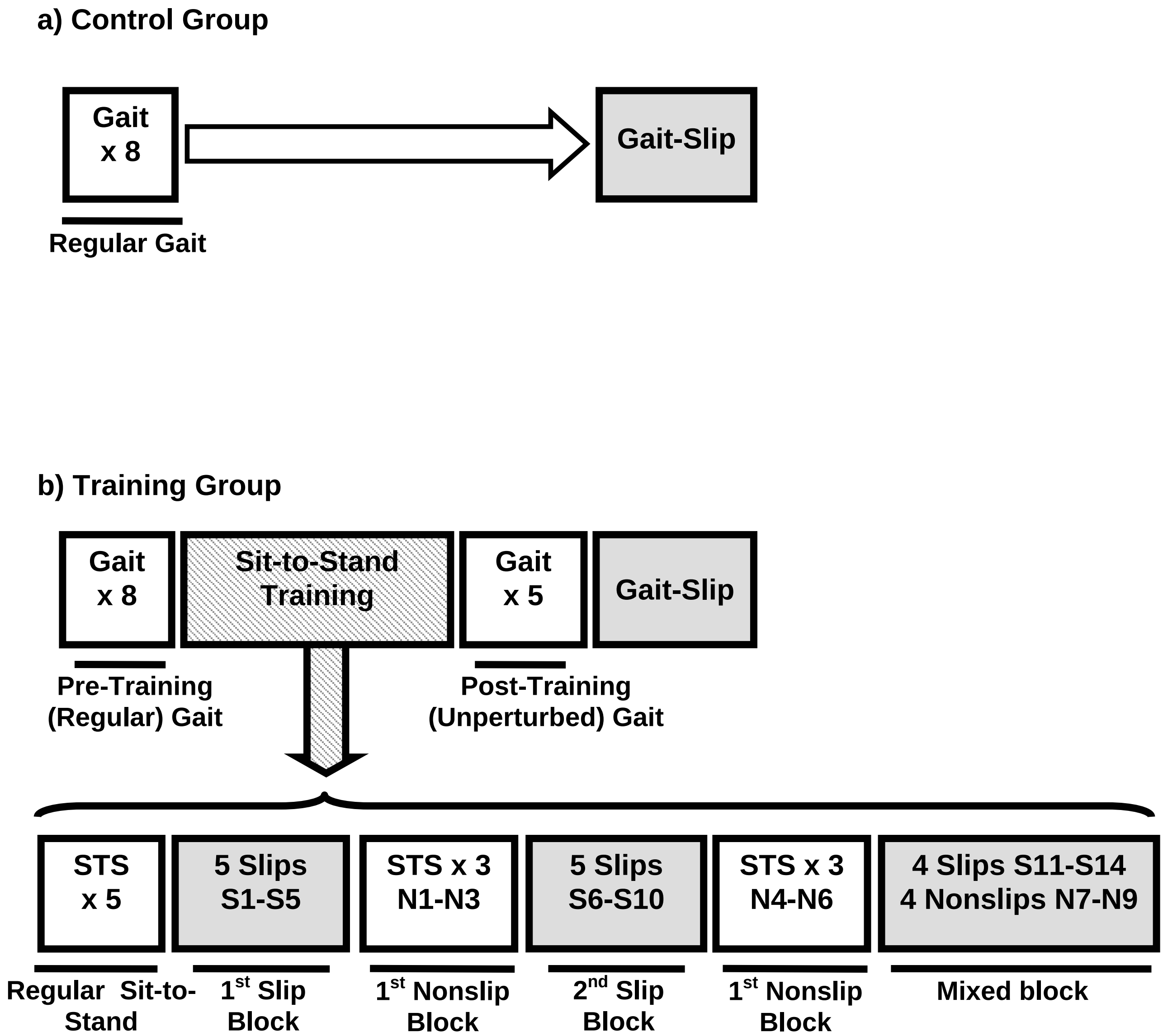

Figure 2

Figure 3

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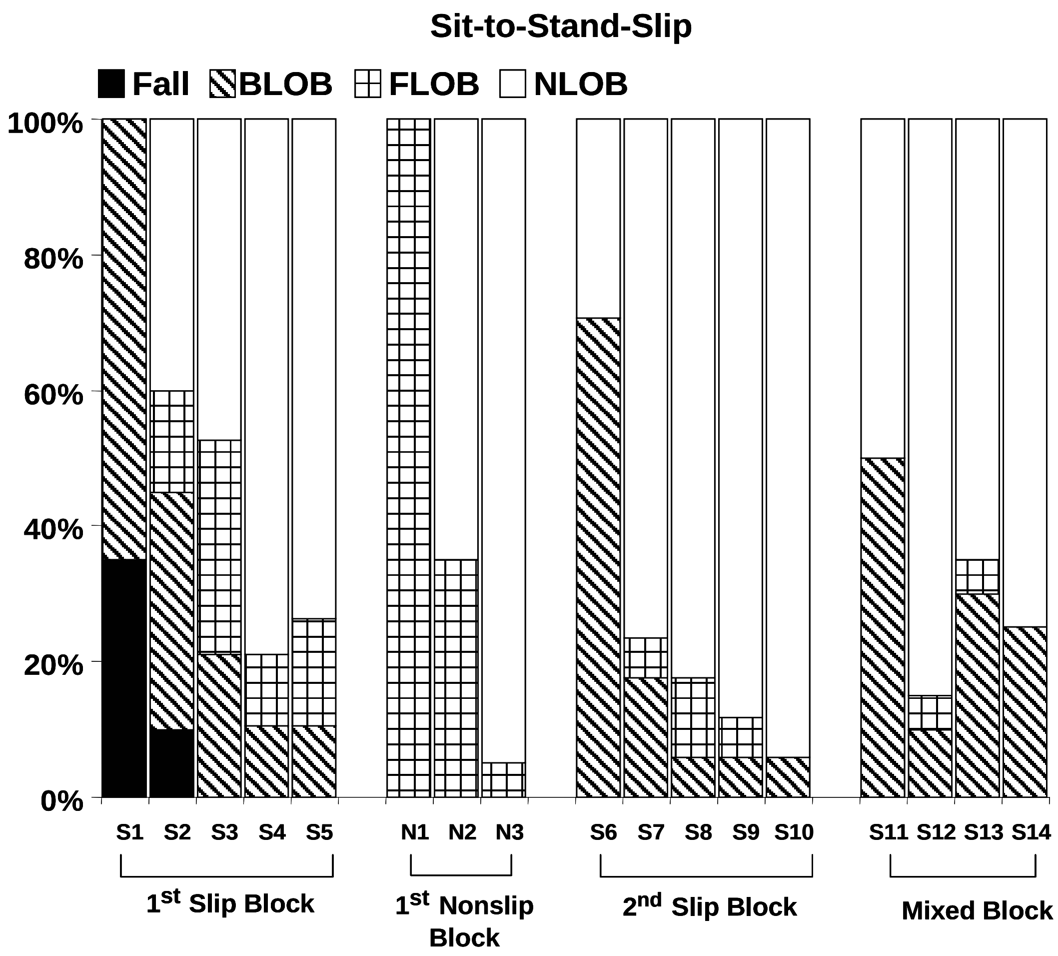

Figure 3

Figure 4
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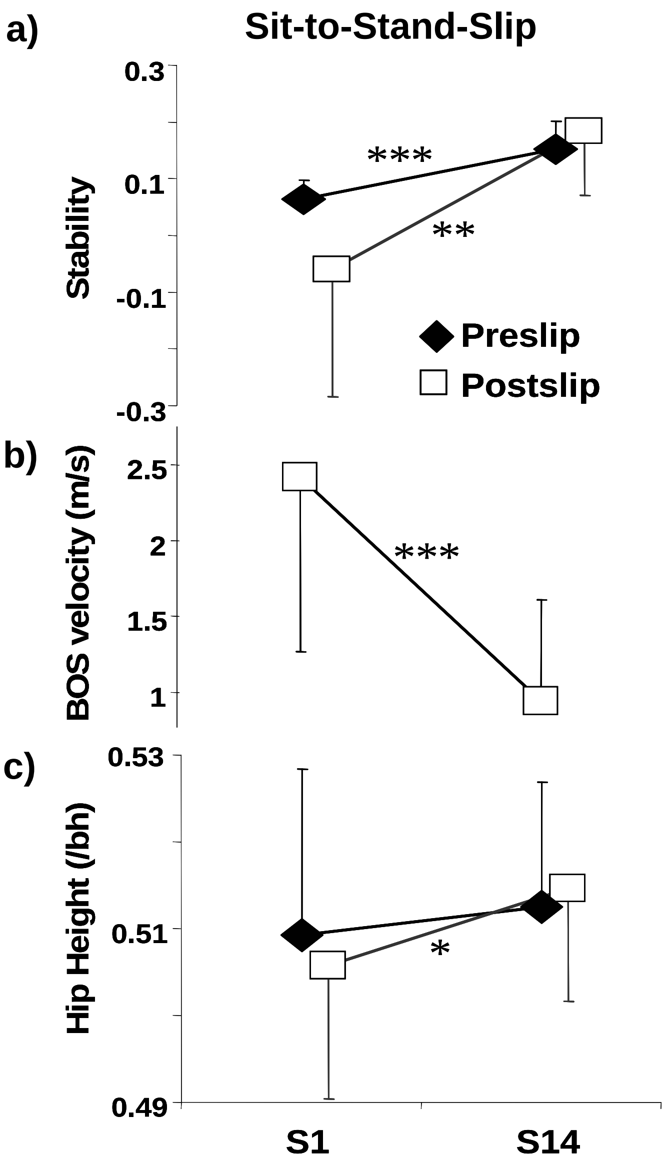

Figure 4

Figure 5
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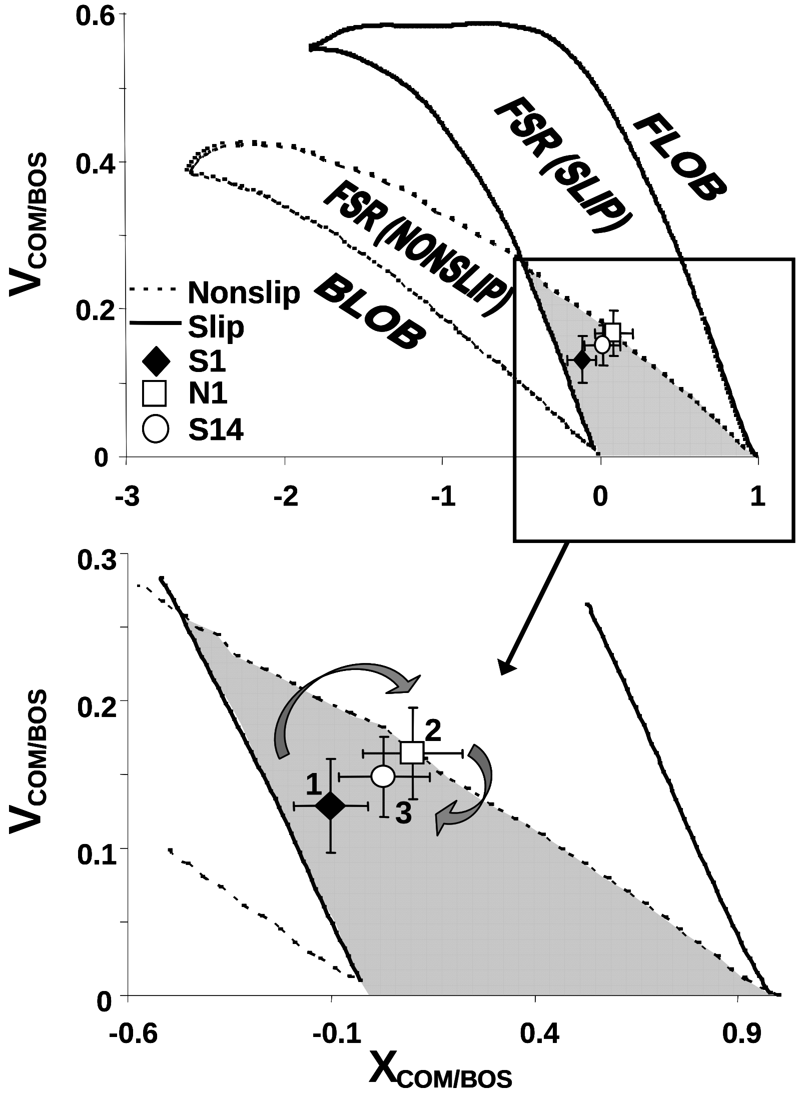

Figure 5

Figure 6
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Regular and Unperturbed Gait

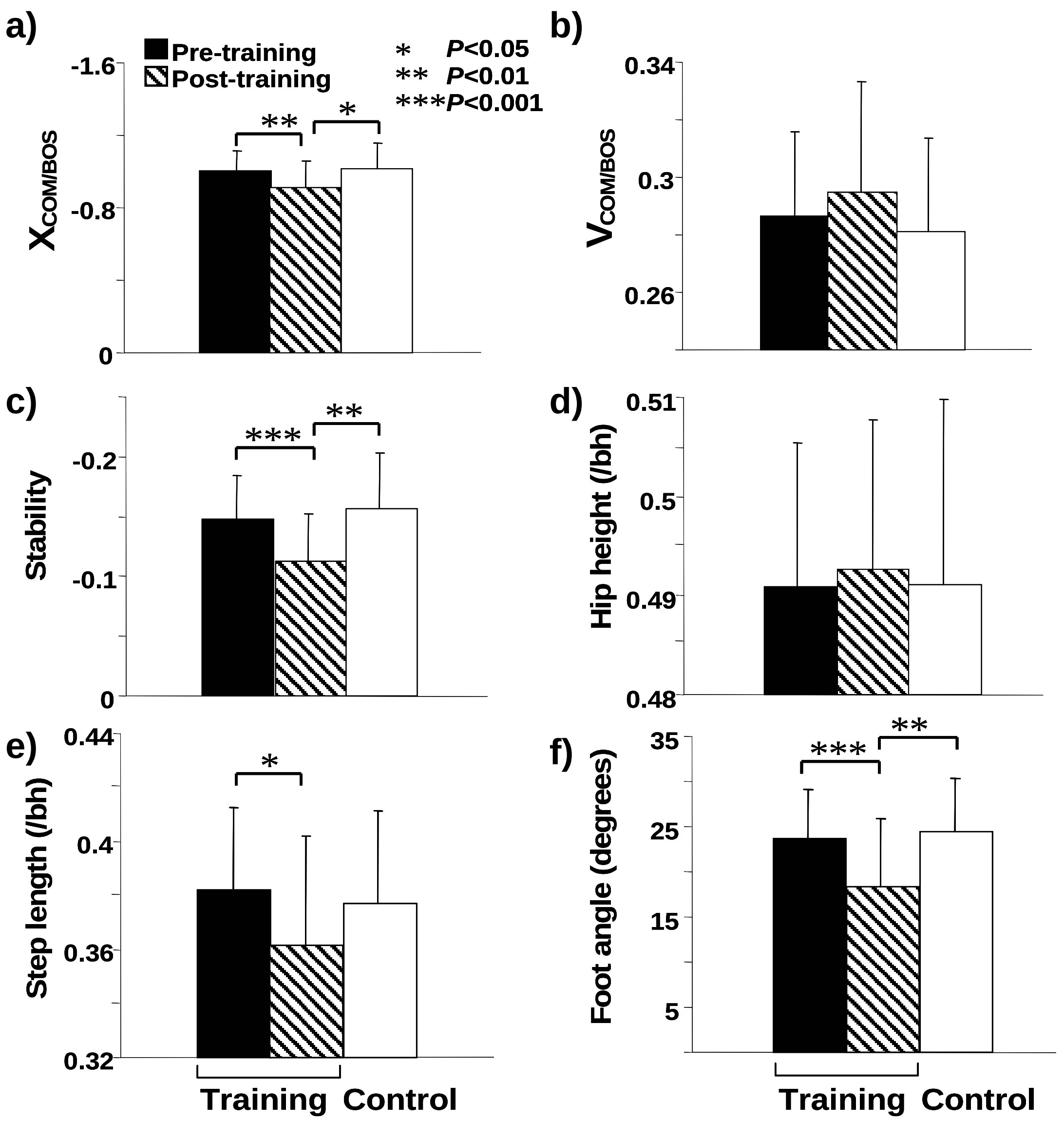

Figure 6

Figure 7
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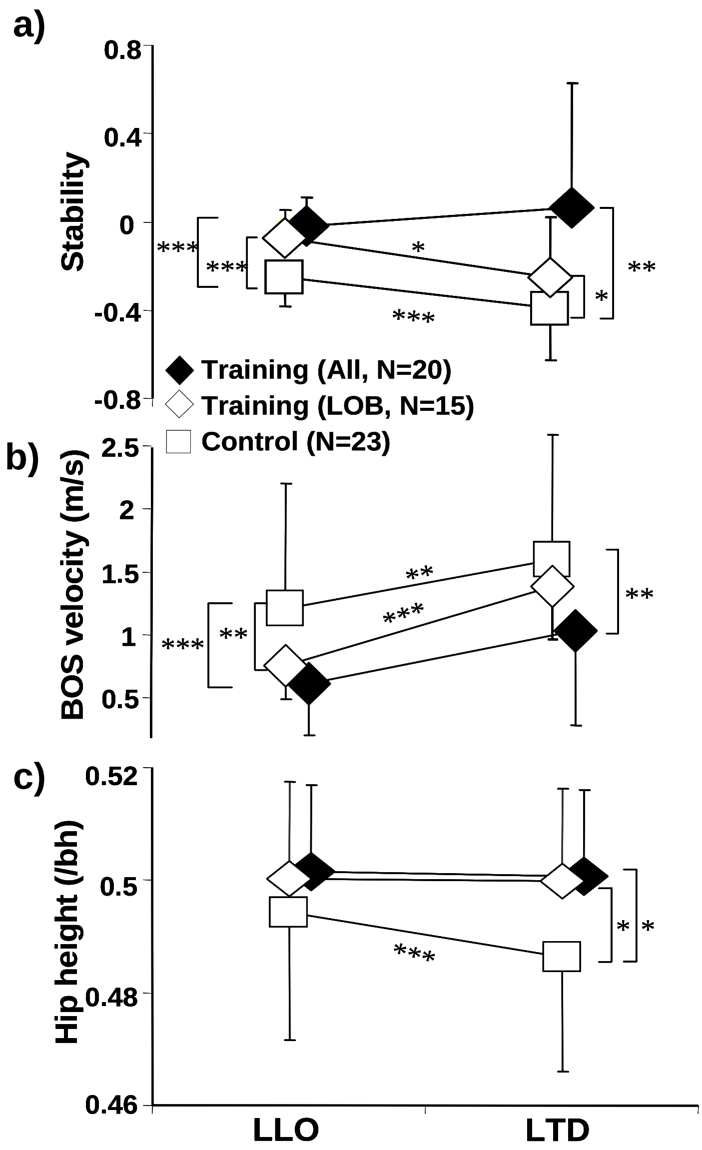

Figure 7