Exp Brain Res
DOI 10.1007/s00221-008-1547-x

RESEARCH ARTICLE

Inter-limb transfer of learned ankle movements

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Received: 3 January 2008 / Accepted: 7 August 2008

Abstract Inter-limb learning transfer (ILT) between the upper-limbs has been well documented, but no corresponding study of the lower limbs has been done. We investigated ILT in the lower limbs of subjects who learned to move a cursor toward targets within 800 ms using ankle movements: plantar/dorsi-flexion and inversion/eversion. Twenty-two healthy right-dominant subjects were divided into two groups: half performed the tasks first using the right foot (group RL), and the other half performed it first with the left foot (group LR). Targets appeared on a computer screen at head-height while subjects were seated with one foot on a goniometric ankle platform. Subjects were required to move the cursor toward one of three randomly appearing targets under two conditions: (1) neutral or no visual motor rotation, and (2) with a 30° visuo-motor rotation. Performance was quantified by computing the z-score for direction and position errors for each subject and ILT was assessed by comparing group performances for each foot. Results demonstrated that group LR but not group RL experienced significant ILT of directional as well as positional information in both tasks in a manner reflective of the distinctly different functional roles played by the upper and lower limbs.

Keywords Inter-limb transfer · Motor learning · Ankle · Cross hemispheric transfer · Limb dominance · Visuomotor rotation · Lower limb

Introduction

While central motor control of the limbs is primarily contralateral, there is increasing evidence that specific types of learned motor actions can transfer across the hemispheres (Sainburg 2002). Inter-limb transfer (ILT) of acquired motor skills, i.e., the ability of a limb to perform a task learned by the opposite limb, has been demonstrated for many activities such as drawing, writing, mirror tracing, ball catching, and pointing (Ketterlinus 1931; Cook 1933a, b; Hellebrandt et al. 1947). Most ILT research focuses on the upper limbs and shows ILT to be either symmetric (bi-directional) or asymmetric, depending on the task studied. The learning of simple tasks, such as grasping, lifting small objects, or anticipatory timing, transfers across hemispheres symmetrically (Lee and Carroll 2007). ILT of more complex learned movements, such as reaching in the presence of visuo-motor (VM) rotations is generally asymmetric and correspondingly more complex. In these studies, the two major determinants of reaching effectiveness, initial trajectory and final hand position, are selectively learned and transferred by opposite hemispheres. Specifically, initial trajectory information transfers from the non-dominant (L) arm to the dominant (R) arm but not vice-versa, and the opposite occurs for final position information (Sainburg and Wang 2002; Criscimagna-Hemminger et al. 2003; Wang and Sainburg 2006). This type of asymmetric ILT may reflect hemispheric specialization, wherein the dominant hemisphere specializes in movement trajectory information while the non-dominant hemisphere specializes in final position (Sainburg 2002). According to this theory, both hemispheres receive similar information on visual rotation but specialized controllers in each hemisphere use it differently.

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The possibility of ILT between the lower limbs has been investigated, with mixed results. In one study, subjects walked on a split-belt treadmill requiring each leg to adapt to a different speed, but no evidence of learning transference to the mirror condition was found (Prokop et al. 1995). Similar absence of ILT was found in another study in which subjects learned a one-legged hopping task on a treadmill (Anstis 1995). Positive evidence for ILT was reported by van Hedel et al. (2002), whose subjects learned to step over an obstacle with the lowest clearance possible while walking on a treadmill. In this study, obstacle avoidance skill was primarily manifested as improved knee control, which transferred symmetrically between the legs. Ankle adaptation and transfer, in contrast, were not observed, presumably due to the greater complexity and hence variability of the ankle joint. It was postulated that the positive finding in this study could have occurred because the task involved learning by knee flexors, rather than the extensors as tested in the two earlier studies (van Hedel et al. 2002). According to this hypothesis, knee flexors are more receptive to ILT than extensors during walking because they are inherently more centrally coupled than knee extensors via reciprocal inhibition.

The goal of the present study was to systematically test for ILT in a single lower limb joint: the ankle. Our learning paradigm was patterned after earlier studies of ILT in the upper limb and involved target reaching by the foot without, and with presence of VM rotations (Sainburg and Wang 2002; Wang and Sainburg 2006). We report the existence of significant ILT between the lower limbs, and note its clinical implications.

Methods

Subjects

Twenty-two neurologically intact right-footed adults (mean age 27.1, range 21–36 years, 10 males and 12 females) participated in this study; twenty of the subjects completed the entire protocol, and an additional two subjects only performed the neutral protocol. Subjects were randomly divided into either group RL or LR. Group demographics did not differ with respect to age, weight and height. Written, informed consent was obtained from each subjec prior to participation, and was approved by the Rutgers University Internal Review Board. The inclusion criterion consisted of being right foot dominant. All subjects had normal ranges of ankle motion and experienced no pain o stiffness.

Footedness was assessed using the modified Waterl footedness questionnaire that addressed the preference a foot manipulating an object (kicking a ball, smoothing sand, etc.), and the preference for the foot in providing support during tasks such as hopping on one foot, etc. (Elias et al. 1998). A written version of the Waterloo test was followed by an active physical version in which subjects were asked to demonstrate use of their feet, according to the written questions. To ensure that only right-dominant subjects were used, only those with foot dominance scores greater than 5 were included.

Experimental set-up

Subjects sat in a height-adjustable chair with feet hip-width apart, and shank oriented vertically, as depicted in Fig. 1. The foot was secured to a custom isokinetic ankle platform, and chair height was adjusted to bring the foot in contact with the platform with minimal vertical load (Morris et al. 2007). The ankle platform was mounted on a universal joint fitted with potentiometers for goniometric registration of dorsiflexion and plantar flexion on the y-axis and inversion–eversion motions on the x-axis. The goniometer output was digitized and sent to a computer to control cursor movement. Subjects thus could move the cursor up and down with dorsiflexion and plantar flexion respectively, and left and right by everting/inverting the right foot or oppositely for the left foot. Subjects viewed the cursor and targets on a 16″ screen with 800 × 600 pixels resolution updated at 60 Hz. Subjects fixated on the screen, which was head-height, and did not directly observe their feet during testing. Goniometric accuracy was 0.64 ± 0.17° and data were sampled at 13 Hz.

Each subject performed two tasks adapted from Sainburg and Wang (2002), as shown in Table 1. Group RL subjects performed the tasks first with the right foot, and then with the left foot; group LR subjects did the opposite. During task (1), the cursor moved in proportion to the biaxial ankle rotations of the user. Throughout task (2), a VM rotation was imposed, wherein the previously learned ankle motions now moved the cursor 30° counter

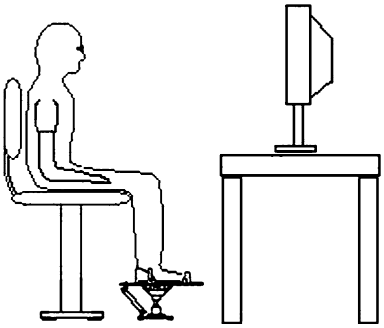


Fig. 1 Experimental setup. Subjects were seated in a height adjustable chair that allowed the knee to be flexed at a 90° angle. One foot was strapped onto the ankle platform. Subjects watched a computer screen as they controlled a cursor with ankle motions

Table 1 Experimental design

Group	Task 1: Neutral 144 Trials 11 Subjects per group		Task 2: VM Rotate 144 Trials 10 subjects per group		Catch:Neutral 4 Trials 5 subjects
RL	R	L	R	L	ID_L
LR	L	R	L	R	ID_R

In Task 1, the second, OFT foot of each group is compared with the corresponding naïve foot of the other group, as denoted by *arrows*. Identical comparison is made for task 2. In the catch trial, the first four initial directions (IDs) of the OFT feet of both groups are compared

clockwise (ccw) relative to the starting circle, causing the subject to learn a new motion, that needed to be rotated 30° clockwise (cw) to hit each target. Each task consisted of 24 trials to each of three (random) targets, for a total of 72 trials per task for each foot; each subject performed 288 trials in total. In addition, five subjects were presented with a catch-trial, in which the VM rotation was removed. The arrows denote the cross-group and within-group comparisons (Table 1).

At the start of each trial, subjects positioned the cursor inside of a start circle located in the center of the screen and held it for 0.3 seconds, using the foot attached to the platform. After receiving an audio and visual “go” cue, the subjects were given 800 ms to move the cursor to one of three targets that appeared at random. Targets were located around the base at radial distances of 250 pixels from its center, which represented approximately 5° of ankle rotation. Illustration of the experimental protocol for group LR is shown in Fig. 2. The arrows depict the ideal movement vectors to the targets, for the left neutral and VMR conditions.

Knowledge of results was given to the subjects by a score and audio feedback, which were both based on the final position of the cursor. Errors less than 42 pixels (0.84°) received ten points, errors within 42 and 84 pixels (0.84° and 1.68°) received three points, and errors within 84 and 126 pixels (1.68° and 2.52°) received 1 point. The subjects performed the task with each foot first without a VM rotation and then during a VM rotation in which the cursor was rotated 30° counterclockwise relative to the start circle. During VM rotation, target 3 was along the *x*-axis, and was reached by almost pure inversion by the right foot and eversion by the left; target 1 was centered after rotation.

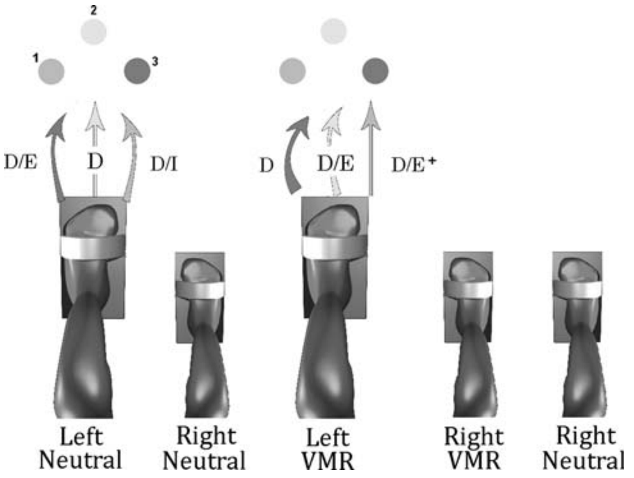


Fig. 2 Experimental Protocol for group LR. The task sequence and ideal direction of movements toward targets for a member of group LR are illustrated. Targets and trajectories to them (1, 2, 3 from *left to right*) are coded as *shades from light to dark*. The left foot (*left neutral*) initially trains to hit each target 24 times, using (ideally) dorsiflexion and inversion (*D/I*) for target 1, dorsiflexion only (*D*) for target 2, and dorsiflexion and eversion (*D/E*) for target 3. The right foot (*right neutral*) then performs the same task, however, movements from targets 1 and 3 are reversed (*arrows omitted*). For left VM rotation (30° ccw), movements must be shifted cw, as shown. For right VM rotation, the movements are also shifted cw (*arrows omitted*). For the neutral (catch) trial, the ccw rotation is removed (*arrows omitted*)

Evaluation

A custom MATLAB program quantified the movement data using three measures of performance: final position (FP) error, initial direction (ID) error, and final direction (FD) error. FP error was measured by the Euclidean distance between the center of the target and the foot-path position at the end of movement and reported as the percentage ratio of final position error to the distance from the center of the base to the center of each target (250 pixels). ID error was calculated as the difference between the vector defined by the foot-path position at the start of movement to the center of the target and the vector defined by the start of movement to the point of maximum velocity. FD error was determined by calculating the difference between the vector defined by the foot-path position at the start of movement to the center of the target and the vector defined by the start of movement to the foot-path position at the end of movement.

To standardize subjects according to basic skill level, the z-score as shown in Eq. 1 was computed for each of the three measures. Since the goal was to normalize each subject, and not each trial, scores from all 288 trials were pooled to compute one mean and standard deviation value for each subject. Since the distribution of the subjects’ data was logarithmic, the log-normal mean, μ, and standard deviation, σ, were computed as shown in Eqs. 2 and 3, respectively.

$$Z_i = \frac{x_i - \mu_{\log}}{\sigma_{\log}} \tag{1}$$

$$\mu_{\log} = e^{\mu + \frac{\sigma^2}{2}} \tag{2}$$

$$\sigma_{\log} = \sqrt{(e^{\sigma^2} - 1)e^{-2\mu + \sigma^2}} \tag{3}$$

To test for ILT, the transfer (second) foot of one group was compared with the naïve (first) foot of the other group in both tasks. The statistical approach was identical to previous studies (Sainburg and Wang 2002) and consisted of comparing the performance of the two groups during the first epochs (average of four trials) for each foot using a post-hoc group comparison. The percent of measurement error decrease was computed for both ankles as the ratio of the difference between the group average z-scores to the average of the naïve foot (Eq. 4).

$$\mathrm{ILT} = \frac{\mu_{\text{naive}} - \mu_{\text{OFT}}}{\mu_{\text{naive}}} \times 100\% \tag{4}$$

where μ_{naive} is the average z-score of motor skill for the first epoch of the first group that performed the task with the ankle of interest, and μ_{OFT} is the average z-score of the first epoch of the group that performed the task with the ankle of interest following opposite foot training (OFT).

A repeated measure analysis of variance (ANOVA) was performed using SPSS 15.0 (SPSS Inc, Chicago IL, USA) with group (RL or LR) as the between subjects variable, and target and foot (R or L) as the within-subject factors. Post hoc pair-wise comparisons using a Bonferroni correction were implemented to test the differences among targets, and to determine if there were differences between the naïve foot and that receiving OFT.

To assess subjects' adaptation to the VM rotation, a catch trial was done with five subjects (three RL and two LR) who performed four repetitions in the neutral condition after having completed the VM task with the final foot. Task adaptation was defined as the difference between the initial direction errors of the first post-training trial and those of the final neutral trial.

Results

Subjects

Subject demographics and selected results from the footedness survey are presented in Table 2. The mean written footedness assessment scores for group RL and LR were 12.5 and 12.0, respectively, and the mean physical footedness scores were 10.9 and 10.1, respectively. These scores are all well above the required score of 5, indicative of right dominance. All subjects completed the neutral task and ten subjects in each group completed both the neutral and rotated tasks.

Table 2 Demographics

	Group RL ($n = 11$)	Group LR ($n = 11$)
Age	26.2 ± 5.0	25.7 ± 4.3
Weight (lbs)	146.9 ± 35.4	146.1 ± 27.7
Height (in)	66.2 ± 3.4	66.2 ± 2.7
Physical footedness assessment	10.9 ± 4.6	10.1 ± 3.2
Written footedness questionnaire	12.5 ± 3.4	12.0 ± 3.6

A written footedness questionnaire was the primary determinant of footedness and physical footedness assessment was used to confirm the written results

Task sequence and overall performance

To illustrate the protocol, cursor trajectories for a representative subject from each group during all tasks are shown in Fig. 3. The RL subject is outlined in red (solid) and the LR subject is outlined in blue (dashed); trajectories to their respective targets (1, 2, and 3 from left to right) are coded as shades from light to dark. Tracking the RL subject, beginning with the first column, first row, it can be seen that trajectories during the final trial of task 1 were generally aimed near the targets. Note that the initial direction toward target 1 was off course, but corrected quickly.

Accuracy during the first trial after VM rotation was markedly reduced (second column, first row) with increased errors in initial and final direction, as well as final position. Initial performance of his left foot following OFT is shown in the third column, second row, and left (transfer) foot performance after several trials is shown in the fourth column, second row. Targeting accuracy improved by the last VM trial.

To determine if adaptation to the VM counter-clockwise rotation occurred, five subjects performed the neutral task immediately following the last VM rotation trial (post-exposure). Most of the trajectories (fifth column, second row) were rotated clockwise to the targets.

Average performance for both tasks from both groups is summarized in Fig. 4; more detailed views and comparisons are presented in later figures. Each data point represents the average and standard error of the z-normalized target errors from 12 trials. Each row of panels shows curves made by the first and second feet in the baseline and VM rotated conditions for both groups. The three rows show performance in terms of FP, ID and FD. One general observation is that the beginning trials of both groups in the neutral condition exhibited the worst performance (highest

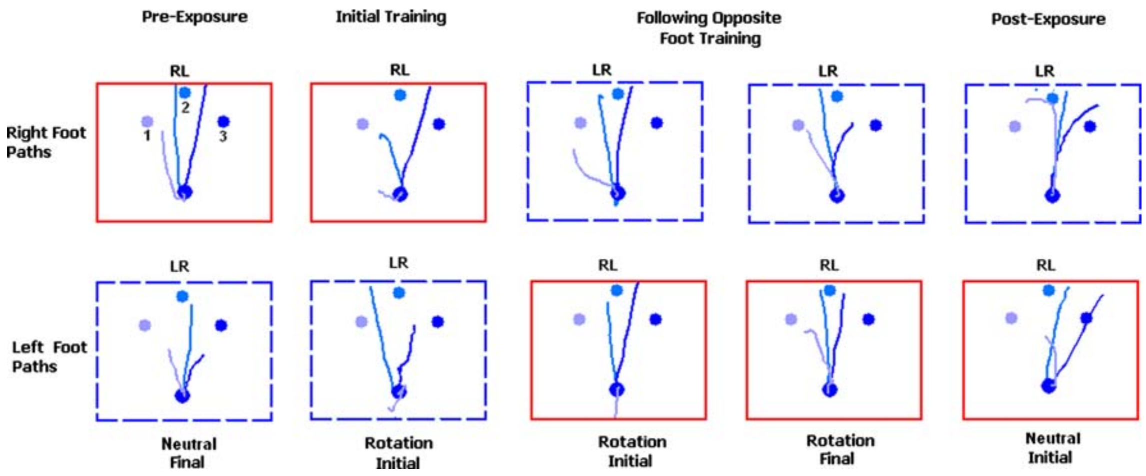
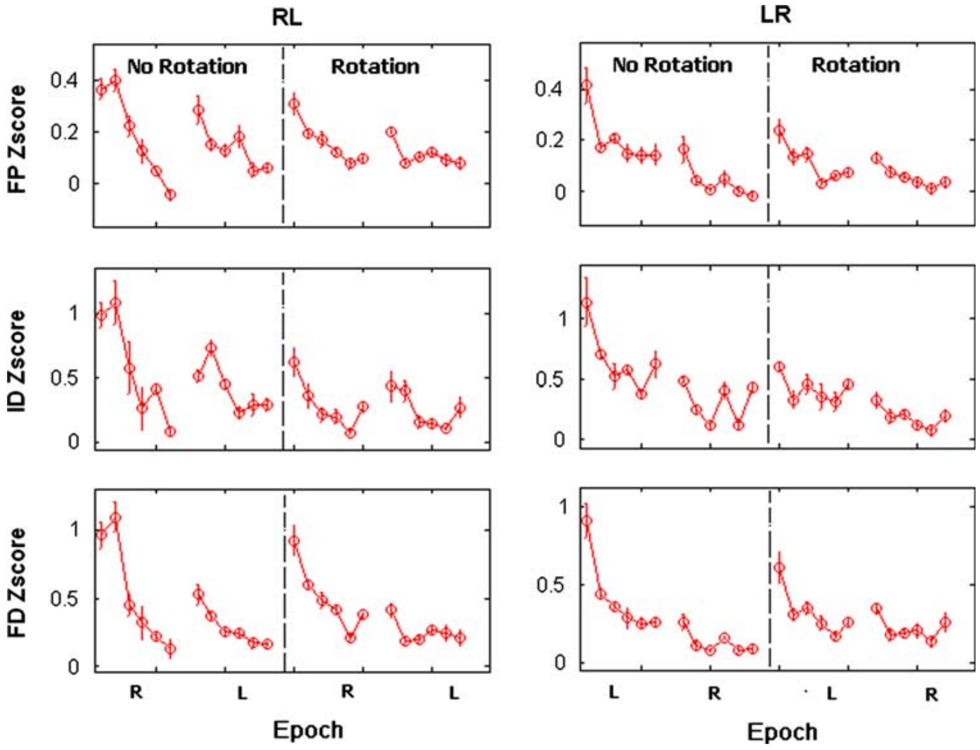


Fig. 3 Sample movement trajectories of representative subjects. Trajectories from a subject in group RL are in *solid boxes*, and trajectories from a subject in group LR are in *dashed boxes*. Trajectories are *shaded* in accord with the target. The *first column* shows the last cycle of movements of each foot during the baseline condition. The *second column* shows the first cycle of movements during the initial training session. The *third and fourth columns* show the first and last cycle of movements following OFT

Fig. 4 Performance Curves for both groups in chronological order. *Each data point* represents the average of 12 consecutive trials (mean ± SE). The *first two curves in each panel* are from the first and second foot that performed the task in the neutral condition



z-scores) in all three categories, as expected. Also evident from Fig. 4 is that all performance curves trended downwardly, meaning that errors decreased from the first to last of the six epochs in all tasks.

ILT during task 1: neutral

Since the task space of the ankle was in a different plane from the target effector space, and ankle movements were not mapped to that of the cursor in absolute coordinates, subjects needed to make VM transformations for the task, which constituted a novel learning challenge. Therefore, performance curves of the baseline (neutral) condition were compared to determine possible occurrence of ILT, as shown in Fig. 5. ANOVA of all three measures showed a significant interaction between foot and group ($P < 0.05$), but not between foot and target ($P > 0.05$). Comparing the initial left foot performance of both groups (right panels of Fig. 5), it can be seen that the right foot z-scores of group LR are lower than those of group RL for both FP

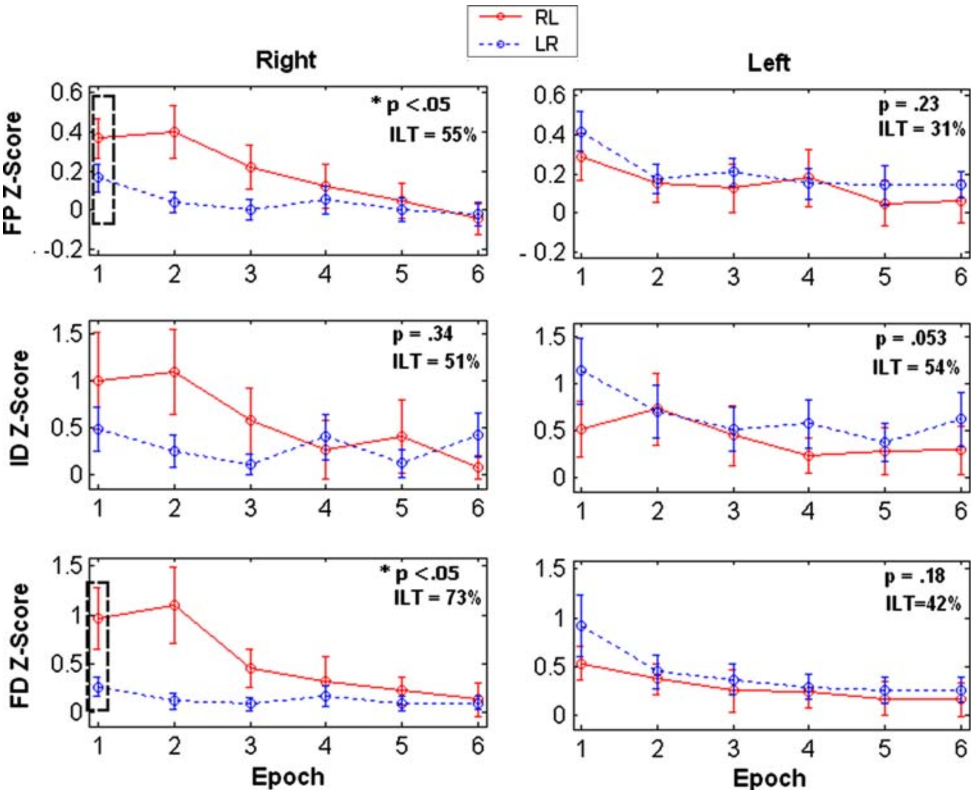


Fig. 5 Performance curves showing the mean z-scores from the neutral trials for the right and left feet. *Each data point* represents the average of 12 consecutive trials (mean ± SE). The performances for group RL and group LR are shown separately for the right and left feet. For the right foot, Group RL is naïve to the task; for the left foot, group LR is naive to the task

(0.16 ± 0.06 versus 0.36 ± 0.06, $P < 0.05$), and FD (0.26 ± 0.21 and 0.96 ± 0.21, $P < 0.05$). Right foot ID scores for group LR were lower than those of group RL but the two scores did not significantly differ (0.49 ± 0.37 versus 1.0 ± 0.37, $P = 0.34$). Left foot z-scores showed slight trends for FP (0.29 ± 0.08 vs. 0.42 ± 0.08, $P = 0.23$), ID (0.51 ± 0.22 vs. 1.1 ± 0.22; $P = 0.053$) and FD (0.53 ± 0.20 and 0.91 ± 0.20, $P = 0.18$), but the differences between the two groups were not significant. ILT measures are annotated in upper right of each panel; note that the right ankle improvements in both FP and FD are significant ($P < 0.05$).

ILT during task 2: VM rotation

Analysis of variance showed a significant interaction between foot and group for the FD measure ($P < 0.05$), but not for FP ($P = 0.10$) or ID ($P = 0.13$). Between-group comparisons were made to study the foot group interaction in more detail (Fig. 6). Group LR experienced significant ILT in terms of both FP and FD, but the RL group did not. The average z-score for FP of the right foot of group LR was significantly lower than that of group RL (0.14 ± 0.06 vs. 0.37 ± 0.06; $P < 0.05$). The left foot z-score of group LR, in contrast, did not significantly differ from those of group RL (0.27 ± 0.06 vs. 0.22 ± 0.06; $P = 0.61$). Likewise, FD scores were also lower for the right foot of group LR (0.33 ± 0.15 vs. 0.88 ± 0.15; $P < 0.05$). The difference between the groups is evident also by comparing the performance curves of the right and left feet. In the case of the right foot, the performance curves of the RL group are consistently higher than those for the LR group for all epochs in all measures, unlike the left foot, in which the group curves cross.

Since the off-center targets seemed to be more difficult for the subjects, pair-wise comparisons were done to detect the presence of systematic effects. ANOVA did not show a significant interaction between foot and target for any of the scores ($P \gg 0.05$ for FP and ID, $P = 0.051$ for FD). The mean scores for all epochs for the three targets are shown in Fig. 7a–c. As seen in Fig. 7a, b, target 2 (center) produced the lowest errors and target 3 produced the highest for both feet in terms of both FP and FD. FP error differed significantly between targets 2 and 3 (0.01 ± 0.07 vs. 0.50 ± 0.10; $P < 0.01$) for the left but not the right foot. FD errors (Fig. 7c) were also significantly higher at target 3 for the left foot compared to the center target (0.89 ± 0.19 vs. 0.04 ± 0.08; $P < 0.01$). Target 3 required the left foot to dorsiflex and evert and the right foot to dorsiflex and invert and thus although left foot eversion was less accurate than right foot inversion, the difficulty with target 3 does not relate to the type of movement, but its position. Note that targets 1 and 3 did not differ significantly for either foot, and hence there is no evidence for movement preference along the x-axis.

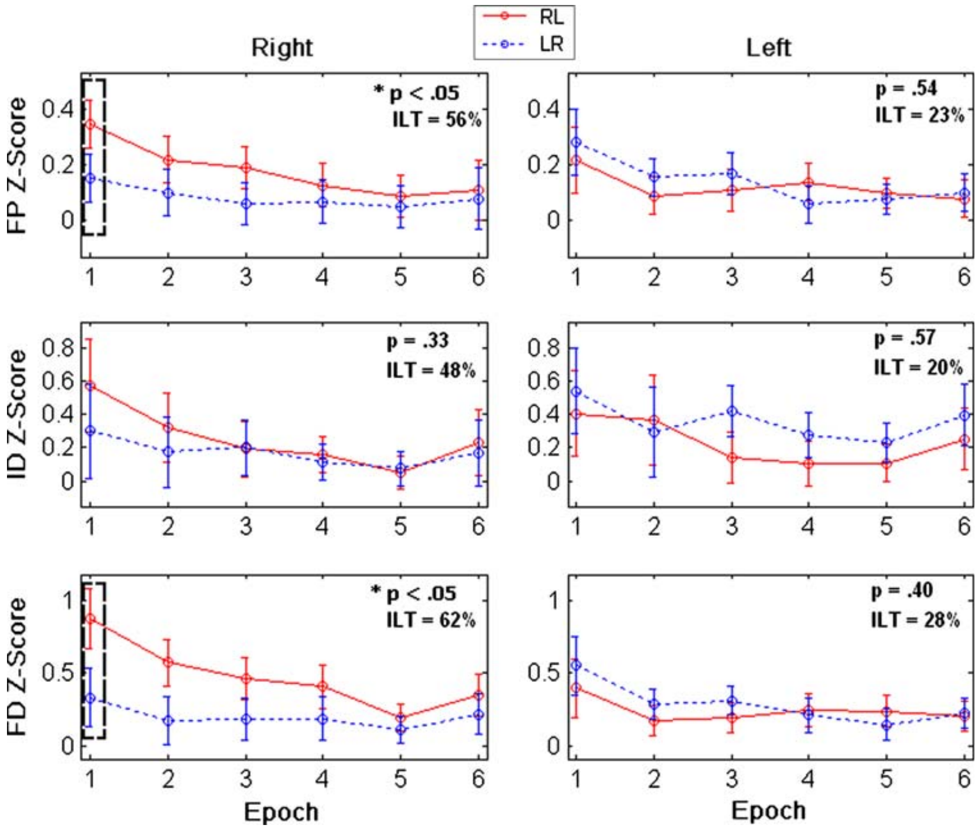


Fig. 6 Performance curves showing the mean z-scores from the VM rotation trials for the right and left feet. *Each data point* represents the average of 12 consecutive trials (mean ± SE). The performances for group RL and group LR are shown separately for the right and left feet. For the right foot, group RL is naïve to the task; for the left foot, group LR is naive to the task

Catch trials

Five subjects were exposed to a catch trial to determine th after-effects of the VM rotation. After the final VM rotation trial, the 30° ccw rotation was removed, and four successive trials were run. Changes in ID errors were computed for all three targets for both groups, with negative differences representing a cw rotation. Mean ID differences were similar for targets 1 and 2 (−27.8 ± 19.9° and −27.9 ± 17.7°, respectively). The mean ID difference was lower for target 3 (−17.7 ± 23.3°), but there were no significant differences among the three targets. The clos approximation to 30° cw errors in the after-effect test indicates that adaptation occurred during VM rotation.

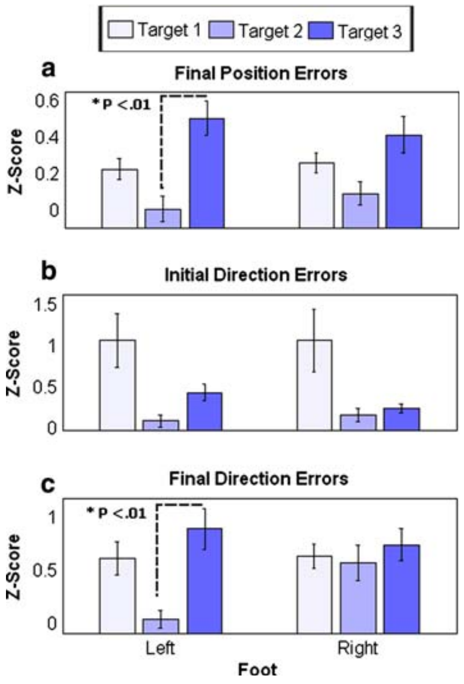


Fig. 7 Target performance comparison. The mean scores for all visuomotor rotation trials for each foot are shown above. *Error bars* represent ± SE. **a** FP errors; **b** FD errors; **c** ID errors

Discussion

Validity of study

Herein we report the first systematic study of ILT of learned movements by the ankle. We studied 22 health subjects, separated into two groups. Using a target reachin VM rotation task similar to that developed for the upper-limb, we demonstrated ILT occurring from the non-dominant (left) to the dominant (right) foot, but not vice-versa. As seen in the between-group comparisons in Fig. 6, the learning transfer included information about final movement direction and position ($P < 0.05$). Significant improvements in performance ranging from 55 to 74%

were seen following OFT. A test of adaptation in a subset of subjects using a catch trial after removing the 30-degree ccw VM rotation, revealed a cw after-effect in all three targets, with two of the targets having after-effects close to 30°, indicating nearly complete adaptation. Furthermore, we showed ILT occurring for a novel task involving coordinate transformation between foot and cursor motion. In this test, the learning transfer pattern was identical to the VM task, with right foot final movement direction and position errors decreasing after OFT. These results, with preferential L to R transfer in both tasks, are consistent with previous studies in which exercise training of the left leg improved the performance of the right leg, but not vice versa (Haaland and Hoff 2003).

Thus, ILT can be generalized to the ankle and extend the results of van Hedel et al. (2002), who showed that movements learned at the knee to avoid an obstacle on a treadmill are transferred from one leg to the other, non-preferentially. In that study, the ankles did not experience significant ILT and their negative finding was attributed to the greater variability and complexity of the ankles as compared with knees. Herein, by studying isolated ankle movements in a single-joint targeting paradigm, with between-group comparisons, we found positive evidence for ILT of ankle motor control.

Our analysis differs from that of Sainburg et al. (2002), mainly in terms of baseline testing. In their studies, the task and effector space was common, since the cursor was projected onto the hand. Our subjects were required to make coordinate transformations in all tests since their feet operated near floor level, while the cursor moved at eye-level while seated. Furthermore, cursor movement was in the frontal plane, while foot motion was three-dimensional. Learning this transformation was an integral part of the experiment, and indeed, we found evidence for significant ILT in the baseline (neutral) trials. It was thus not possible to use baseline performance as a normalization factor as done by Sainburg et al. (2002). Instead, we computed z-normalization scores for each subject, in order to minimize skill-differences.

The possible influence of musculoskeletal differences between ankles on the ILT results during VM rotation was investigated by analyzing performance difference among targets (Fig. 7). For the left foot, target 3 was significantly more difficult, in terms of both FP and FD errors, based on pair-wise comparison with target 2. Since target 3 required eversion by the left foot, a motion which was amplified by VM rotation (see Fig. 2), it could be argued that left foot performance suffered relative to that of the right because eversion was more difficult than inversion, which is the motion the right foot needed to reach target 3. This argument, however, is not strongly supported by the evidence, since, (1) the right foot tallied more errors toward target 3 (inversion), than toward target 1 (although not significantly, Figure 7); (2) there was no significant difference between targets 1 and 3 for either foot; (3) ANOVA showed no interaction between foot and target. Thus, the target difference may not have significantly influenced the ILT asymmetry of our results in terms of VM rotation, and the consistency of the latter with those of the non-rotated test argue against a major influence.

Comparison with upper-limb ILT

Direct comparison of ILT characteristics of the upper and lower-limbs is not straightforward due to fundamental differences in their function. Upper-limbs specialize in fine manipulation, with infinite degrees of freedom, usually cooperating in the same workspace whereas the lower limbs specialize in relatively gross rhythmic alternations, usually operating in separate workspaces, where stability and balance are the primary objectives. For manipulation tasks, the foot task space, i.e., pedals and levers, is usually removed from the effector space, i.e., vehicles or equipment. Accordingly, motor strategies for upper and lower limbs differ widely, as documented by their relative cortical activities. Upper-limb activity involves primarily the contralateral sensorimotor cortex, and the ipsilateral cerebellum, whereas ankle movements exhibit more ipsilateral activity in the motor and pre-motor cortices and are continually under reciprocal control (Ciccarelli et al. 2005; Dietz 2002; Kapreli et al. 2006). Thus, the upper limbs operate with more independence, and less cross-hemispheric interaction than the lower limbs.

It has been suggested that ILT expresses as asymmetric when there is a large degree of hemispherical interactions (Wang and Sainburg 2006). In arm experiments, when workspace is common, ILT is asymmetric; when arms operate in separate workspaces, i.e. both task and effector space are separate, ILT is symmetric (Wang and Sainburg 2006). Although our subjects' feet manipulated a common effector (cursor on screen), they were technically in separate workspaces, a situation that is somewhat in between the two protocols used by Sainburg et al. Nevertheless, our finding of asymmetric ILT is consistent with previous interpretation, since lower-limbs have inherently greater cross-hemispheric activity.

Lateralization of the arms, i.e. handedness, manifests as preferential use of the left hand (for right-handers) for holding objects in position while the right arm manipulates a tool, such as in the case of handwriting (Sainburg and Wang 2002). This behavioral specialization of the arms, when working in a common space, provides an explanatory context for the asymmetric transfer of information between them. Asymmetry is also reflected in the cortex, wherein left hand motions are much more bilaterally represented in the sensorimotor cortex compared with the right (Kapreli et al. 2006).

Lateralization of the feet, i.e. footedness, may be less prominent than handedness, and may vary depending on the context. For example, during unilateral balance, the right foot is the favored postural stabilizer, with the ankle being the most important joint (Gabbard 1997). Thus during gait initiation, the right foot is likely to be the primary stabilizer. Our results on ILT of both position and direction going to the right foot are consistent with the fact that the feet are not involved in common manipulation, but rather each ankle, during the single stance phase, is alternately required to control both position and trajectory. The primary lead ankle, i.e. the right, may be endowed with a more adaptive control system that would be more responsive to ILT. This concept is concordant with upper-limb ILT, where each limb receives benefit only according to its specialty, i.e. the right arm learns trajectory information and the left, position. It should be noted that our experimental condition of sitting, with one ankle moving while the leg was partially weight-supported, simulates a common position for ankle exercise, and does not closely simulate either standing or gait.

Whether the present results represent cross-hemispheric transfer (CHT) of learning, or transfer at a lower level, such as spinal, cannot be concluded. Recent studies have provided strong evidence for CHT by showing that subjects who had left hemispheric damage due to stroke exhibited deficits in arm trajectory, whereas those with right hemispheric damage had deficits in final position accuracy (Schaefer et al. 2007). These specific hemispheric lateralizations correlate well with behavioral specializations of the arms noted above. Further support for CHT was demonstrated in a study showing that muscular strength gained by upper or lower-limb transfers to the opposing limb (Munn et al. 2004). Meta-analysis of randomized, controlled studies of limb training transfer revealed that a strength increase of 35% in a trained lower-limb was accompanied by a 7.8% strength increase in the contralateral limb even though it experienced no substantial muscle activity during training, and did not increase cross-sectional muscle area (Munn et al. 2004). These ‘cross-educational’ strength gains were limited to the homologous muscle of the opposite untrained limb, and to the same movement task performed by the trained limb. The specificity of this phenomenon and the lack of detectible morphological changes in muscle suggests that transfer is due to alterations in neural control at a central, possibly hemispheric level (Lee and Carroll 2007).

Clinical implications

This study of ILT has important implications for functional rehabilitation of clients with hemiparesis due to stroke, CP or other central injury. Most hemiparetics cannot fruitfully exercise their affected leg due to severe control deficiency, and therefore do not generally participate in directed physical therapies. Therapeutic options are further limited since the affected ankle is generally immobilized in an orthosis in order to restore a semblance of gait. If the affected limb could be improved by sustained exercises of the contralateral limb, this could ameliorate the complications caused its disuse and maximize the effectiveness of rehabilitation. In particular, restoring even a limited degree of ankle control could restore un-assisted gait and/or postural balance to many clients. The present results thus provide clear evidence for the potential benefit to the affected limb afforded by contralateral limb training, and studies are underway to test its efficacy (Morris et al. 2007).

Acknowledgments We thank, Dr. Steven Escaldi, Carey Glass, C.P.O, Nam Hun Kim, Ph.D. and Richard Thomas for technical help. This study was funded by a U.S. Department of Education NIDRR RERC grant.

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