Published in final edited form as:

Gait Posture. 2017 July ; 56: 24–30. doi:10.1016/j.gaitpost.2017.04.032.

Interlimb Transfer of Motor Skill Learning during Walking: No evidence for asymmetric transfer

Chandramouli Krishnan, PT, PhD¹, Rajiv Ranganathan, PhD², and Manik Tatarbe¹

¹Department of Physical Medicine and Rehabilitation, University of Michigan Medical School, Ann Arbor, MI, USA

²Department of Kinesiology, Michigan State University, East Lansing, MI, USA

Abstract

Several studies have shown that learning a motor skill in one limb can transfer to the opposite limb—a phenomenon called as interlimb transfer. The transfer of motor skills between limbs, however, has shown to be asymmetric, where one side benefits to a greater extent than the other. While this phenomenon has been well-documented in the upper-extremity, evidence for interlimb transfer in the lower-extremity is limited and mixed. This study investigated the extent of interlimb transfer during walking, and tested whether this transfer was asymmetric using a foot trajectory-tracking paradigm that has been specifically used for gait rehabilitation. The paradigm involved learning a new gait pattern which required greater hip and knee flexion during the swing phase of the gait while walking on a treadmill. Twenty young adults were randomized into two equal groups, where one group (right-to-left: RL) practiced the task initially with the dominant right leg and the other group (left-to-right: LR) practiced the task initially with their non-dominant left leg. After training, both groups practiced the task with their opposite leg to test the transfer effects. The changes in tracking error on each leg were computed to quantify learning and transfer effects. The results indicated that practice with one leg improved the motor performance of the other leg; however, the amount of transfer was similar across groups, indicating that there was no asymmetry in transfer. This finding is contradictory to most upper-extremity studies (where asymmetric transfer has been reported) and points out that both differences in neural processes and types of tasks may mediate interlimb transfer.

Keywords

Skill learning; cross-transfer; cross education; asymmetry; motor task; rehabilitation

Address for Correspondence: Chandramouli Krishnan, Director, Neuromuscular & Rehabilitation Robotics Laboratory (NeuRRo Lab), Department of Physical Medicine and Rehabilitation, University of Michigan, 325 E Eisenhower Parkway (Suite 3013), Ann Arbor, MI - 48108, Phone: (319) 321-0117, Fax: (734-615-1770), mouli@umich.edu.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

INTRODUCTION

The issue of “motor transfer” – i.e., the ability to learn a new motor skill and transfer it to another task or situation – is fundamental to learning and development, and is considered to be a key factor for motor recovery after neurologic or orthopedic injuries [1, 2]. One specific type of transfer is interlimb transfer where the neuromotor system retrieves information relevant to learning from the trained limb, and transfers it to the opposite, untrained limb [3–7]. This phenomenon of interlimb transfer is not only interesting from a theoretical standpoint of how movements are represented, but also to rehabilitation specialists, as it has therapeutic implications for individuals with unilateral deficits like stroke.

The concept of interlimb transfer has been studied extensively in the upper-limb, and various factors (e.g., type of task, conception of the task, spatial reference frame, duration of training, motor variability during training, ageing, sleep) have been identified to affect the extent and stability of transfer [8–14]. One specific finding is that the amount of interlimb transfer of motor learning appears to be asymmetric or side-specific, with one limb showing greater ability to learn from practice on the other limb [3, 5, 15–17]. Whether it is the dominant or non-dominant limb that shows greater transfer seems to be a function of the task, and this asymmetry has been linked to the idea of hand/hemispheric dominance [16, 18–20]. However, while there is strong evidence for this asymmetry in the upper limb, the evidence for inter-limb transfer in the lower-limb has been mixed. van Hedel et al. used a novel obstacle avoidance task to study the extent and asymmetry of transfer of motor skill learning from one leg to the other [21]. They observed a significant transfer of motor skills between limbs, but reported no asymmetry in the amount of transfer between limbs. In contrast, Houldin et al. evaluated the extent of interlimb transfer using a unipedal walking task and reported limited transfer of locomotor adaptations from the right leg to the left leg [22]. Finally, a recent study by Stockel and Wang [11] showed that the asymmetry in the lower limb was mediated by the task context, depending on whether the feedback was spatial (kinematic) or dynamic (force).

Given the paradigms used to investigate interlimb transfer in the lower limb have been varied, we investigated the amount of interlimb transfer in a paradigm that we have specifically used for gait rehabilitation [23, 24]. The paradigm involves a foot trajectory-tracking task that necessitates participants to produce greater hip and knee flexion by coordinating their muscle activation patterns during the swing phase of the gait, and has been used to promote motor recovery after stroke [23–28]. Here, we used this functional paradigm to study the extent of interlimb transfer and test whether there is an asymmetry in the amount of transfer between the dominant and the non-dominant legs. We hypothesized that significant improvement in performance would be observed in the transfer leg after training with the other leg, and that this transfer would be asymmetric between the dominant and the nondominant leg.

METHODS

Participants

Twenty right-legged (as determined by their preferred leg to kick a ball) healthy adults (Age: 22.8 ± 5.8 years, Height: 1.7 ± 0.1 m, Weight: 66 ± 15.9 kg) participated in this study. All participants signed an informed consent document that was approved by the University of Michigan Institutional Review Board.

Experimental Protocol

The schematic of the experimental protocol is shown in Figure 1. Prior to the experiment, participants were randomized into two experimental groups: (1) right-to-left (RL) and (2) left-to-right (LR) group. Participants in the RL group practiced the motor learning task with the right leg during the training phase and were tested for transfer effects with the left leg. Participants in the LR group used the legs in the opposite order. Throughout the paper, the terms “training leg” and “transfer leg” will be used to refer to the leg which was used to learn the task first (i.e. for RL group: training leg – right leg, transfer leg-left leg; for LR group: training leg – left leg, transfer leg – right leg)

The experiment consisted of four phases: (1) pre-test phase, (2) training phase, (3) post-test phase, and (4) transfer phase (Figure 1). During the *pre-test phase*, the initial performance of the transfer and the training leg was established using a foot-trajectory tracking paradigm [23, 25, 27–30], where the participant changed their gait to match a target projected on the monitor. The target was created from the ensemble average of the baseline walking (B) trajectory by scaling the hip and knee angles by 30% during the swing phase of the gait and projecting it in the end-point space (further details are provided below). Target-matching performance was evaluated both with (TM) and without visual feedback (NVF) of their actual trajectory – this design allowed us to evaluate interlimb transfer both with and without feedback. The *training phase* consisted of repeated practice of the foot-trajectory tracking task – 8 blocks of practice was performed with each block lasting for one minute. In the *post-test phase*, the changes in target-tracking performance of the trained leg (i.e., learning) and the initial change in the performance of the untrained, opposite leg (i.e., interlimb transfer) were evaluated. During the *transfer phase*, the effects of the interlimb transfer on final performance level (if any) was evaluated. Here, the participant repeated the same sequence of events performed in the training phase using their transfer leg. Following which, improvements in performance of the transfer leg was evaluated. Throughout the experiment, each block was separated by a one minute rest-period. On average, each block consisted of $43 (\pm 4)$ gait cycles.

The target template trajectory for the motor learning task was created for each leg (training leg and the transfer leg) from the participant’s hip and knee joint kinematics data obtained from the respective legs during baseline walking. For this, retroreflective spherical markers (19 mm) were placed on the participant’s greater trochanter, lateral epicondyle of the femur, and lateral malleolus of the ankle. The participant then walked on a motorized treadmill (Woodway USA) at 2.0 mph with their hands placed over a custom-built treadmill rail system (Figure 2a). The sagittal plane kinematics of the participant while walking on the

treadmill was recorded using a high-definition camera and tracked in real-time using an established algorithm that has been described elsewhere [28]. After a two minute warm-up period, baseline kinematic data were recorded for one minute. The ensemble averages of the hip and knee joint angles recorded during baseline walking were then scaled to create a target template trajectory. The template corresponded to a gait pattern that necessitated greater hip and knee joint angle by a scale of 30% during the swing phase of the gait (Figure 2b) [23, 25–27]. To prevent any abrupt scaling both in the beginning and at end of swing phase, the trajectory was smoothed using a Hanning window [24, 28, 30]. This template was then projected in the end-point space (i.e., spatial path of participant's lateral malleolus relative to the hip on the sagittal plane) using a forward kinematic equation [26, 28, 31]:

$$\begin{bmatrix} X_a \\ Y_a \end{bmatrix} = \begin{bmatrix} \sin \Theta_h & -\sin(\Theta_k - \Theta_h) \\ -\cos \Theta_h & -\cos(\Theta_k - \Theta_h) \end{bmatrix} \begin{bmatrix} l_1 \\ l_2 \end{bmatrix}$$

where X_a and Y_a are the x and y positions of the ankle lateral malleolus (referred to as the foot trajectory) relative to the hip, l_1 is the distance between hip and knee markers, l_2 is the distance between knee and ankle markers, Θ_h is the anatomical hip angle relative to a vertical pelvis, and Θ_k is the anatomical knee angle. The target template trajectory was then displayed concurrently with the participant's actual foot trajectory on a computer monitor placed in front of the participant (Figure 2c). The duration of the concurrent visual feedback on the screen was adjusted such that the participant could see the entire trajectory produced over the previous gait cycle. Throughout the experiment, the participant was instructed to match the target, as precisely as possible, by changing their gait during the swing phase of the gait.

Data Analyses

Task performance during target-tracking (i.e. how closely the actual trajectory matched the target trajectory) was quantified by computing the tracking error observed during each block. The tracking error was computed for each gait cycle as the non-overlapping area (in pixels) between the target trajectory and the actual foot trajectory produced in that gait cycle (Figure 2c). This area was normalized to area within the participant's target foot trajectory and averaged across strides during each block..

Statistical analysis

To evaluate whether baseline performance of the training leg and transfer leg was similar between groups, repeated measures analysis of variance (ANOVA) with block (Tr-TM Pre and Tf-TM Pre) as a within-subjects factor and group (RL and LR) as a between-subjects factor was performed. To evaluate whether training improved performance in the trained leg (i.e., whether learning occurred) and whether learning differed by group, repeated measures analysis of variance (ANOVA) with block (Tr-TM Pre and Tr-TM Post) as a within-subjects factor and group (RL and LR) as a between-subjects factor was performed.

To evaluate whether training improved performance of the untrained leg (i.e., whether transfer of motor learning occurred between legs) and whether interlimb transfer differed by

group, another repeated measures ANOVA with block (initial transfer: Tf-TM Pre and Tf-TM; final transfer: Tf-TM Pre and Tf-TM Post) as a within-subject factor and group (RL and LR) as between-subjects factor was performed. A similar analysis was also performed on the no visual feedback trials (learning: Tr-NVF Pre and Tr-NVF post or Tf-NVF Pre and Tf-NVF Post, transfer: Tf-NVF Pre and Tf-NVF) to examine if learning and transfer were dependent on visual feedback.

To evaluate the amount of interlimb transfer with respect to the training leg, we compared the relationship between (TF-TM pre – Tr-TM post) and (TF-TM pre – Tf-TM) using linear regression analysis. A significant main or interaction effect was followed by post-hoc analysis with appropriate corrections for multiple comparisons. A significance level of $\alpha = 0.05$ was used for all statistical analysis.

RESULTS

Baseline Performance

Exemplar data showing tracking performance of a subject in the RL group during key time points of the experiment are shown in Figure 3. There were no significant differences in baseline performance (i.e., tracking error) between the training and the transfer leg for both the target-matching with visual feedback ($F[1,18] = 0.047$, $p = 0.831$) and no visual feedback conditions ($F[1,18] = 0.5$, $p = 0.489$). There were also no significant group (TM: $F[1,18] = 1.098$, $p = 0.308$; NVF: $F[1,18] = 0.387$, $p = 0.541$) or group $\times$ block interaction (TM: $F[1,18] = 1.730$, $p = 0.205$; NVF: $F[1,18] = 1.704$, $p = 0.208$) effects on baseline tracking performance.

Training Leg Learning

During target-matching with visual feedback, there was a significant effect of block on tracking error ($F[1,18] = 25.464$, $p < 0.001$; Figure 4a), indicating a significant learning effects with practice. There were no significant group ($F[1,18] = 0.006$, $p = 0.940$) or group $\times$ block interaction ($F[1,18] = 0.602$, $p = 0.448$) effects on tracking error. Similarly, during target-matching with no visual feedback, there was a significant effect of block on tracking error ($F[1,18] = 4.452$, $p = 0.049$; $19.9 \pm 1.3\%$ vs. $17.4 \pm 1.3\%$), but no significant group ($F[1,18] = 0.053$, $p = 0.821$) or group $\times$ block interaction ($F[1,18] = 1.368$, $p = 0.257$) effects on tracking error.

Interlimb Transfer Effects (Initial Transfer)

During target-matching with visual feedback, there was a significant effect of block (Tf-TM Pre = 17.8% and Tf-TM = 13.9%, $F[1,18] = 11.976$, $p = 0.003$) on tracking error, indicating that the performance of the untrained leg improved significantly with training of the opposite leg (Figure 4a). There were no significant group ($F[1,18] = 1.430$, $p = 0.247$) or group $\times$ block interaction ($F[1,18] = 2.814$, $p = 0.111$) effects on tracking error. There were also no significant group ($F[1,18] = 1.054$, $p = 0.318$), block ($F[1,18] = 2.682$, $p = 0.119$), or group $\times$ block interaction ($F[1,18] = 0.255$, $p = 0.620$) effects on tracking error for the no visual feedback condition. Regression analysis indicated that there was a linear relationship between the amount of learning on the training leg and the amount of transfer to the

untrained leg ($p < 0.001$; Figure 5). Evaluation of regression slope indicated that for every 1% change in target-matching error of the training leg there was a change of 0.84% on the transfer leg (i.e., ~84% of transfer of learning between legs).

Interlimb Transfer Effects (Final Transfer)

Finally, to examine if practice on the training leg had any effects on subsequent learning of the transfer leg, we examined the target-matching performance of the transfer leg during the transfer phase. During target-matching with visual feedback, there was a significant group $\times$ block interaction ($F[1,18] = 10.595$, $p = 0.004$, Figure 4b) effect. Post-hoc analysis with Bonferroni's correction indicated that tracking performance improved significantly in both the groups, but the improvements were greater in RL group in comparison to the LR group because of differences in the pre-test (RL: Tf-TM Pre = 19.7%, Tf-TM Post = 12.1%, $p < 0.001$; LR: Tf-TM Pre = 15.9%, Tf-TM Post = 12.8%, $p = 0.005$). For the no visual feedback condition, there were no significant group ($F[1,18] = 1.013$, $p = 0.327$), block ($F[1,18] = 0.651$, $p = 0.430$), or group $\times$ block interaction ($F[1,18] = 0.385$, $p = 0.543$) effects.

DISCUSSION

In this study, we tested the amount of interlimb transfer during walking and evaluated whether this transfer was asymmetric — i.e., transfer occurred to a greater extent from one leg to the other than vice versa. Two participant groups (RL and LR) practiced a motor learning task that has been previously used for gait rehabilitation. The RL group trained with their right leg and tested for transfer in their left leg, whereas the LR group trained with their left leg and tested for transfer in their right leg. Thus, the entire practice schedule was similar between the two groups, except that the leg that was used for training and transfer differed between the groups. The principal finding of this study was that both the RL and the LR groups exhibited significant interlimb transfer after training with their opposite leg, albeit only when visual feedback was provided. However, contrary to our hypothesis, we did not observe any asymmetry in the amount of transfer between legs. Further, the improvements in performance of the transfer leg after training with the transfer leg were also similar in both groups, indicating that there was no asymmetric transfer observed in the final level of performance in the transfer leg.

The interlimb transfer of motor learning has often shown to be asymmetric in upper-extremity studies. The direction of transfer, however, varies across studies, in that some studies have shown greater transfer after initial practice with the dominant hand [13, 32], while others have shown greater transfer after initial practice with the nondominant hand [15, 17, 33]. The precise reason for this asymmetric transfer is currently not clear, although scientists have linked this observation to the idea of hemispheric specialization for certain movement variables (e.g., kinematic vs. dynamic) [16, 18, 20]. Unlike upper-extremity studies, the evidence for asymmetric transfer effects is not consistent in lower-extremity studies. While some studies support the notion of asymmetric interlimb transfer [11, 34], others have shown equal transfer between legs [21]. Interestingly, a few studies have even reported limited interlimb transfer of locomotor adaptations [22, 35], which questions the

very idea that learned skills can be transferred between legs. The precise reason for this inconsistent finding is not clear; however, it appears that the type/nature of task may partly contribute for this observation. For example, a significant transfer effect is often observed when the learning paradigm involves movements that are typically encountered during day-to-day activities (e.g., leg extension or ankle movements) [11, 34], whereas little or no transfer is observed when the movements involved in the learning paradigm are atypical (e.g., split-belt adaptation or unipedal walking) [22, 35]. Further, it appears that interlimb transfer is more symmetric when the task is functionally/biologically relevant [21]. Thus, the findings of this study add to our current understanding of interlimb transfer of leg motor learning during walking and provide further evidence indicating that training of one leg can improve subsequent performance of the opposite leg. Further, the results show that this interlimb transfer effect is symmetric, in that both sides benefit to a similar extent from training of its opposite counterpart. These findings are consistent with those of van Hedel et al. [21], who also reported that improvements in performance of the transfer leg due to the training of the opposite leg were symmetrical and were not side-specific.

We note, however, that significant transfer was observed only during the visual feedback condition. This observation does not necessarily imply that there was no “true” learning in the transfer leg, as evidence indicates that no visual feedback condition (though an important test of learning) is not the only test of learning and that evidence for motor learning can be obtained even in tests with visual feedback [36]. In fact, many current experimental paradigms in interlimb transfer examine learning and re-learning in the presence of visual feedback [3, 11, 12]. The reason for improvements in tracking performance during the no visual feedback condition only in the training leg, but not the transfer leg is not clear and deserves attention in future studies. It is likely that the amount of practice (8×1 -min block) provided in this study was not sufficient to produce a meaningful effect in the no visual feedback condition, although prior research indicates that prolonged training does not affect the extent of interlimb transfer [37]. Alternatively, “guessing strategies” introduced by the no visual feedback tests [38, 39] could have created higher between-subject variability thereby masking the learning effects.

Previous research indicates that the conception of a motor task (i.e., how the task is perceived) could also influence the direction of transfer. For example, Stockel and Wang showed that right leg benefitted from initial training with the left leg, if the task was conceived as a spatial task, whereas left leg benefitted from initial training with the right leg, if the task was conceived as a dynamic task [11]. When applying these results to our study, one would expect that the interlimb transfer would be greater in the LR group when compared to the RL group, as we used a spatial task. However, we did not find any directional transfer; rather, both legs benefitted from opposite leg training. This is surprising considering that our experimental design was very similar to their study. There are two likely explanations for this difference – first, their task was discrete and participants received only offline feedback about their motor performance, whereas our task was continuous and participants received concurrent visual feedback on their motor performance. Further, the amount of learning observed in their motor learning task was relatively small, which could have resulted in a different pattern of interlimb transfer than the one that was observed in this study. Second, in their task (and in other unimanual tasks), the “transfer” limb was not

used during the training phase, whereas in our study (and the one by van Hedel et al. [21]) because participants were walking, both limbs were moving during the training phase even though the learning task was presented only for one limb. We believe that there are advantages to both types of paradigms – stopping the transfer limb from moving during training provides a “cleaner” theoretical test of transfer (since the transfer limb can only learn from the training limb). On the other hand, paradigms in which both limbs are allowed to move during training have a more direct functional relevance for gait rehabilitation, where participants have to relearn functional tasks such as walking that require coordination between both limbs [40–43].

There are some limitations to this study. First, similar to others, our experimental design involved baseline evaluation of the transfer leg prior to the training leg in the initial pre-test phase (Figure 1). Therefore, the baseline performance of the training leg could have been confounded by the evaluation of the transfer leg due to interlimb transfer. However, when comparing the tracking error between Tf-TM Pre and Tr-TM Pre, there were no significant main or interaction effects, indicating that there were no short-term transfer effects and that initial evaluation of the transfer leg did not confound the study results. Second, we only evaluated short-term improvements in motor performance and did not test delayed retention of the learned skill. Thus, it is unclear if interlimb transfer effects could be asymmetric after consolidation of learning. Future studies should evaluate this issue. Finally, while the participants received concurrent feedback of their tracking performance, there was no knowledge of results after each block of training. It is likely that the training and transfer effects could have been much larger if the participants were provided with feedback of the tracking error after completion of each block of training.

In summary, we tested the extent of interlimb transfer during walking and examined whether this transfer was asymmetric between legs. We found evidence of interlimb transfer of motor learning during walking. However, contradictory to most upper-extremity studies, we found no evidence for asymmetry in interlimb transfer of motor performance in the lower limb during walking. These results point out that both differences in neural processes and types of tasks may mediate interlimb transfer.

Acknowledgments

This work was supported in part by Grants R03HD069806 and R01EB019834 from the National Institutes of Health and grants from the University of Michigan Office of Research and Undergraduate Research Opportunities Program. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

1. Kitago T, Krakauer JW. Motor learning principles for neurorehabilitation. *Handb Clin Neurol*. 2013; 110:93–103. [PubMed: 23312633]
2. Krakauer JW. Motor learning: its relevance to stroke recovery and neurorehabilitation. *Curr Opin Neurol*. 2006; 19:84–90. [PubMed: 16415682]
3. Sainburg RL, Wang J. Interlimb transfer of visuomotor rotations: independence of direction and final position information. *Exp Brain Res*. 2002; 145:437–47. [PubMed: 12172655]
4. Latash ML. Mirror Writing: Learning, Transfer, and Implications for Internal Inverse Models. *J Mot Behav*. 1999; 31:107–11. [PubMed: 11177624]

5. Taylor HG, Heilman KM. Left-hemisphere motor dominance in righthanders. *Cortex*. 1980; 16:587–603. [PubMed: 7226856]
6. Laszlo JJ, Baguley RA, Bairstow PJ. Bilateral transfer in tapping skill in the absence of peripheral information. *J Mot Behav*. 1970; 2:261–71. [PubMed: 23941320]
7. Bhatt T, Pai YC. Immediate and latent interlimb transfer of gait stability adaptation following repeated exposure to slips. *J Mot Behav*. 2008; 40:380–90. [PubMed: 18782713]
8. Carroll TJ, de Rugy A, Howard IS, Ingram JN, Wolpert DM. Enhanced crosslimb transfer of force-field learning for dynamics that are identical in extrinsic and joint-based coordinates for both limbs. *J Neurophysiol*. 2016; 115:445–56. [PubMed: 26581867]
9. Lefumat HZ, Vercher JL, Miall RC, Cole J, Buloup F, Bringoux L, et al. To transfer or not to transfer? Kinematics and laterality quotient predict interlimb transfer of motor learning. *J Neurophysiol*. 2015; 114:2764–74. [PubMed: 26334018]
10. Joiner WM, Brayanov JB, Smith MA. The training schedule affects the stability, not the magnitude, of the interlimb transfer of learned dynamics. *J Neurophysiol*. 2013; 110:984–98. [PubMed: 23719204]
11. Stockel T, Wang J. Transfer of short-term motor learning across the lower limbs as a function of task conception and practice order. *Brain Cogn*. 2011; 77:271–9. [PubMed: 21889250]
12. Wang J, Przybyla A, Wuebbenhorst K, Haaland KY, Sainburg RL. Aging reduces asymmetries in interlimb transfer of visuomotor adaptation. *Exp Brain Res*. 2011; 210:283–90. [PubMed: 21424842]
13. Pereira EA, Raja K, Gangavalli R. Effect of training on interlimb transfer of dexterity skills in healthy adults. *Am J Phys Med Rehabil*. 2011; 90:25–34. [PubMed: 20975521]
14. Bhatt T, Pai YC. Role of cognition and priming in interlimb generalization of adaptive control of gait stability. *J Mot Behav*. 2009; 41:479–93. [PubMed: 19592361]
15. Hicks RE. Asymmetry of bilateral transfer. *The American Journal of Psychology*. 1974:667–74.
16. Pan Z, Van Gemmert AW. The effects of aging on the asymmetry of inter-limb transfer in a visuomotor task. *Exp Brain Res*. 2013; 229:621–33. [PubMed: 23831848]
17. Kumar S, Mandal MK. Bilateral transfer of skill in left- and right-handers. *Laterality*. 2005; 10:337–44. [PubMed: 16020370]
18. Wang J, Sainburg RL. Interlimb transfer of novel inertial dynamics is asymmetrical. *J Neurophysiol*. 2004; 92:349–60. [PubMed: 15028745]
19. Wang J, Sainburg RL. The dominant and nondominant arms are specialized for stabilizing different features of task performance. *Exp Brain Res*. 2007; 178:565–70. [PubMed: 17380323]
20. Sainburg RL, Duff SV. Does motor lateralization have implications for stroke rehabilitation? *J Rehabil Res Dev*. 2006; 43:311–22. [PubMed: 17041817]
21. van Hedel HJ, Biedermann M, Erni T, Dietz V. Obstacle avoidance during human walking: transfer of motor skill from one leg to the other. *J Physiol*. 2002; 543:709–17. [PubMed: 12205202]
22. Houldin A, Chua R, Carpenter MG, Lam T. Limited interlimb transfer of locomotor adaptations to a velocity-dependent force field during unipedal walking. *J Neurophysiol*. 2012; 108:943–52. [PubMed: 22592310]
23. Krishnan C, Ranganathan R, Dhaher YY, Rymer WZ. A pilot study on the feasibility of robot-aided leg motor training to facilitate active participation. *PLoS One*. 2013; 8:e77370. [PubMed: 24146986]
24. Krishnan C, Ranganathan R, Katak SS, Dhaher YY, Rymer WZ. Active robotic training improves locomotor function in a stroke survivor. *J Neuroeng Rehabil*. 2012; 9:57. [PubMed: 22906099]
25. Srivastava S, Kao PC, Kim SH, Stegall P, Zanotto D, Higginson JS, et al. Assist-as-Needed Robot-Aided Gait Training Improves Walking Function in Individuals Following Stroke. *IEEE Trans Neural Syst Rehabil Eng*. 2015; 23:956–63. [PubMed: 25314703]
26. Kao PC, Srivastava S, Agrawal SK, Scholz JP. Effect of robotic performance-based error-augmentation versus error-reduction training on the gait of healthy individuals. *Gait Posture*. 2013; 37:113–20. [PubMed: 22832470]

27. Kao PC, Srivastava S, Higginson JS, Agrawal SK, Scholz JP. Short-term Performance-based Error-augmentation versus Error-reduction Robotic Gait Training for Individuals with Chronic Stroke: A Pilot Study. *Phys Med Rehabil Int.* 2015;2.
28. Krishnan C, Washabaugh EP, Seetharaman Y. A low cost real-time motion tracking approach using webcam technology. *J Biomech.* 2015; 48:544–8. [PubMed: 25555306]
29. Kim SH, Banala SK, Brackbill EA, Agrawal SK, Krishnamoorthy V, Scholz JP. Robot-assisted modifications of gait in healthy individuals. *Exp Brain Res.* 2010; 202:809–24. [PubMed: 20186402]
30. Ranganathan R, Krishnan C, Dhaher YY, Rymer WZ. Learning new gait patterns: Exploratory muscle activity during motor learning is not predicted by motor modules. *J Biomech.* 2016; 49:718–25. [PubMed: 26916510]
31. Banala SK, Kim SH, Agrawal SK, Scholz JP. Robot assisted gait training with active leg exoskeleton (ALEX). *IEEE Trans Neural Syst Rehabil Eng.* 2009; 17:2–8. [PubMed: 19211317]
32. Galea JM, Miall RC, Woolley DG. Asymmetric interlimb transfer of concurrent adaptation to opposing dynamic forces. *Exp Brain Res.* 2007; 182:267–73. [PubMed: 17703286]
33. Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX. Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task. *PLoS One.* 2016; 11:e0152228. [PubMed: 27050168]
34. Morris T, Newby NA, Wininger M, Craelius W. Inter-limb transfer of learned ankle movements. *Exp Brain Res.* 2009; 192:33–42. [PubMed: 18830590]
35. Choi JT, Bastian AJ. Adaptation reveals independent control networks for human walking. *Nat Neurosci.* 2007; 10:1055–62. [PubMed: 17603479]
36. Russell DM, Newell KM. On No-KR tests in motor learning, retention and transfer. *Hum Mov Sci.* 2007; 26:155–73. [PubMed: 17050022]
37. Lei Y, Wang J. Prolonged training does not result in a greater extent of interlimb transfer following visuomotor adaptation. *Brain Cogn.* 2014; 91:95–9. [PubMed: 25282328]
38. Johnson RE, Rosenthal E. Influence of guessing on measurements of immediate and delayed retention. *Journal of Educational Measurement.* 1968; 5:175–80.
39. Ranganathan R, Newell KM. Influence of augmented feedback on coordination strategies. *J Mot Behav.* 2009; 41:317–30. [PubMed: 19508958]
40. Sousa AS, Silva A, Santos R, Sousa F, Tavares JM. Interlimb coordination during the stance phase of gait in subjects with stroke. *Arch Phys Med Rehabil.* 2013; 94:2515–22. [PubMed: 23871877]
41. Sousa AS, Silva A, Tavares JM. Biomechanical and neurophysiological mechanisms related to postural control and efficiency of movement: a review. *Somatosens Mot Res.* 2012; 29:131–43. [PubMed: 23094940]
42. Sousa AS, Silva A, Tavares JM. Interlimb relation during the double support phase of gait: an electromyographic, mechanical and energy-based analysis. *Proc Inst Mech Eng H.* 2013; 227:327–33. [PubMed: 23662349]
43. Sousa AS, Tavares JM. Interlimb Coordination During Step-to-Step Transition and Gait Performance. *J Mot Behav.* 2015; 47:563–74. [PubMed: 25893693]

HIGHLIGHTS

- Interlimb transfer of motor skills can be therapeutic for individuals with stroke
- We tested the amount of interlimb transfer during walking in college-aged adults
- We also examined whether this interlimb transfer was asymmetric between legs
- Participants showed significant transfer of motor skills between legs
- In contrast to upper-limb literature, there was no evidence for asymmetric transfer

Figure 1. Schematic of the experimental protocol. Note that the right leg was the training leg for the RL group and the left leg was the training leg for the LR group. Baseline indicates normal walking blocks, target-matching indicates blocks in which participants performed a foot-trajectory tracking task, and no visual feedback indicates blocks in which participants performed the tracking task without any visual feedback of their performance. Each block was separated by about one minute of rest.

Figure 2.

(A) Schematic of experimental set-up for the foot target-trajectory paradigm. Participants viewed a target-trajectory on a computer monitor placed in front of them and attempted to match their own foot-trajectory with the target. (B) Schematic of construction of target template – target template was constructed by scaling the hip and knee angle by 30% during the swing phase of the gait and projecting it in the end-point space (i.e., ankle position relative to the hip). (C) Schematic of computation of tracking error – tracking error was computed as the non-overlapping area between the target template and the actual foot trajectory produced in that gait cycle (shaded region). The resulting area (i.e., the error) was normalized to the area within the participant's target foot trajectory.

Figure 3.

Representative data showing foot trajectory and tracking performance of a subject in the RL group during key time points of the experiment. Tf-TM Pre and Tr-TM Pre are baseline target-matching performance of the transfer and training leg, respectively (pre-test phase). Tr-TM Post is the target-matching performance of the training leg after the training phase. Tf-TM is the target-matching performance of the transfer leg immediately after the training phase. Tf-TM Post is the target matching performance of the transfer leg after training with the transfer leg (transfer phase). Note that the target-matching performance of the trained and untrained legs improved substantially after training.

Figure 4.

(A) Plots showing the changes in tracking performance of the untrained, transfer leg (Tf) due to repeated practice of the novel gait task with the training leg (Tr) in the right-to-left (RL) and left-to-right (LR) groups. Note that the tracking errors were similar between the two groups on the transfer leg after practicing with the training leg. (B) Plots showing the changes in tracking performance of the transfer leg after practicing with the same leg in the RL and the LR groups. The two pre-test blocks (Tf-TM Pre and Tf-NVF Pre) are shown again at the start to provide a clearer visual comparison. Note that the tracking error as a function of practice of the transfer leg was similar between groups. The shaded gray region indicates the training leg, the bolded circles indicate no visual feedback trials, and the error bars represent standard error of the mean.

Figure 5.

Scatterplot showing the extent of interlimb transfer and the relationship between the amount of learning on the training leg and the amount of transfer to the untrained leg. The solid black line indicates the slope of the actual data and the broken line indicates the unity line for comparison. Note that a slope of 1 will indicate complete transfer.