**RESEARCH ARTICLE**

# Inter-limb transfer of ballistic motor skill following non-dominant limb training in young and older adults

**Mark R. Hinder · Timothy J. Carroll · Jeffery J. Summers**

**Abstract** We recently reported considerably less inter-limb transfer in older, compared to young, adults following dominant (right) hand motor training (Hinder et al. in J Appl Physiol 110:166–175, 2011). This occurred despite the fact that both age groups exhibited similar performance improvements in the trained limb. However, asymmetries can exist with respect to the degree of transfer observed in some tasks, depending upon which limb undertakes the training. Accordingly, here we investigated inter-limb transfer following left hand ballistic motor training in young ($n = 15$; mean age 21.2 years) and older ($n = 15$; mean age 70.3 years) right handers. Following motor training that required participants to maximally abduct the left index finger, both groups exhibited significant performance improvements in the trained left hand. Moreover, the extent of inter-limb transfer was substantial and indistinguishable between the two age groups. Transcranial magnetic stimulation revealed that both age groups exhibited bilateral increases in cortical excitability following unilateral training, indicating that unilateral training affects both the trained and untrained hemisphere. However, only for young adults was the extent of the performance gain in the trained hand able to predict the degree of transfer. These findings suggest that different mechanisms may mediate inter-limb transfer of ballistic motor tasks for older and young adults.

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Because such tasks evoke similar neural responses to those observed following strength training (Selvanayagam et al. in J Appl Physiol 111:367–375, 2011; Carroll et al. in Acta Physiol 202:119–140, 2011), our findings have important implications for rehabilitation paradigms following stroke or limb immobilisation due to injury.

## Introduction

Repeated practice of a unilateral motor task not only results in performance improvements in the trained limb, but can also result in improvements in the contralateral limb (which undertakes no physical practice). This phenomenon is known as inter-limb, or cross-limb, transfer. A number of recent studies have investigated whether inter-limb transfer is manifested to a similar extent following training of the dominant or non-dominant limbs in a number of different adaptation paradigms. Criscimagna-Hemminger et al. (2003) and Wang and Sainburg (2004) reported that following a training protocol in which the dominant arm learned to compensate for external forces (i.e., dynamic force field learning), the non-dominant (untrained) arm showed improved performance compared to naïve performance levels. Transfer to the dominant limb following non-dominant limb practice was not, however, observed in either study. In contrast, Sainburg and Wang (2002) considered inter-limb transfer following adaptation to a novel visuomotor mapping. In this instance, transfer occurred from the dominant to non-dominant limb with respect to endpoint accuracy of movements, whereas transfer from non-dominant

to dominant limbs occurred in terms of initial movement directional accuracy.

While these behavioural studies permit some insight into how those mechanisms encoding adaptation to novel forces or visual environments may operate, adaptation to complex visual and dynamical perturbations often involves a distributed network of visual and motor regions within the brain, and it is not clear how principles of inter-limb transfer obtained from sensorimotor adaptation studies may relate to motor learning in other contexts. For example, given the common observations of muscle atrophy and loss of strength in paretic limbs following stroke, and following (even short) periods of immobilisation due to trauma (Urso et al. 2006; Lundbye-Jensen and Nielsen 2008), a better understanding of the mechanisms underlying inter-limb transfer of training-induced strength gains might lead to applications in clinical rehabilitation contexts. In this regard, Farthing et al. (2005) reported a study in which right-handed participants underwent a 6-week (4 sessions per week) training regime involving maximal isometric ulnar deviation torque training. Those participants who trained with their right limb manifested significant transfer of strength to the (untrained) left limb, whereas those who trained with the left limb did not exhibit transfer to the right limb. This result, which is consistent with the aforementioned findings of Criscimagna-Hemminger et al. (2003) and Wang and Sainburg (2004), suggests a distinct limitation to the benefits that could be conferred by unilateral strength training (of the non-dominant limb) following paresis or fracture/immobilisation of the dominant limb.

A limitation of Farthing et al. (2005) study, however, was that neurophysiological tools such as transcranial magnetic stimulation (TMS) were not used to assess the neural adaptations that may have underpinned the asymmetric transfer effects. Indeed, a limitation of strength training protocols for assessing the neural mechanisms thought to underpin inter-limb transfer of strength is the fact that many weeks are required to evoke a strength (behavioural) gain, even though the neural changes may occur much more quickly (Lee et al. 2009). Changes in the excitability of neural circuits are most affected in the early stages of adaptation, with later adaptation being associated with more structural changes not directly detectable with TMS (Carroll et al. 2011; Selvanayagam et al. 2011). To address this issue, we have conducted a number of studies investigating the transfer of ballistic (fast-as-possible) motor actions. The mechanisms that mediate performance improvements and transfer in these ballistic motor tasks appear to be similar to those underlying the acquisition and transfer of strength gains (Selvanayagam et al. 2011). Moreover, other benefits of adopting ballistic motor tasks as a model system are that performance gains are thought to be mediated primarily by adaptations within the trained primary motor cortex (Lee et al. 2010;

Muellbacher et al. 2002; Liepert et al. 2001) with transfer mediated by adaptations within the contralateral (untrained) motor cortex (Lee et al. 2010). These adaptations include bilateral increases in corticospinal excitability (Muellbacher et al. 2002; Lee et al. 2010) and a bilateral release of intracortical inhibition (Hinder et al. 2011). Importantly, the neural and behavioural adaptations can be observed over the course of a single experimental session, permitting TMS to be used to directly assess adaptive changes to excitatory and inhibitory circuits within the motor cortex contralateral and ipsilateral to the performed motor task. To date, however, we have only considered transfer effects following motor training of the dominant limb (Carroll et al. 2008; Hinder et al. 2011; Lee et al. 2010). The first aim of the current study was to assess whether inter-limb transfer was manifested following ballistic motor training of the non-dominant (left) limb and to characterise the neural mechanisms mediating the performance improvement in the trained limb and, if present, in the untrained limb.

Healthy ageing is associated with well-categorised changes in brain activation during movement. These include frontal shifts in brain activation patterns (likely indicating a greater cognitive component) during planning and execution of even relatively simple motor tasks (Heuninckx et al. 2005), together with greater bihemispheric activation of motor cortices during unilateral motor tasks (Ward et al. 2008). The HAROLD (hemispheric asymmetry reduction in older adults) model (Cabeza et al. 2002) theorises that this additional activation is functional (i.e., associated with improved task performance) and compensates for age-related degradation in other brain regions. While some motor learning studies are consistent with the model (Heuninckx et al. 2005; Mattay et al. 2002), others indicate that the additional bihemispheric activation may simply represent dedifferentiation (Langan et al. 2010; Li et al. 2001), that is, an inability to deactivate ipsilateral motor areas, possibly due to breakdown of inter-hemispheric inhibitory function (Talelli et al. 2008). In a recent study, we reported that while young (<35 years) adults exhibit substantial transfer of the performance gains manifested in a ballistic motor task undertaken with their dominant (right) index finger to the non-dominant (left) hand, transfer was negligible for a group of older (>60 years) adults (Hinder et al. 2011). This finding occurred despite the fact that all the older adults exhibited reliable performance gains in the trained hand and as a group exhibited increases in cortical excitability in both hemispheres commensurate with the young group. The older adults also exhibited greater mirror activity during the unilateral task than did young adults, indicative of greater bilateral cortical activation, which we had postulated would *increase* the degree of transfer under the cross-activation hypothesis of cross-limb transfer (Hinder et al. 2011; Carroll et al. 2008). As such, seemingly greater drive

to the ipsilateral (untrained) cortex did not result in greater transfer as was hypothesised. Accordingly, it may be the case that changes in brain activation patterns with advancing age result in mechanisms of cross-limb transfer that are different from those that predominate in young adults. This has important potential implications for the use of inter-limb transfer effects in rehabilitation, since the prevalence of limb fractures and stroke is higher in older adults. The present study was therefore conducted with groups of right-handed young and older adults with the aim of determining whether age differences in the extent of transfer (Hinder et al. 2011) were also apparent in the following motor training paradigm undertaken with the non-dominant limb.

## Methods

### Participants

Fifteen young (mean age ± 95 % confidence intervals = 21.2 ± 1.5 years, range 18–27 years; 7 males) and fifteen older (70.3 ± 2.8 years; 60–78 years; 5 males) adults, self declared as being strongly right handed, participated in the study having given their written informed consent which had received ethical approval from the University of Tasmania's Human Research Ethics Committee. Participants were screened for contraindications to TMS, had normal or corrected-to-normal vision and were free from neurological and neuromuscular disorders.

### Movement task

With their forearms resting on a horizontal board designed to standardise hand position and isolate movements of the index fingers (Hinder et al. 2011), participants placed their palms facing down and performed ballistic abductions of their right or left index finger, attempting to isolate the movements to the second metacarpo-phalangeal joint with the goal of maximising the peak acceleration of each movement. Accelerometers (Dytran Instruments, Chatsworth, CA, USA/Endevco Corp. San Juan Capistrano, CA, USA) were used to capture horizontal acceleration.

### Experimental design

The protocol was designed to investigate the effect of motor training with the non-dominant left hand on subsequent motor performance in the (untrained) dominant right hand. Prior to motor training (i.e., pre-test), corticospinal excitability and intracortical inhibition were measured in both hemispheres (neurophysiological testing, see Transcranial magnetic stimulation section, below) and motor performance was assessed in both the left and right hands

(performance testing). Performance testing involved 10 trials per hand (in the absence of performance feedback) at 0.5 Hz prompted by an audio tone. Training involved 2 blocks of 150 trials (at a rate of 0.5 Hz) with the non-dominant left hand. Verbal encouragement and visual feedback were provided. Feedback from each trial was presented in the form of a data point on a graph on which the y-axis represented peak acceleration and the x-axis represented trial number. Participants were encouraged to increase their peak accelerations over the course of the training. Short rest breaks (~30 s) every 10 movements aimed to minimise possible fatigue effects. Between (mid-test) and following (post-test) these training blocks, neurophysiological and performance tests were repeated to assess training-induced changes in excitability/inhibition and motor performance in both limbs. The order of the neurophysiological (left/right cortex) and performance (left/right hands) tests was counterbalanced. However, neurophysiological (TMS) testing always preceded the performance testing to ensure that any neurophysiological changes were a result of the preceding unilateral training and not due to the test phases. The mid- and post-test TMS blocks commenced approximately 1.5 (first cortex tested) or 4 (second cortex tested) min after completion of the preceding training block, and thus should reflect training-induced changes in excitability rather than transient movement- or activation-related potentiation of corticospinal excitability (e.g., Chen et al. 1998).

### Muscle activity

Muscle activity (during task execution and during TMS) was recorded using a belly-tendon montage of Ag/AgCl electrodes (Meditrace 130, Tyco Healthcare, Mansfield, MA) from the left and right first dorsal interosseus (FDI), the primary agonist for finger abduction. These signals were fed into a CED 1401 amplifier (Cambridge, UK) where a notch filter (50 Hz) was applied prior to amplification (gain 300–1,000). Muscle activity was monitored by the experimenter to ensure that participants relaxed between trials and that the task was undertaken with strong FDI bursts.

### Transcranial magnetic stimulation

Transcranial magnetic stimulation was delivered using two Magstim 200 units (Magstim Company, Dyfed, UK) connected via a Bistim unit and a single figure of eight coil (external diameter of each loop 70 mm). Motor 'hotspots' for left and right FDI (with posterior- to anterior-induced current in the cortex) were determined and resting motor thresholds (RMT) were established as the minimum intensities required to elicit MEPs > 50 μV in the right and left FDI muscles in 3 out of 5 consecutive trials when stimulating at the hotspots (Carroll et al. 2001; Hinder et al. 2010).

Participants were instructed to relax their limbs while assuming the same posture as that adopted during the movement task (see above). Visual feedback of muscle activity helped to keep muscle activity to a minimum.

During all TMS test sessions, 20 stimulations (at a rate of 0.2 Hz) were administered to the right (trained) and left (untrained) motor hotspots. Half of the stimulations involved a single 'test' pulse (130 % RMT) to assess the net excitability of the corticospinal projections to the trained/untrained hand, while half the trials involved paired-pulse stimulation (Kujirai et al. 1993) in which a subthreshold conditioning pulse (70 % RMT) preceded the same test pulse. The ratio of the average motor evoked potential (MEP) evoked following paired-pulse trials (within one TMS test block) to the average MEP amplitude evoked in the single-pulse trials (within the same TMS test block) is referred to as the short-interval intracortical inhibition ratio, SICI (Kujirai et al. 1993), and is used as an indication level of activity of the intrahemispheric inhibitory circuits. The order of single- and paired-pulse stimulations was randomised within each TMS block.

### Data acquisition and analysis

Kinematic and EMG data associated with each of the volitional finger movements were sampled at 2 kHz using CED (Cambridge, UK) Signal programs for 1,500 ms beginning 500 ms before the 'go' tone. Data analysis was performed offline using custom-written signal routines (Hinder et al. 2011). Acceleration data were low-pass filtered at 20 Hz prior to analysis. For each movement, peak abduction acceleration was determined as the first peak in the horizontal acceleration. Performance during the pre-, mid- and post-tests was calculated as the average peak acceleration across the 10 trails in each test and was then normalised (for each participant) to the pre-test acceleration for each hand (i.e., left hand values were normalised to average acceleration in left pre-test block, while right hand accelerations were normalised to the right pre-test block) for the purposes of statistical comparisons and graphical representation.

Responses to TMS were sampled at 10 kHz from 3 s before to 2 s after the test pulse. Any trial in which background rms EMG exceeded 0.025 µV in a 40-ms time window immediately prior to TMS stimulation was excluded from further analysis. The peak-to-peak amplitudes of the evoked (MEP) response were measured in the period 15–50 ms post-stimulation in the limb contralateral to the cortex being stimulated. Average MEP amplitudes were determined for single- and paired-pulse trials of each stimulation block separately and normalised to the corresponding pre-test value (we refer to these normalised values as nMEP: nMEP > 1 indicates facilitatory changes, while nMEP < 1

indicates suppression of evoked responses, relative to pre-test responses). The SICI ratio for each muscle was determined as the average (non-normalised) MEP amplitude in the paired-pulse stimulations divided by the average MEP amplitude in the single-pulse stimulations in the same test phase. These data are presented as an indication of the efficacy of the paired-pulse TMS paradigm at inducing SICI. To assess the extent of any training-induced changes in SICI, we divided the SICI ratio in the mid- and post-test trials by the SICI ratio in the pre-test and refer to this as nSICI (Hinder et al. 2011). nSICI < 1 indicates increased inhibition relative to the pre-test test, while nSICI > 1 indicates a release of inhibition, relative to SICI expressed in the pre-test.

Movement-related EMG data was rectified and low-pass filtered (20 Hz). The peak EMG amplitude in the FDI of the hand undertaking the task was then determined. Movement onset was defined as the time when FDI activity in the active hand first exceeded 4 times background EMG determined in the period 50–100 ms prior to the 'go' tone. Movement offset was defined as the time when FDI activity in the active hand first dropped below 0.2 times the peak amplitude (Carroll et al. 2008; Hinder et al. 2011). This technique allows us to consistently determine movement offset even if tonic muscle activity is present at the final (abducted) finger position. Average burst-related EMG of the FDI in the hand executing the ballistic action was calculated in this time window, minus the average value of background EMG. In a similar manner, we determined the average FDI EMG in the contralateral hand during the same time window (i.e., mirror activity). Using this methodology, EMG values for both muscles represent muscle activity associated with the ballistic actions and do not include any ongoing activity that could have been present for postural maintenance/stabilisation. EMG values were then averaged over the 10 trials of each test phase. The values for the right FDI (in left and right hand test trials) were normalised to the EMG value obtained for the right FDI during the right hand pre-test. Values for left FDI activity (during left and right hand trials) were normalised to the left FDI EMG value obtained for the left hand pre-test. This normalisation method enabled us to assess changes in the FDI of the hand undertaking the task relative to that activity exhibited prior to training and permitted the extent of mirror activity to be expressed as a proportion of the level of activity observed when that hand was actively undertaking the task (Hinder et al. 2011).

The normalisation methods that we employed for *all* dependent variables are beneficial in that they remove possible confounds in the statistical results that may otherwise exist due to the inherent inter-group variability in the pre-test values, that is, statistical analyses of normalised values are not biased by the data of any one participant who has a particularly low, or high, pre-test value.

## Statistical analysis

### Task performance

To assess whether there were pre-training differences in absolute performance between hands and groups, we compared non-normalised (raw) peak accelerations in the pre-test using ANOVA with hand (left, right) as a within-subjects factor and age (young, older) as a between-subjects factor. Training-induced changes in performance of the right and left hands, relative to the respective pre-tests, were compared using normalised peak accelerations in the mid- and post-tests using repeated measures ANOVA with hand (left, right) and time (mid- and post-tests) as within-subject factors and age (young, older) as a between-subjects factor.

### Muscle activity during task performance

Muscle activity in the FDI muscle of the hand instructed to undertake the task was compared using repeated measures ANOVA with hand (left, right) and time (mid- and post-tests) as within-subjects factors and age (young, older) as a between-subjects factor. Mirror activity in FDI of the contralateral hand was assessed using ANOVA with hand (left, right) and time (pre-, mid- and post-tests: repeated measures) as within-subjects factors and age (young, older) as a between-subjects factor.[1]

### TMS measures

Pre-test measures of corticospinal excitability (MEP amplitude) and intracortical inhibition (SICI) were compared using ANOVA with the factors hand (within group) and age (between group). Training-induced changes in corticospinal excitability were assessed using normalised MEP amplitudes (nMEP) in the FDI muscle in both the trained and untrained hands. Similarly, changes in short-interval intracortical inhibition (SICI) were assessed in the right and left FDI by nSICI. In both instances, we undertook repeated measures ANOVA with hand (right, left) and time (mid- and post-test) within-subjects factors and age group as a between-subjects factor.

For all ANOVAs, Huynh–Feldt corrections were applied if the assumption of sphericity was violated ($\varepsilon < 0.7$). Partial eta-squared ($\eta_p^2$) values are presented as a measure of effect size to aid the interpretation of the tests of significance.

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[1] Because the extent of mirror activity is reported relative to the level of activity in that same hand when it undertook the task (i.e., mirror activity in the left hand during right hand movements is reported relative to the activity in the left hand during left hand movements) pre-test values are not unity and, as such, are included in the ANOVA.

Statistical significance was set at $P < 0.05$. For all dependent variables, Bonferroni-adjusted post hoc tests were undertaken to further investigate statistically significant main effects and interactions.

## Results

Task performance

Motor performance prior to motor training (i.e., pre-test) was compared using non-normalised peak acceleration values in the pre-test trials. Young adults (right hand: 15.79 ms$^{-2}$; left hand: 15.80 ms$^{-2}$) exhibited somewhat faster movement accelerations than the older group (right hand: 10.90 ms$^{-2}$; left hand: 11.20 ms$^{-2}$), although the difference was not statistically significant ($F_{(1,28)} = 2.93$, $P = 0.10$, $\eta_p^2 = 0.10$). The main effect of hand ($F_{(1,28)} = 0.04$, $P = 0.85$, $\eta_p^2 < 0.01$) and interaction between age and hand ($F_{(1,28)} = 0.03$, $P = 0.86$, $\eta_p^2 < 0.01$) were not significant.

Normalised performance improvements in the mid- and post-tests (relative to performance observed in the pre-test) are shown in Fig. 1 for both the trained (left) and untrained (right) hands, for both participant groups. Upon completion of training (i.e., during post-testing), young adults' performance had improved relative to pre-test levels by 76 % and 49 % in the trained and untrained hands, respectively, with 37 % (trained hand) and 26 % (untrained hand) improvements exhibited by the older group. Greater performance improvements were apparent in the post-test (47 % improvement) compared to the mid-test (25 % improvement; time main effect: $F_{(1,28)} = 31.36$, $P < 0.01$, $\eta_p^2 = 0.53$), indicating a progressive performance improvement across the training regime. Gains in the trained left hand (44 % improvement) outweighed those in the untrained right hand (28 % improvement); although this just failed to reach statistical significance ($F_{(1,28)} = 3.80$, $P = 0.06$, $\eta_p^2 = 0.12$), it was associated with a medium effect size. Similarly, the main effect of age ($F_{(1,28)} = 3.60$, $P = 0.07$, $\eta_p^2 = 0.11$) just failed to reach statistical significance, but the marginal $P$ value and medium effect size are indicative of a trend for young adults (50 % improvement averaged across both hands and both mid- and post-tests) to exhibit larger performance improvements than the older adults (22 % improvement). All two-way and three-way interactions were not significant (all $P > 0.27$).

It was apparent from assessment of individual participants' data that a number of participants, especially those in the older cohort, did not exhibit improved performance with the left (trained) hand in the post-test, relative to the pre-test (Fig. 2). The absence of learning was particularly evident in older adults, of whom 6 of the 15 participants exhibited no, or negligible, performance improvement in
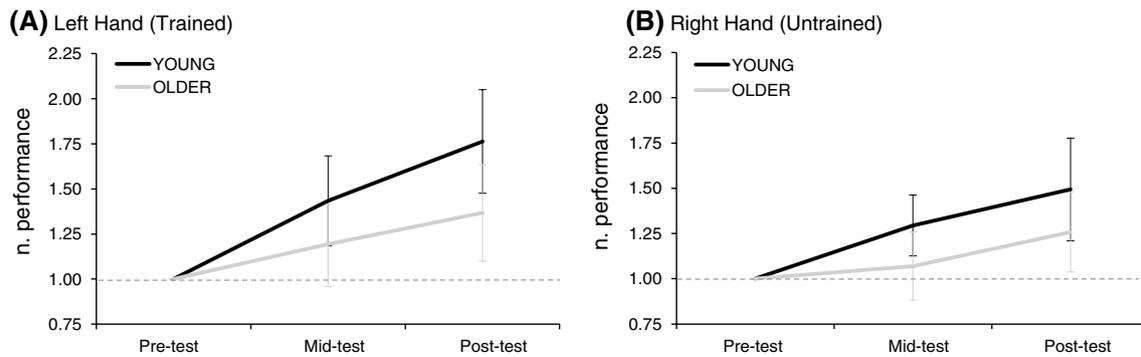
**(A)** Left Hand (Trained)



**(B)** Right Hand (Untrained)

**Fig. 1** Average normalised performance in **a** *left* (trained) and **b** *right* (untrained) hands for the young (*black*) and older (*grey*) groups. *Error bars* show 95 % confidence intervals (CIs) and *horizontal dotted lines* represent pre-test performance
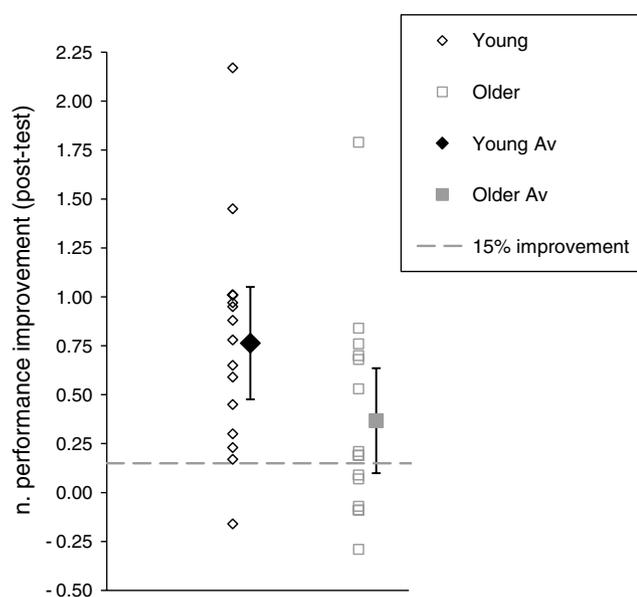


**Fig. 2** Normalised performance gains (in post-test trials) for the 15 young (*left—unfilled diamonds*) and 15 older (*right—unfilled squares*) participants. Group averages are shown with the *larger filled symbols*. *Error bars* show 95 % CIs. *Horizontal dotted line* represents 15 % improvement relative to pre-testing

the trained hand. We note that there was no correlation between (non-normalised) pre-test performance and the ability to exhibit training-induced performance improvements, that is, the 'non-learners' did not exhibit particularly low or high pre-test performance (in the left, or right, hand).

To assess whether age differences in the magnitude of learning and transfer were apparent in those participants who demonstrated an ability to improve performance in the trained hand, we applied a criteria requiring at least 15 % improvement in the post-test of the trained hand and then undertook a similar three-way ANOVA. In this

instance (with 14 young and 9 older adults), the effect of hand was statistically significant ($F_{(1,21)} = 12.52$, $P < 0.01$, $\eta_p^2 = 0.37$), indicating greater improvement in the trained left hand (60 % improvement) compared to untrained (32 % improvement) right hand (Fig. 3). The effect of age was not significant ($F_{(1,21)} = 0.33$, $P = 0.47$, $\eta_p^2 = 0.03$), indicating that those older adults who improved performance in the trained hand post-test by at least 15 % exhibited performance improvements of similar magnitude (in both the trained and untrained hands) to the young adults. As with the initial omnibus ANOVA, improvements were larger in post-training relative to mid-training (58 % vs. 34 % improvement; time main effect $F_{(1,21)} = 24.89$, $P < 0.01$, $\eta_p^2 = 0.54$). All two- and three-way interactions were not significant (all $P > 0.31$). The lack of age × hand interaction indicates no age-related difference in the degree of transfer observed in the untrained hand relative to the extent of learning exhibited in the trained hand.

To assess whether the degree of transfer in untrained right limb could be predicted from the degree of training-induced performance gain exhibited in the left limb, we undertook linear regression analyses for each group (Fig. 4a, b). For the young group, this relationship was associated with a high correlation coefficient and was statistically significant ($r^2 = 0.52$, $P < 0.01$), while for the older group, the association was weak and not statistically significant ($r^2 = 0.13$, $P = 0.18$). If the regressions were restricted to those adults in each group who exhibited at least 15 % performance improvement in the trained hand (see above), similar results were obtained (young group: $r^2 = 0.68$, $P < 0.01$; older group: $r^2 = 0.18$, $P = 0.26$, Fig. 4c, d), indicating in particular that the lack of relationship between left and right hand improvements for the older group was not driven by those participants who exhibited minimal performance improvements in the trained hand.
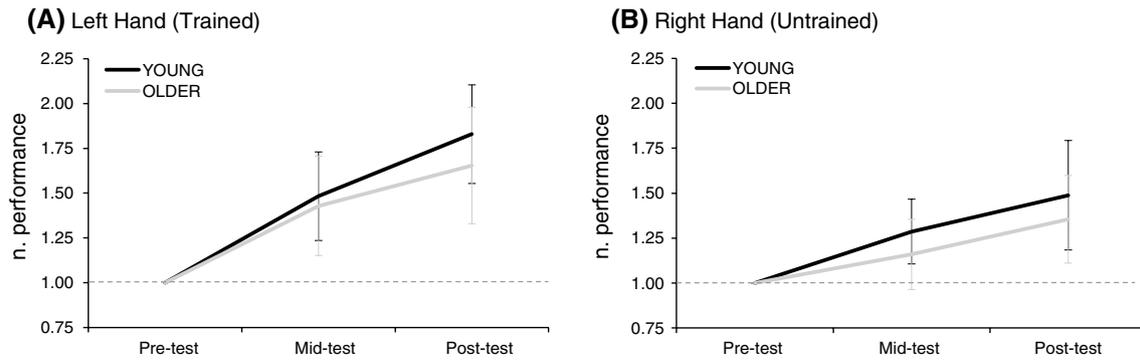
**(A)** Left Hand (Trained)

**(B)** Right Hand (Untrained)

**Fig. 3** Average normalised performance in **a** *left* (trained) and **b** *right* (untrained) hands for the young and older adults who exhibited at least 15 % improvement at the post-test in the trained limb. *Error bars* show 95 % CIs and *horizontal dotted lines* represent pre-test performance

**(A)** Young

**(B)** Older

**(C)** Young (learners only)
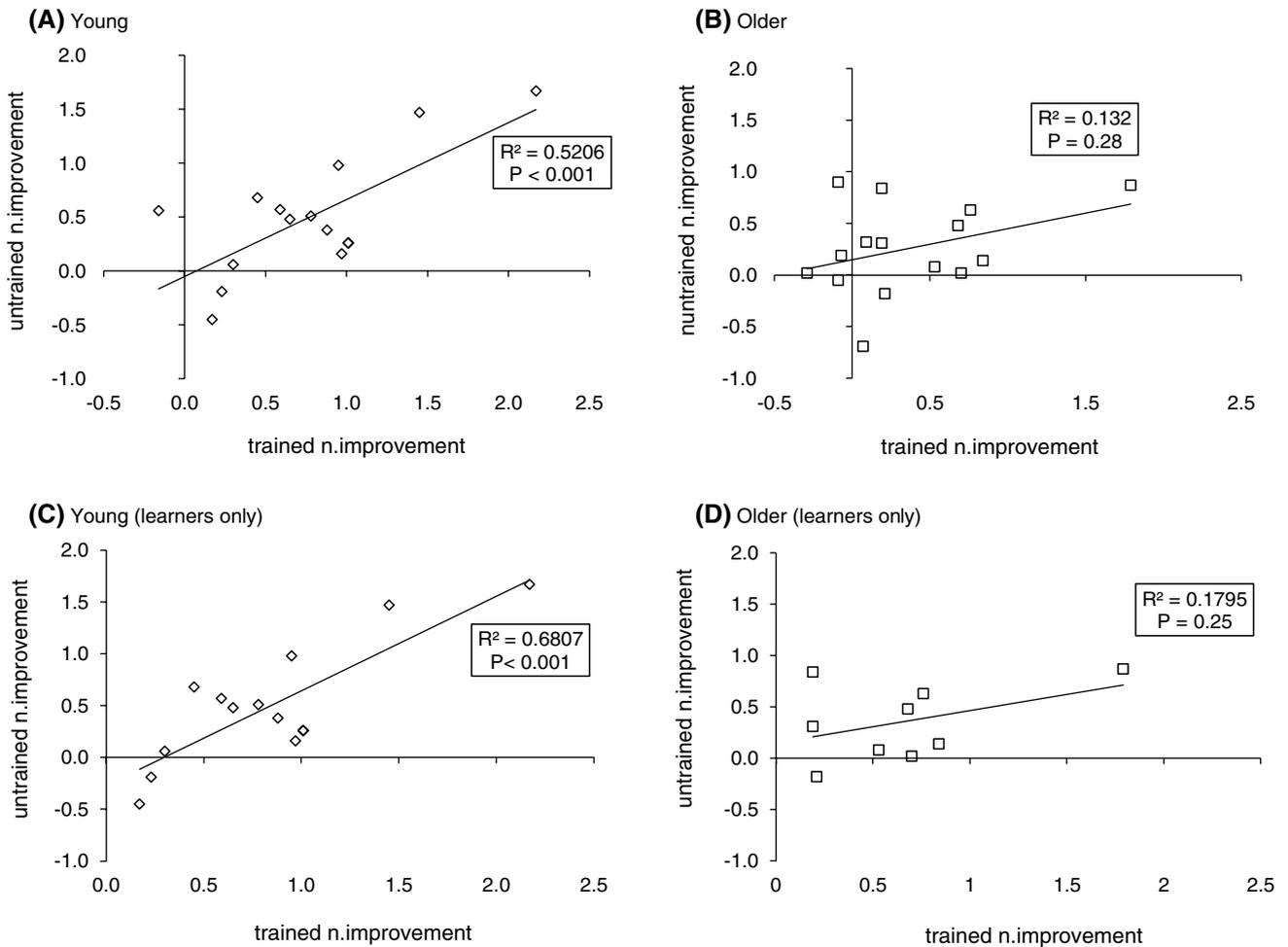
**(D)** Older (learners only)

**Fig. 4** Normalised performance improvement in the untrained *right hand* (*ordinate*) plotted against the normalised performance of the trained *left hand* (*abscissa*) for all **a** young and **b** older participants and for those participants who exhibited performance improvements in the trained hand of at least 15 % (**c** *young*; **d** *older*)

Neurophysiological measures

Resting motor thresholds (RMT), expressed as a percentage of maximum stimulator output (mean ± 95 % CI), were (for the left and right FDI muscles, respectively) 51.7 ± 4.2 % and 49.3 ± 4.3 % (young group) and 50.9 ± 4.3 % and 49.7 ± 4.0 % (older group). ANOVA revealed that there was no significant difference between hands ($F_{(1,28)} = 2.17$, $P = 0.16$, $\eta_p^2 = 0.09$) or age groups ($F_{(1,28)} = 0.04$, $P = 0.84$, $\eta_p^2 < 0.01$), and no interaction between the two factors ($F_{(1,28)} = 0.65$, $P = 0.43$, $\eta_p^2 = 0.03$). Corticospinal excitability prior to training was assessed by way of MEP amplitudes in the FDI muscle of each hand in the pre-tests. Group average MEP amplitudes (±95 % CI) were 1.84 ± 0.81 mV (right) and 1.00 ± 0.44 mV (left) for the young group and 0.59 ± 0.16 mV (right) and 0.41 ± 0.18 mV (left) for the older group. The effect of hand ($F_{(1,28)} = 6.15$, $P = 0.02$, $\eta_p^2 = 0.18$) and that of age ($F_{(1,28)} = 10.98$, $P < 0.01$, $\eta_p^2 = 0.28$) were both statistically significant; the interaction between the hand and age ($F_{(1,28)} = 2.57$, $P = 0.12$, $\eta_p^2 = 0.08$) did not reach significance.

To assess the effect of unilateral left hand training on the corticospinal excitability of projections to the left and right index fingers, we measured MEP sizes following 150 (mid-test) and 300 (post-test) training movements which were subsequently normalised to pre-test MEP sizes (Table 1) and compared using (repeated measures) ANOVA. Averaged over time (mid and post), hand and age group, unilateral left hand training resulted in a 26 % increase in excitability relative to the pre-test, which was statistically significant (grand mean nMEP = 1.26; $F_{(1,28)} = 6.75$, $P = 0.01$, $\eta_p^2 = 0.19$). The main effects of hand, time and age were not significant (all $P > 0.32$; all $\eta_p^2 < 0.04$), indicating that this increased excitability was equally apparent in both the trained and untrained hands, in mid- and post-tests, and by young and older adults. All two-way interactions were not significant (all $P > 0.33$, all $\eta_p^2 < 0.03$), while the three-way interaction of age, time and hand was marginal ($F_{(1,28)} = 3.37$, $P = 0.08$, $\eta_p^2 = 0.11$).

**Table 1** Average (±95 % confidence intervals) normalised MEP (nMEP) amplitude relative to the pre-test

| nMEP size (mV) (mean ± 95 % confidence interval) | Pre-test | Mid-test | Post-test |
|---|---|---|---|
| Young—L (trained) hand | 1.00 ± 0.00 | 1.43 ± 0.60 | 1.12 ± 0.46 |
| Young—R (untrained) hand | 1.00 ± 0.00 | 1.05 ± 0.16 | 1.35 ± 0.42 |
| Older—L (trained) hand | 1.00 ± 0.00 | 1.15 ± 0.37 | 1.50 ± 0.45 |
| Older—R (untrained) hand | 1.00 ± 0.00 | 1.22 ± 0.43 | 1.26 ± 0.32 |

**Table 2** Average (±95 % confidence intervals) normalised SICI ratios (nSICI) with respect to the pre-test

| nSICI ratio (mean ± 95 % confidence interval) | Pre-test | Mid-test | Post-test |
|---|---|---|---|
| Young—L (trained) hand | 1.00 ± 0.00 | 1.48 ± 0.39 | 1.13 ± 0.27 |
| Young—R (untrained) hand | 1.00 ± 0.00 | 0.95 ± 0.16 | 0.99 ± 0.21 |
| Older—L (trained) hand | 1.00 ± 0.00 | 1.12 ± 0.39 | 1.10 ± 0.27 |
| Older—R (untrained) hand | 1.00 ± 0.00 | 1.08 ± 0.16 | 1.07 ± 0.21 |

SICI ratios prior to unilateral left hand training (i.e., pre-test SICI) for the young group were 0.63 ± 0.22 and 0.51 ± 0.34 for the left and right hands, respectively. For the older group, SICI was 0.60 ± 0.30 and 0.77 ± 0.46 for the left and right hands, respectively. ANOVA revealed that the effects of hand ($F_{(1,28)} = 0.11$, $P = 0.74$, $\eta_p^2 < 0.01$) and age ($F_{(1,28)} = 1.21$, $P = 0.28$, $\eta_p^2 = 0.04$) were not significant, while the two-way interaction was marginal ($F_{(1,28)} = 3.76$, $P = 0.06$, $\eta_p^2 = 0.12$). To assess the effect of unilateral left hand training on SICI, we undertook repeated measures ANOVA using normalised SICI ratios, that is, nSICI (Table 2). Averaged over time (mid and post), hand, and age group, the training resulted in a 12 % release of inhibition relative to the pre-test, however, this was not statistically significant (grand mean nSICI = 1.12; $F_{(1,28)} = 3.31$, $P = 0.08$, $\eta_p^2 = 0.11$). The main effects of hand ($F_{(1,28)} = 2.42$, $P = 0.13$, $\eta_p^2 = 0.08$), time ($F_{(1,28)} = 1.64$, $P = 0.21$, $\eta_p^2 = 0.06$) and age ($F_{(1,28)} = 0.12$, $P = 0.73$, $\eta_p^2 < 0.01$) all failed to reach significance. The two- and three-way interactions did not reach statistical significance (all $P > 0.10$).

Electromyographic recordings—volitional muscle burst and mirror activity

Increases in muscle burst intensity were apparent in the untrained right hand (9 % increase, statistically significant, $P < 0.05$) but not for the left (trained) hand (0.2 % decrease, not significant), relative to pre-test levels (hand main effect $F_{(1,28)} = 5.18$, $P = 0.03$, $\eta_p^2 = 0.16$). The main effects of time ($F_{(1,28)} = 2.15$, $P = 0.15$, $\eta_p^2 = 0.07$) and age ($F_{(1,28)} = 1.67$, $P = 0.21$, $\eta_p^2 = 0.06$) were not significant. The significant interaction between hand and age ($F_{(1,28)} = 5.83$, $P = 0.02$, $\eta_p^2 = 0.17$) alludes to the fact that burst intensity increased in the right hand trials in the young group (19 % increase), but that burst intensity was not significantly affected by training in the right hand in the older group (4 % decrease) or the left hand of either group (0 % change for either group).

The level of mirror activity (i.e., average EMG in the FDI contralateral to the volitional muscle burst) did not vary as a function of hand, time or age (all main effects not significant, all $P > 0.39$, all $\eta_p^2 < 0.03$). The two- and three-way interactions were also not significant (all $P > 0.40$, all $\eta_p^2 < 0.03$, except hand $\times$ age interaction $P = 0.16$, $\eta_p^2 = 0.06$).

## Discussion

The present study investigated the extent of inter-limb transfer exhibited in the dominant right hand following a period of ballistic motor training with the non-dominant left hand in young and older adults. Transcranial magnetic stimulation was used to evaluate the neurophysiological adaptations that occurred in conjunction with training to provide information about the neural mechanisms underlying the adaptation and transfer processes. We observed a substantial degree of performance gain in the trained limb for the young adults, with only one participant in this group failing to exhibit performance gains of at least 15 % in the trained limb. These performance gains transferred well to the untrained limb, a finding consistent with our previous studies for dominant to non-dominant limb transfer (Carroll et al. 2008; Hinder et al. 2011; Lee et al. 2010). With respect to the older adults, a noticeable finding was that 40 % of participants in this group (6 of 15 participants) failed to exhibit at least 15 % performance gain in the trained limb. This finding may indicate learning deficits in non-dominant limb control with advancing age, which may occur as a result of lower coordination with the non-dominant limb. It is unlikely that low levels of motivation were responsible for the lack of learning shown by these individuals as we have shown that young and older participants enrolled via the same recruitment process and provided with the same task feedback and encouragement, all improved their performance in a ballistic finger task undertaken with their dominant right hand (Hinder et al. 2011). Despite the quite variable levels of performance gain in the trained left limb, the older adults exhibited a significant degree of transfer of performance gains to the untrained right limb, and this was at a level commensurate with the degree of transfer observed in the young group. This finding presents an important contrast to our previous work, in which, despite significant performance gains in the trained right limb, older adults did not exhibit significant transfer to the untrained left limb (Hinder et al. 2011).

Transfer is manifested symmetrically in young adults following ballistic motor learning

The present findings, in conjunction with our previous work (Hinder et al. 2011), suggest a symmetrical pattern of transfer is observed with respect to ballistic motor skills for young

adults. That is, there appears to be a substantial degree of transfer following training of the dominant or non-dominant limb in young adults. This finding adds to the existing literature on whether inter-limb transfer is manifested following dominant and/or non-dominant arm training, and the specific aspects of the task that may be transferred. Following training in which participants made reaching movements while learning to compensate for external forces, it has been reported (in young adults) that transfer occurs following dominant arm training, but not following non-dominant arm training (Criscimagna-Hemminger et al. 2003; Wang and Sainburg 2004). Sainburg and Wang (2002), in contrast, reported that when compensating for visual distortions during reaching, young adults exhibited transfer of endpoint accuracy only following dominant limb training, whereas transfer of initial directional errors only occurred following non-dominant limb training. These asymmetries have been attributed to hemispheric specialisation for specific aspects of complex sensorimotor transformations needed for multi-joint reaching under visual guidance (Sainburg and Wang 2002; Wang and Sainburg 2003) or to a tendency to attribute errors produced by the non-dominant limb to intrinsic rather than extrinsic factors (Berniker and Kording 2008). The current results suggest that motor learning associated with producing more efficient neural drive in ballistic tasks transfers equally well in both directions, at least for young adults. Given that these ballistic tasks are thought to rely predominantly on processing within M1 (Lee et al. 2010; Muellbacher et al. 2002), symmetrical transfer in this context appears consistent with the 'higher order' mechanisms proposed to explain asymmetrical transfer of complex sensorimotor adaptations.

Given that the ballistic tasks utilised in the current paper and our previous transfer studies (Carroll et al. 2008; Hinder et al. 2011; Lee et al. 2010) appear to involve similar neural mechanisms to those which mediate strength gains (Selvanayagam et al. 2011), the most relevant previous transfer study is perhaps that of Farthing et al. (2005). In that study, right-handed young adults exhibited significant transfer of ulnar deviation torque following right limb training, but not following left limb training. It is not clear why our current results are different from those of Farthing et al. (2005), but there are a number of possibilities to consider. One possibility is that the wrist adduction task used by Farthing and colleagues required the acquisition of a more difficult coordination pattern between finger (to grip the device) and wrist musculature than our finger abduction task and that this involved hemispherically specialised higher order cortical centres. Alternatively, it is possible that control of the different muscle groups involves different inter-hemispheric interactions between dominant and non-dominant limbs. In this regard, it is known that short latency inter-hemispheric inhibition induced via TMS is stronger

for distal than proximal muscle groups (Harris-Love et al. 2007). A final possibility is that the mechanisms underlying transfer are different between early phases of training (e.g., after a single session as shown here) and later phases (e.g., after 24 sessions as shown in study reported in Farthing et al. 2005). Indeed, although Lee et al. (2009) showed that the capacity of the motor cortex to drive untrained muscles in the limb contralateral to that which had been engaged in a strength training program are enhanced 4 weeks later, the cortical adaptations underlying this effect are indeterminate.

With respect to older adults, it appears that transfer of ballistic skill *can* occur in older adults, but that this is only apparent following training of the non-dominant hand: in the present study, the untrained (dominant) hand improved by 25.9 % ($t_{14} = 2.29$, $P = 0.03$), whereas in our previous study, dominant limb training did not elicit improvements in the untrained (non-dominant) limb (7.7 % change, $t_{11} = 1.58$, $P = 0.18$, NS). This has important practical implications for the use of inter-limb transfer effects in rehabilitation, in that it suggests that the transfer effect is more likely to be beneficial for older people with dominant limb deficits. Another crucial finding of our current study is that some older adults appear to have deficits in the ability to acquire ballistic skill with the non-dominant limb following a training paradigm targeting that limb. It will be important to establish the characteristics of this effect and the physiological mechanisms responsible. Further work should therefore focus on the role of performance feedback (e.g., varying types of real-time and post-movement visual feedback for example) in promoting training-induced performance improvement.

### Extent of inter-limb transfer predicted by training-induced performance gains in young but not older adults

The present data indicate a significant correlation between the degree of transfer manifested in the untrained right limb and the degree of performance improvement in the trained left (non-dominant) limb for young, but not older, adults. To assess whether this finding was also observed following dominant right hand training, we conducted a regression analyses on our previously published data (Hinder et al. 2011). Consistent with the regressions from the current data set, we observed a strong correlation ($r^2 = 0.52$, $P < 0.001$) between the degree of performance improvement in the trained (right) and untrained (left) hands for the young adults, with no significant correlation for the older cohort ($r^2 = 0.04$, $P = 0.38$). It appears, therefore, that in ballistic learning paradigms, a consistent finding is that the degree of learning manifested in the trained hand may predict the extent of transfer to the untrained limb in young, but not older adults. While we acknowledge that participant

numbers (i.e., degrees of freedom) may limit the strength of the conclusions that can be drawn on the basis of these regressions, the fact that we observed consistent finding across two experiments with different participant cohorts lends weight to our supposition.

### Bilateral increases in corticospinal excitability associated with unilateral training

The present data indicate that in conjunction with unilateral left hand motor training there occurs a bilateral increase in corticospinal excitability, irrespective of age. We did not, however, observe a significant relationship between our neurophysiological measures (change in MEP and SICI in either hemisphere) and change in performance in either limb. The finding of bilateral cortical changes following a non-dominant limb training regime is consistent with our previous reports that indicate bilateral increases in corticospinal excitability in young (Carroll et al. 2008; Hinder et al. 2011; Lee et al. 2010) and older adults (Hinder et al. 2011) following unilateral right (dominant) hand ballistic learning together provide evidence suggesting that the neural responses to unilateral motor training are symmetric, that is, independent of which hand undertakes the training regime. The fact that the increase in excitability was equally apparent in both cortices suggests a high degree of motor cortex involvement in the present task together with a high degree of inter-hemispheric communication between the primary motor cortices in both age groups. In conjunction with our behavioural data indicating symmetrical transfer of ballistic motor tasks in young adults, the TMS data suggest that the mechanisms of transfer for ballistic motor learning in young adults may be fundamentally different from those involved in sensorimotor adaptations, which often give rise to asymmetrical transfer effects. Indeed ballistic motor learning (and transfer thereof) appears to involve a substantial contribution from primary motor regions (Muellbacher et al. 2002; Carroll et al. 2008; Lee et al. 2010) compared to sensorimotor adaptations which involve a more complex and diffuse network of associated brain regions. With respect to older adults, symmetric increases in cortical excitability following motor practice do not appear to be sufficient to produce symmetric transfer of ballistic motor skill. It may therefore be the case that the transfer of ballistic motor skill in older adults is not primarily mediated by the cross-activation hypothesis which appears to underlie this transfer in young adults (Lee et al. 2010). Alternatively, it is possible that changes in MEP amplitude reflect generalised inter-hemispheric interactions, rather than the specific neuronal adaptations that underlie improved performance. Further studies are therefore warranted to elucidate the specific underlying mechanisms of inter-limb transfer in older age.

## Concluding remarks

Because the current ballistic paradigms have been shown to evoke neural responses comparable to those following strength training (Selvanayagam et al. 2011), our findings have implications for the potential use of inter-limb transfer programs for rehabilitation. For example, the transfer effect may be beneficial following limb immobilisation due to traumatic injury (e.g., limb fracture) or stroke, where regaining strength in a compromised limb is paramount.

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