

# Degree of handedness affects intermanual transfer of skill learning

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**Abstract** Intermanual transfer of skill learning has often been used as a paradigm to study functional specialization and hemispheric interactions in relation to handedness. This literature has not evaluated whether degree of handedness impacts learning and intermanual transfer. Because handedness scores are related to factors that might influence intermanual transfer, such as engagement of the ipsilateral hemisphere during movement (Dassonville et al. in Proc Natl Acad Sci USA 94:14015–14018, 1997) and corpus callosum volume (Witelson in Science 229:665–668, 1985; Brain 112:799–835, 1989), we tested whether degree of handedness is correlated with transfer magnitude. We had groups of left and right handed participants perform a sensorimotor adaptation task and a sequence learning task. Following learning with either the dominant or nondominant hand, participants transferred to task performance with the other hand. We evaluated whether the magnitude of learning and intermanual transfer were influenced by either direction and/or degree of handedness. Participants exhibited faster sensorimotor adaptation with the right hand, regardless of whether they were right or left handed. In addition, less strongly left handed individuals exhibited better intermanual transfer of sensorimotor adaptation, while less strongly right handed individuals exhibited better inter-

manual transfer of sequence learning. The findings suggest that involvement of the ipsilateral hemisphere during learning may influence intermanual transfer magnitude.

**Keywords** Handedness · Learning · Transfer · Sequence learning · Sensorimotor adaptation · Motor

## Introduction

Handedness is associated with lateralization of behavioral proficiency, and structural and functional differences in the motor system (for a recent review see Goble and Brown 2008a, b). Intermanual transfer of skill learning has often been used as a paradigm to study functional specialization and hemispheric interactions in relation to handedness. This literature has yielded complex patterns of intermanual transfer that are dependent on motor task and the variables used to assess performance. Interestingly, some studies report transfer occurring from only the dominant (DOM) to the nondominant (NON) hand (Gordon et al. 1994; Halsband 1992; Laszlo et al. 1970; Parlow and Kinsbourne 1989), from the NON to the DOM hand (Hicks 1974; Parlow and Kinsbourne 1990; Taylor and Heilman 1980), equal transfer between the hands (Morton et al. 2001), or no intermanual transfer (Baizer et al. 1999; Kitazawa et al. 1997).

Several studies report greater transfer of learning when participants first practice with the DOM hand and then subsequently perform the task with the NON hand (Gordon et al. 1994; Halsband 1992; Laszlo et al. 1970; Parlow and Kinsbourne 1989). Theories that have been put forth to explain transfer from the DOM to the NON limb include the proficiency model (Laszlo et al. 1970) and the cross-activation model (Parlow and Kinsbourne 1989). The

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proficiency model proposes that motor programs are formed and stored contralaterally to the arm being trained, and that the left-sided motor control system houses a superior motor program due to its proficiency with limb control. Thus, the NON arm can benefit from the better program created during DOM arm training, but transfer does not occur in the opposite direction. This model also predicts better learning with the DOM than the NON arm (Laszlo et al. 1970). In contrast, the cross-activation model proposes that dual motor programs are formed in each hemisphere during DOM arm training, and that the one in the more dominant, left hemisphere is superior. When performing with the NON hand, the system relies on the inferior motor program, independently of the superior motor program found in the dominant hemisphere. It should be noted that although these models have been framed in terms of interhemispheric transfer via the corpus callosum, alternative interpretations exist. For example, Criscimagner-Hemminger et al. (2003) demonstrated transfer of skill learning from the DOM to the NON hand in a split-brain patient. They suggest that the dominant hemisphere may have a greater degree of ipsilateral projections, allowing for control of both the DOM and NON arms. Other studies have shown reduced interhemispheric transfer in split-brain and acallosal patients, however (De Guise et al. 1999; Lassonde et al. 1995).

It has also been demonstrated that variables used to describe performance of a single task can exhibit differential intermanual transfer. For example, in a figure drawing task, Thut et al. (1996) found that movement time showed better transfer from the DOM to the NON arm while spatial accuracy transferred best from the NON to the DOM arm. Additionally, Teixeira (2000) showed that force control transferred better from the DOM to the NON hand in a visually guided force production task, while anticipatory timing transferred equally in both directions. Sainburg and colleagues have also conducted a body of work documenting asymmetric transfer of learning between the two limbs, and have proposed the dynamic dominance hypothesis to explain their results (Sainburg 2002, 2005; Sainburg and Wang 2002; Wang and Sainburg 2004). They have found that NON arm adaptation to a visuomotor rotation improves trajectory control of the DOM arm when subsequently adapting to the same transformation. In contrast, DOM arm adaptation improves endpoint position, but not trajectory control of the NON arm. Sainburg and colleagues propose that acquired information about trajectory and endpoint position is stored in two distinct memory resources located in each hemisphere (Wang and Sainburg 2003), with the arm used during adaptation determining the nature of the information transferred across the limbs.

The previously reviewed literature presents a complex picture of intermanual transfer of learning that appears to

be dependent on both the task and the variables used to quantify performance. The bulk of this literature has tested only right handed individuals, making it difficult to interpret the role of handedness in intermanual transfer, even though the studies do typically evaluate transfer from the DOM to the NON hand and vice versa. There are a few exceptions, however, in which studies have tested both right and left handed individuals. Schmidt et al. (2000) tested right and left handed men and women in the learning and intermanual transfer of a grooved pegboard task, and found that transfer only occurred for the left handed men. Inui (2005) tested both right and left handers in the learning and transfer of a temporally paced force tapping task. They found that positive intermanual transfer occurred (measured as the variance of force production) from the NON to the DOM hand for both right and left handers. Sainburg et al. have recently extended their paradigm to test left handed individuals and found similar results (Wang and Sainburg, 2006). That is, they found that the DOM (left) arm is specialized for trajectory control and the NON (right) arm for position control in this population as well. They also found some slight, but interesting differences with respect to their previous work with right handers, suggesting that use of the NON arm may differ between right and left handers. These studies suggest that left handers may show the mirror image pattern of intermanual transfer in comparison to right handers, but that some differences may exist.

Studies of intermanual transfer do not typically take into account both degree (how strongly handed one is) and direction (whether one is right or left handed) of handedness. There are several reasons to believe that degree of handedness may play an important role in intermanual transfer, however. First, Dassonville et al. (1997) have demonstrated that there is a relationship between the degree of handedness and the laterality of functional brain activation in the primary motor cortex (M1). They report that, the less strongly handed one is, the more symmetrical the brain activation is in M1 during motor task performance. This increase in symmetry was due to greater ipsilateral M1 activation, and was present for less strongly handed participants regardless of whether they were right or left handed. Second, the corpus callosum is enlarged in both left handed and more ambidextrous individuals compared to strongly right handed individuals (Witelson 1985, 1989). In combination, these data suggest that less strongly handed individuals may have greater involvement of the ipsilateral motor cortex during learning, and a facility for sharing information between the two hemispheres, both of which would predict better intermanual transfer of learning.

Thus, the purpose of the current study was to determine whether degree of handedness plays a role in intermanual transfer. We predicted that less strongly handed individuals

would exhibit greater transfer from both the DOM to the NON hand and vice versa than more strongly handed individuals. We evaluated transfer effects for both a sensorimotor adaptation task and a sequence learning task. Researchers studying skill learning divide motor learning tasks into these two categories, which are thought to be neurally and strategically different from each other (Willingham 1998; Doyon and Benali 2005). That is, sequence learning relies more heavily on basal ganglia and medial motor area circuitry, while adaptation relies more heavily on cerebellar and parietal regions (Clower et al. 1996; Ghilardi et al. 2000; Hikosaka et al. 1999; Imamizu et al. 2000; Inoue et al. 1997, 2000; Jueptner et al. 1997a, b; Seidler et al. 2002). Pertinent to the current investigation, both types of learning engage M1 (Lu and Ashe 2005; Paz et al. 2003; Seidler et al. 2005), which Dassonville et al. (1997) reported to be the locus of degree of handedness effects. Therefore, we expected that degree of handedness would have a similar impact on transfer of both types of learning.

We tested transfer of sequence learning to sequences that were either spatially constant (same stimulus locations) or motorically constant (responses made with the homologous fingers) with respect to the trained sequence. There is evidence that perceptual representations are important in sequence learning (Mayr 1996; Remillard 2003), as well as motor representations (Willingham 1999; Seidler et al. 2005). We predicted that transfer to the motorically constant sequence would depend on degree of handedness, but that transfer to the spatially constant sequence would not. We expected this because it has been shown that movement-related facilitation of the ipsilateral M1 is specific to the homologous muscles, which would be engaged in the same sequence for the motorically constant but not the spatially constant sequence. It is not possible to assess the same type of transfer dissociation with kinematic sensorimotor adaptation tasks, because this type of learning appears to be represented exclusively in extrinsic, spatial coordinates (Wigmore et al. 2002). That is, transfer to a mirror image distortion results in negative rather than positive intermanual transfer.

## Methods

### Participants

Fourteen left handed (7 women) and 14 right handed (8 women) individuals ranging from 18 to 28 years old participated in the study. We made substantial efforts to recruit individuals with a broad range of handedness scores in order to test our hypothesis. The mean handedness score (Oldfield 1971, scaled from  $-100$  to  $100$ ) for the right handed participants was  $70$  ( $SD = 14$ ), and

ranged from  $50$  to  $100$ . The mean handedness score for the left handed participants was  $-55$  ( $SD = 23$ ) and ranged from  $-15$  to  $-90$ .

Participants were compensated for their participation, which took approximately 2 h. All participants signed a consent form approved by the Institutional Review Board of the University of Michigan. Participants filled out an activity questionnaire and the Edinburgh Handedness Inventory (Oldfield 1971), and then performed an intermanual transfer of learning paradigm for both a sequence learning and a sensorimotor adaptation task, in a counterbalanced order.

### Sensorimotor adaptation paradigm

We elected to use a kinematic sensorimotor adaptation task in which participants adapt goal-directed movements to a rotated visual feedback display. This task is widely used in the literature to study visuomotor integration and sensorimotor adaptation (Pine et al. 1996; Ghilardi et al. 2000), and we utilized task parameters similar to those employed previously. Participants moved a joystick using the hand and fingers to control a cursor moving in real time on a computer display. Movements were always initiated from a central home position on the display screen. A target appeared every 4 s, either 4.8 cm to the right, left, above, or below the centrally located home position. Participants were instructed to move the cursor representing the joystick position into the target as quickly as possible upon target appearance, and to hold the cursor within the target until it disappeared (2 s following its appearance). Participants were instructed to release their grip on the joystick handle at this point, allowing the elastic spring-loaded device to re-center for the next trial. The subsequent trial began 2 s later, resulting in an intertrial interval (from one target presentation to the next) of 4 s. Each block consisted of 28 trials, including 7 movements to each of the 4 target locations. Some blocks were performed with veridical movement feedback, whereas for the adaptation blocks, the feedback display was rotated by  $45^\circ$  in the clockwise direction about the central home location. Although it is possible that the direction of the rotation may have a differential effect on left and right handed participants, there is no evidence to suggest that this is true. In addition, it is not possible to test transfer to both a constant ( $45^\circ$  CW) and a mirror image rotation ( $45^\circ$  CCW), because sensorimotor adaptation appears to be represented exclusively in extrinsic, spatial coordinates (Wigmore et al. 2002). The blocks were presented as outlined in Table 1 for transfer from DOM to NON (DOM and NON were transposed for participants training with the NON hand and transferring to DOM). Seven right handers and seven left handers were assigned to each testing and transfer order.

**Table 1** Condition block order for the sensorimotor adaptation task

Block number	Rotated feedback	Hand
1	No	NON
2	No	NON
3	No	DOM
4	No	DOM
5	45°	DOM
6	45°	DOM
7	45°	DOM
8	45°	DOM
9	45°	DOM
10	45°	DOM
11	45°	DOM
12	45°	NON

### Sequence learning paradigm

Participants pressed buttons on a response box using the fingers of one hand, in response to stimuli displayed on a computer screen. For any given block, the stimuli were presented either randomly or following a repeating sequence. Half of the participants learned the sequence first with the DOM hand and were tested for transfer to the NON hand, and the other half performed in the reverse fashion. The sequence consisted of eight elements, with each button represented twice (for example 3 1 2 0 1 3 0 2). Participants were informed in advance of each block as to whether stimuli would appear randomly or sequentially. The stimuli were presented at a constant interstimulus interval of 800 ms in blocks lasting 75 s. The blocks were presented as outlined in Table 2 for transfer from DOM to NON (and in

**Table 2** Condition block order for the sequence learning task

Block number	Stimulus presentation	Hand
1	Random	NON
2	Random	NON
3	Random	DOM
4	Random	DOM
5	Sequence	DOM
6	Sequence	DOM
7	Sequence	DOM
8	Sequence	DOM
9	Sequence	DOM
10	Random	DOM
11	Random	NON
12	Sequence	NON
13	Random	NON
14	Sequence	NON
15	Random	NON

the reverse fashion for participants training with NON and transferring to DOM). Seven right handers and seven left handers were assigned to each testing and transfer order. For blocks 12 and 14, the sequence was either identical in presentation to the one experienced during training (“spatially constant”) or it was the mirror image (“motorically constant”), requiring button pressing of the homologous fingers on the opposite hand. Order of presentation of the spatially constant and motorically constant sequences was counterbalanced across participants.

### Sensorimotor adaptation data analysis

We analyzed the joystick data offline, using custom data analysis routines. We first filtered the data with a dual pass Butterworth digital filter (cf. Winter 1990) using a cutoff frequency of 10 Hz. Then we computed the resultant joystick path by taking the square root of the sum of the squared  $x$  and  $y$  coordinate data at each time point. The tangential velocity profile was then computed via differentiation. Movement onset and offset were calculated by applying the optimal algorithm of Teasdale et al. (1993) to this velocity profile for each movement. We computed direction error (DE) and initial endpoint error (IEE) in order to assess performance during adaptation and transfer of learning. DE is the angle between the line connecting the start and target positions (in joystick coordinates) and the line connecting the start with the spatial location of the joystick at the time of peak velocity. Subjects typically make multiple submovements to achieve targets early in the sensorimotor adaptation process (cf. Cunningham and Welch 1994; Seidler et al. 2001a, b). To compute IEE, we decomposed movements into their primary and secondary submovements (Meyer et al. 1988). We then determined the distance from the target at the end of the initial ballistic impulse (IEE). The algorithm we used searches for a period of acceleration following a period of deceleration or a change in the sign of velocity. Thus, the initial movement has “ended” when there is either a change in movement direction or an additional propulsive action is made. The IEE is the distance from the target center at the end of this initial ballistic movement.

We conducted a handedness (left or right) by order (DOM to NON or NON to DOM) by block by trial ANOVA with repeated measures on block and trial for both DE and IEE. In cases of sphericity violations, the Huynh–Feldt statistic, which corrects degrees of freedom, was reported (Huynh and Feldt 1970). Significant interactions were followed up with simple contrasts. Proficiency with the sensorimotor adaptation task was computed as the change in performance from the first five trials of adaptation (block 5) to the last five trials (block 11). Transfer magnitude was computed as the difference in performance between the *group* mean of the first adaptation block (for

example, right handers learning with the DOM hand for block 5) and an *individual's* block mean at transfer (for example, a right handed participant transferring to the DOM hand at block 12). This ensured that the comparison was made between learning with the DOM (NON) hand and transfer to the DOM (NON) hand. The magnitude of learning and transfer were both tested for correlation with handedness scores. Correlations were evaluated using one-tailed tests (to determine whether less strongly handed individuals show more transfer).

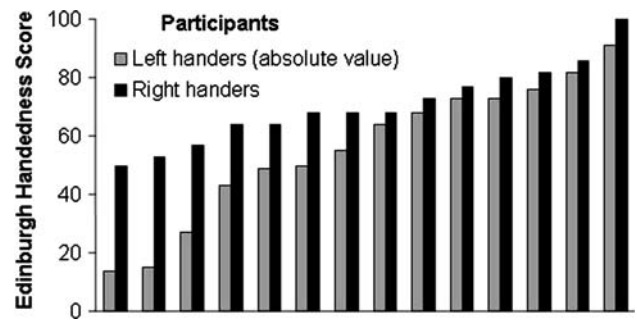
### Sequence learning data analysis

We computed response time as the performance metric for the sequence task. The median response time was computed across trials within each block, because the median is less impacted by outlier responses than the mean. The data were subjected to a handedness (left or right) by order (DOM to NON or NON to DOM) by block by trial ANOVA with repeated measures on block and trial. In cases of sphericity violations, the Huynh–Feldt statistic, which corrects degrees of freedom, was reported (Huynh and Feldt 1970). Significant interactions were followed up with simple contrasts. Proficiency with the learning task was computed as the difference in performance between the last sequence training block (block 9) and the subsequent random block (block 10). Transfer magnitude was computed as the difference in performance for the motorically constant or spatially constant transfer block (block 12 or 14) and the average of their neighboring two random blocks (blocks 11 and 13 or blocks 13 and 15). The magnitude of learning and transfer measures were both tested for correlation with degree of handedness. Correlations were evaluated using one-tailed tests (to determine whether less strongly handed individuals show more transfer).

## Results

Due to technical problems, the data from two right handed participants were lost for the sensorimotor adaptation task. As a result, the analyses are presented on 12 right handed and 14 left handed participants for the sensorimotor adaptation task, and 14 right handed and 14 left handed participants for the sequence learning task. There was a near significant difference in degree of handedness for the two groups, with the right handed participants tending to be more strongly handed than the left handed participants ( $T_{1,13} = 2.0$ ,  $P = 0.06$ ). As shown in Fig. 1, however, there was a good distribution across the range of handedness scores in both groups.

In a couple of instances, participants exhibited negative learning scores, indicating that their performance did not



**Fig. 1** Individual handedness scores are presented for each participant. The absolute value score is presented for the left handers (grey columns), to allow for easier comparison to the right handers (black columns)

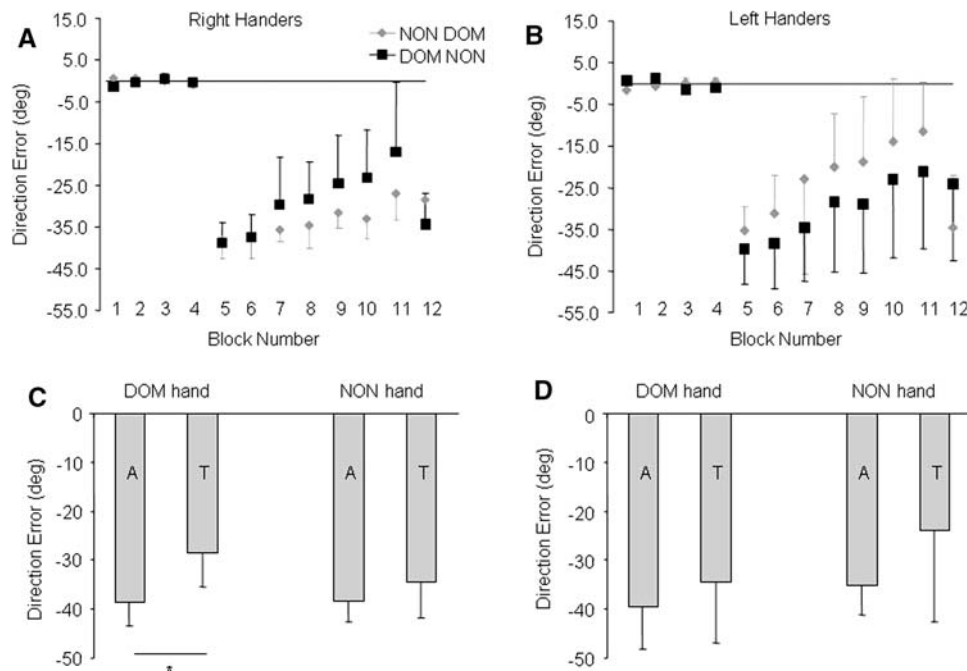
improve with practice. We assumed, in these rare cases, that participants were either not paying attention or did not follow task instructions. They were therefore removed from analyses, as noted below.

### Does handedness affect learning and transfer of sensorimotor adaptation?

The DE data are depicted in Fig. 2. Panels a and c present the data for right handed participants, while panels b and d present the data for the left handed participants. Participants learned at a faster rate with the right hand, regardless of whether they were left or right handed (handedness  $\times$  order  $\times$  block interaction,  $F_{11,58} = 5.0$ ,  $P < 0.01$ ). There was no relationship across participants between the magnitude of learning and the degree of handedness (right handers  $R = 0.05$ ,  $F_{1,11} = 0.03$ ,  $P > 0.10$ , left handers  $R = 0.25$ ,  $F_{1,13} = 0.85$ ,  $P > 0.10$ , two groups combined  $R = 0.26$ ,  $F_{1,26} = 1.8$ ,  $P > 0.10$ ).

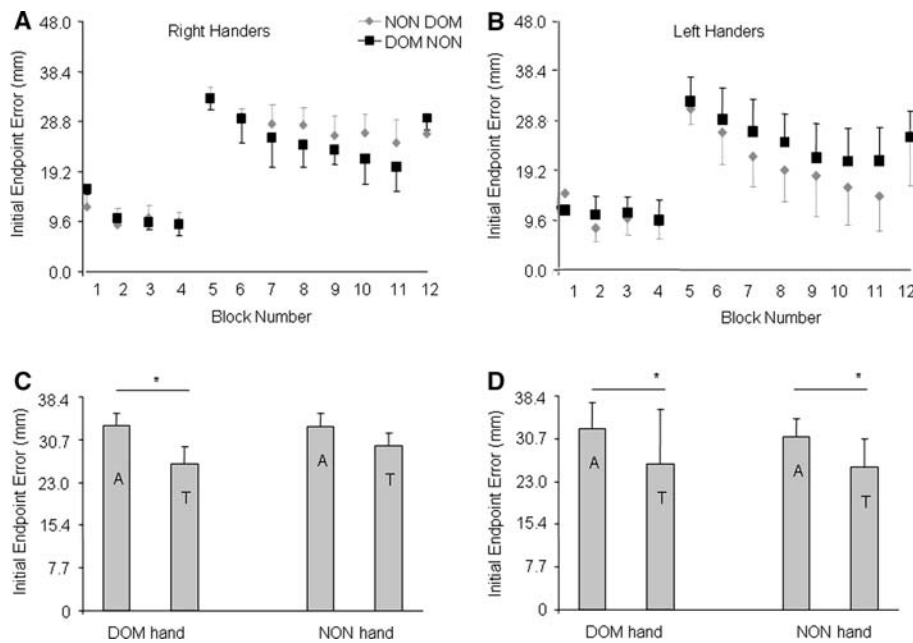
The IEE data are depicted in Fig. 3. Panels a and c present the data for the right handed participants, while panels b and d present the data for the left handed participants. Similar to the results obtained for the DE measure, participants exhibited faster learning with the right hand, regardless of whether they were left or right handed (handedness  $\times$  order  $\times$  block interaction,  $F_{5,106} = 5.5$ ,  $P < 0.01$ ). There was no relationship across participants between the magnitude of learning and the degree of handedness (right handers  $R = 0.38$ ,  $F_{1,11} = 1.8$ ,  $P > 0.10$ , left handers  $R = 0.07$ ,  $F_{1,13} = 0.07$ ,  $P > 0.10$ , two groups combined  $R = 0.20$ ,  $F_{1,26} = 1.1$ ,  $P > 0.10$ ).

Transfer was evaluated by comparing block 12 DOM (NON) performance with block 5 DOM (NON) performance across the two testing order groups (cf. Wang and Sainburg 2006). That is, block 12 transfer performance for the DOM-to-NON group was compared to block 5 performance of the NON-to-DOM group. The right handers showed significant transfer of DE from the NON to the



**Fig. 2 a** Depicts sensorimotor adaptation performance as quantified by DE for the right handed participants. The data have been averaged across trials and participants for each block, with error bars reflecting the standard deviation across participants. Blocks 1–4 are baseline visual feedback, blocks 5–11 are rotated feedback display, and block 12 is the transfer block (see Table 1 for detailed block descriptions). Participants exhibited faster learning with the right hand, depicted by the *square symbols* in

**a** and the *circular symbols* in **b**. **b** Depicts performance for the left handed participants, who also exhibited faster learning with the right hand. **c** Plots the initial adaptation (block 5) and transfer (block 12) performance for the right handers. Transfer of DE was greater to the DOM hand than the NON hand,  $*P < 0.05$ . **d** Plots the initial adaptation (block 5) and transfer (block 12) performance for the left handers. There was a trend for equal, positive transfer of DE to both the DOM and NON hands

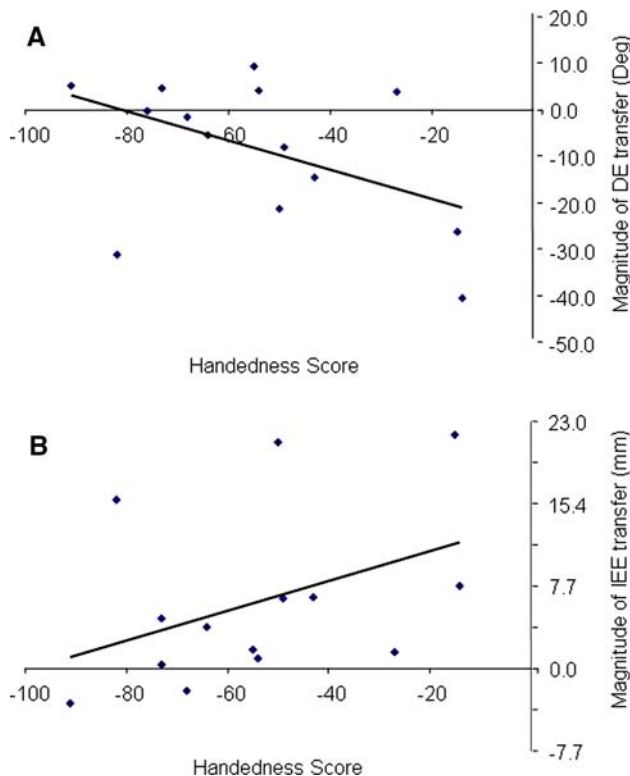


**Fig. 3 a** Depicts sensorimotor adaptation performance as quantified by IEE for the right handed participants. The data have been averaged across trials and participants for each block, with *error bars* reflecting the standard deviation across participants. Blocks 1–4 are baseline visual feedback, blocks 5–11 are rotated feedback display, and block 12 is the transfer block (see Table 1 for detailed block descriptions). Participants exhibited faster learning with the right hand, depicted by the *square sym-*

*bols* in **a** and the *circular symbols* in **b**. **b** Depicts performance for the left handed participants, who also exhibited faster learning with the right hand. **c** Plots the initial adaptation (block 5) and transfer (block 12) performance for the right handers. Transfer of IEE was greater to the DOM hand than the NON hand,  $*P = 0.05$ . **d** Plots the initial adaptation (block 5) and transfer (block 12) performance for the left handers. Transfer of IEE was equal and positive to both the DOM and NON hands,  $*P < 0.05$

DOM hand ( $F_{1,11} = 9.1$ ,  $P < 0.05$ ), but not in the other direction (Fig. 2c,  $F_{1,11} = 1.3$ ,  $P > 0.10$ ). The left handers had a tendency to show DE transfer as well (Fig. 1d,  $F_{1,30} = 3.4$ ,  $P = 0.08$ ), with no interaction between transfer magnitude and direction of transfer. The magnitude of transfer was determined as an individual's mean performance at block 12 compared to the mean of the other group's performance at block 5 (thus ensuring that DOM hand transfer performance is compared to DOM hand original learning). The left handers exhibited a relationship between the magnitude of DE transfer and degree of handedness ( $R = 0.48$ ,  $F_{1,13} = 3.9$ ,  $P < 0.05$ , Fig. 4a, larger *negative* values indicate more transfer), such that less strongly handed individuals showed more transfer of learning. This effect was not present for the right handers ( $R = 0.01$ ,  $F_{1,11} = 0.01$ ,  $P > 0.10$ ), nor for the two groups combined ( $R = 0.08$ ,  $F_{1,26} = 0.17$ ,  $P > 0.10$ ).

For the right handers, there was an interaction between direction of transfer (DOM to NON or NON to DOM) and the size of the transfer effect as assessed by IEE (Fig. 3c,  $F_{1,26} = 4.2$ ,  $P = 0.05$ ), with these participants showing bet-



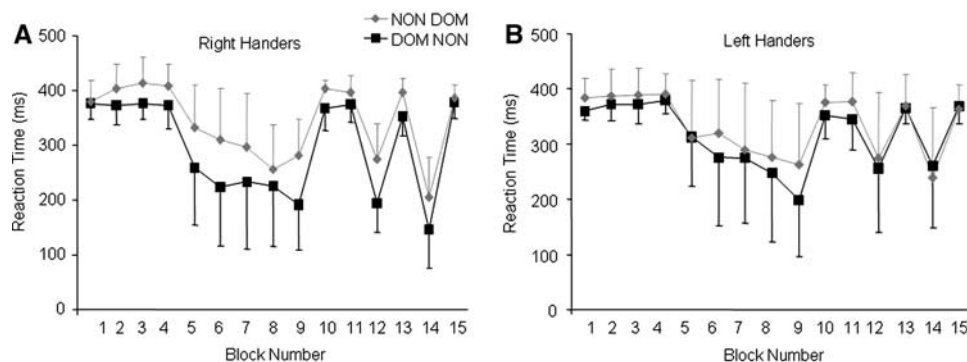
**Fig. 4** **a** Plots handedness scores (x axis) versus the magnitude of DE transfer (y axis) for the left handed participants; larger negative DE values indicate more transfer. Less strongly handed individuals (lower handedness scores) showed more intermanual transfer of learning. **b** Plots handedness scores (x axis) versus the magnitude of IEE transfer (y axis) for the left handed participants; larger positive IEE values indicate more transfer. Less strongly handed individuals (lower handedness scores) tended to show more intermanual transfer of learning

ter transfer of IEE to the DOM hand than the NON hand. The left handers showed significant transfer of IEE (Fig. 3d,  $F_{1,30} = 6.5$ ,  $P = 0.01$ ), the magnitude of which did not differ depending on the direction of transfer. The left handers exhibited a tendency for a relationship between the magnitude of IEE transfer and degree of handedness ( $R = 0.43$ ,  $F_{1,13} = 2.9$ ,  $P = 0.06$ , Fig. 4b, larger *positive* values indicate more transfer) such that less strongly handed individuals showed more transfer of learning. This effect was not present for the right handers ( $R = 0.22$ ,  $F_{1,11} = 0.58$ ,  $P > 0.10$ ), nor for the two groups combined ( $R = 0.10$ ,  $F_{1,26} = 0.25$ ,  $P > 0.10$ ).

Does handedness affect learning and transfer of sequences?

The response time data are depicted in Fig. 5. Panel a presents the data for the right handed participants, while panel b presents the data for the left handed participants. The transfer data have been sorted such that transfer to the motorically constant sequence is presented first (block 12) and the spatially constant sequence second (block 14), although order of presentation was counterbalanced across participants. There were no significant interactions of block with handedness or order, indicating that all participants learned the sequence at the same rate. Performance varied by block, though ( $F_{4,106} = 45.0$ ,  $P < 0.001$ ), with sequence learning improvements evident within the first practice block (repeated contrast on block, difference between blocks 4 and 5,  $P < 0.01$ ). Response time increased when participants were re-introduced to randomly presented stimuli following the sequence training (repeated contrast on block, difference between blocks 9 and 10,  $P < 0.01$ ). There was a relationship between the magnitude of learning and handedness for the right handed participants ( $R = 0.48$ ,  $F_{1,12} = 3.7$ ,  $P < 0.05$ , removal of one participant who had a negative learning score, see Fig. 5 panel a), such that participants who were less strongly handed exhibited better sequence learning. This relationship was not evident for the left handed participants ( $R = 0.28$ ,  $F_{1,12} = 1.0$ ,  $P > 0.10$ ) or for both groups combined ( $R = 0.11$ ,  $F_{1,27} = 0.31$ ,  $P > 0.10$ ).

Response time differences between sequence and random blocks were evident at transfer (repeated contrast on blocks, differences between blocks 11 and 12, 12 and 13, 13 and 14, and 14 and 15,  $P < 0.01$  in all cases, see Fig. 5). Participants showed better transfer when the sequence was spatially congruous with that performed during learning as opposed to motorically congruous (paired *t*-test,  $P < 0.01$ ). For all participants, the amount of learning that occurred predicted the amount of transfer that occurred, with those showing greater learning exhibiting better transfer to both the motorically constant ( $R = 0.85$ ,  $F_{1,24} = 64.6$ ,  $P < 0.01$ , removal of 3 participants with negative transfer scores) and the spatially constant ( $R = 0.83$ ,  $F_{1,24} = 51.6$ ,  $P < 0.001$ ,



**Fig. 5 a** Depicts sequence learning performance as quantified by response time for the right handed participants. The data have been averaged across trials and participants for each block, with the transfer data sorted such that transfer to the motorically constant sequence is

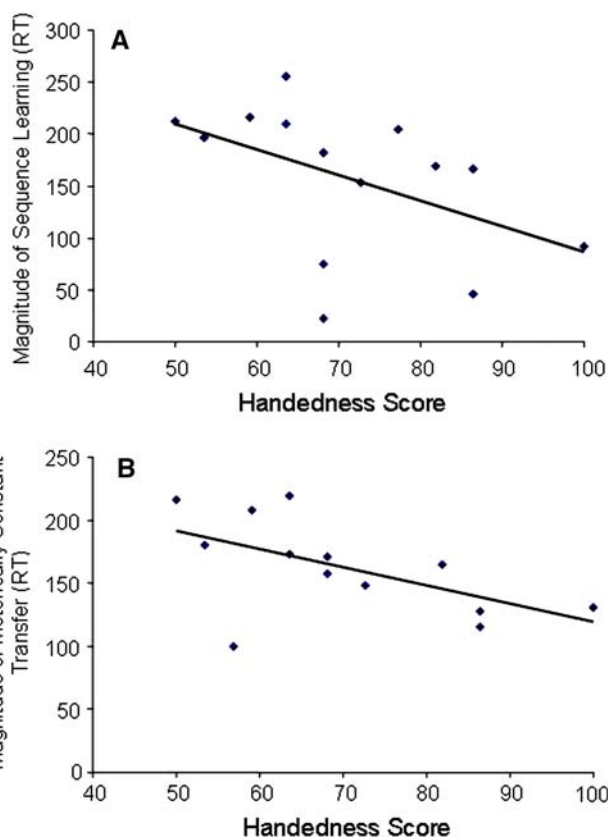
presented first (block 12) and to the spatially constant sequence second (block 14). Table 2 presents detailed block descriptions. **b** Depicts the same variables for left handed participants

removal of 3 participants with negative transfer scores) sequence.

There was no relationship between the magnitude of transfer to the spatially constant sequence and handedness for the right handed participants ( $R = 0.14$ ,  $F_{1,13} = 0.25$ ,  $P > 0.10$ ) or the left handed participants ( $R = 0.01$ ,  $F_{1,12} = 0.0$ ,  $P > 0.10$ ). There was a significant correlation for the two groups combined ( $R = 0.44$ ,  $F_{1,27} = 6.6$ ,  $P < 0.05$ ), due to a greater transfer magnitude for the right handed than the left handed participants (independent  $t$ -test,  $P = 0.01$ ). Right handed participants exhibited a relationship between the magnitude of transfer to the motorically constant sequence ( $R = 0.38$ , removal of two participants with negative transfer scores resulted in  $R = 0.56$ ,  $F_{1,11} = 5.0$ ,  $P < 0.05$ ), such that participants who were less strongly handed exhibited better transfer (see Fig. 6 panel B). This was not the case for left handed participants ( $R = 0.18$ ,  $F_{1,12} = 0.4$ ,  $P > 0.10$ ) or both groups combined ( $R = 0.27$ ,  $F_{1,27} = 2.0$ ,  $P > 0.10$ ). In addition, there was a relationship between the amount of sequence learning that occurred and the amount of transfer to the motorically constant sequence for the right handed participants ( $R = 0.55$ , removal of the two participants with negative transfer scores results in  $R = 0.80$ ,  $F_{1,11} = 20.1$ ,  $P < 0.01$ ). The direction of the relationship was such that those who learn more also transfer more.

## Discussion

In the current study, we investigated whether direction and degree of handedness affect intermanual transfer of skill learning. We hypothesized that less strongly handed individuals would show better intermanual transfer, in light of studies showing more bilateral brain activation (Dassonville et al. 1997) and enlarged corpus callosum (Witelson 1985, 1989) in these individuals. These predictions were partially



**Fig. 6 a** Plots handedness scores (x axis) versus the magnitude of sequence learning (y axis) for the right handed participants; larger positive response time values indicate more learning. Less strongly handed individuals (lower handedness scores) exhibited more sequence learning. **b** Plots handedness scores (x axis) versus the magnitude of transfer to the motorically constant sequence for the right handed participants; larger positive response time values indicate more transfer. Less strongly handed individuals (lower handedness scores) exhibited better transfer of learning

supported by the findings that less strongly handed left handers showed better intermanual transfer of sensorimotor adaptation, and less strongly handed right handers showed

better intermanual transfer of sequence learning to a motorically constant sequence.

At first glance, it is curious that degree of handedness predicts sensorimotor adaptation transfer for only *left* handed participants, while it predicts sequence learning transfer for only *right* handed participants. However, previous literature demonstrates an interaction between handedness and the type of measure used to assess hemispheric interactions. Cherbuin and Brinkman (2006a, b) determined interhemispheric transfer time for both right and left handed individuals using the Poffenberger paradigm (1912). They also had participants perform a within- and across-visual field letter matching task to determine efficiency of hemispheric interactions. They found that degree of handedness was differentially associated with hemispheric interactions for right and left handers. Left-handedness was associated with *reduced* efficiency of hemispheric interactions when assessed by accuracy on the letter matching task, but *greater* efficiency when assessed by reaction time on the same task, with effects modulated by degree of handedness (Cherbuin and Brinkman 2006b). These data, in combination with our findings, underscore the complexity of the relationship between direction and degree of handedness and hemispheric interactions.

The mechanisms underlying a relationship between degree of handedness and the magnitude of intermanual transfer are unclear; at least two possibilities arise from the existing literature. Less strongly handed individuals have been shown to have enlarged corpus callosum (Witelson 1985, 1989), potentially facilitating transfer of information from one hemisphere to the other. Perez et al. (2007) have recently shown that practicing a motor sequence with one hand is associated with reduced interhemispheric inhibition (IHI). This decrease in IHI was correlated with a general performance improvement in the untrained hand, but was not related to the amount of intermanual sequence transfer. Interhemispheric communication via the corpus callosum is not obligatory for observation of intermanual transfer effects, however. Criscimagner-Hemmingner et al. (2003) have demonstrated intermanual transfer of force field adaptation learning effects in a split-brain patient. Another potential mechanism is variations in the degree of ipsilateral control associated with degree of handedness. Dassonville et al. (1997) reported more M1 ipsilateral brain activation when less strongly handed individuals (both right and left handed participants) performed a finger movement task. Volkmann et al. (1998) also found a relationship between symmetry of M1 representations and symmetry of hand performance on a standardized test. A greater degree of ipsilateral hemisphere involvement during skill learning may facilitate access to acquired representations when transferring to the contralateral hand. Future experimentation will be required to dissociate these possibilities.

It is also possible that the differential motoric experiences of less strongly handed participants affected the results. That is, by definition, these participants use their NON hand more frequently. This greater use is likely associated with motor cortical plasticity (cf. Karni et al. 1995; Hutchinson et al. 2003), meaning that NON motor representations may be more developed in these participants than in more strongly handed individuals. We attempted to account for this by evaluating transfer effects relative to baseline performance. However, enhanced motor representations for the NON hand in less strongly handed individuals may facilitate transfer effects.

Our finding that degree of handedness modulates transfer to the motorically constant but not the spatially constant sequence is compatible with the literature on interhemispheric facilitation associated with motor execution. Sohn et al. (2003) used transcranial magnetic stimulation (TMS) to show that, during movement execution, the ipsilateral M1 is both inhibited and facilitated. These effects are temporally modulated with respect to movement onset. Interestingly, ipsilateral facilitation effects were specific to the homologous muscles. This led us to hypothesize that transfer to the motorically constant sequence, which requires use of the homologous fingers to execute the sequence, would be associated with degree of handedness. Due to greater ipsilateral involvement during movements made by less strongly handed individuals (Dassonville et al. 1997), ipsilateral facilitation of homologous muscles may be greater for those with lower handedness scores, thereby increasing intermanual transfer to the motorically constant sequence.

It was not possible for us to test for intermanual transfer to a “motorically constant” version of the sensorimotor adaptation task. This would have required evaluating transfer to a counterclockwise 45° rotation. However, it has previously been demonstrated that when participants are exposed to rotations of opposing directions, interference (negative transfer) occurs (Wigmore et al. 2002), suggesting that learning is represented in an extrinsic, spatial coordinate system. Thus it was not possible for us to evaluate whether the relationship between degree of handedness and transfer magnitude to a motorically constant task version in right handers applies across different tasks.

Participants learned the sensorimotor adaptation task faster with the right hand, regardless of whether they were left or right handed. In addition, right handed participants who were less strongly handed exhibited better sequence learning. These same participants showed better intermanual transfer to the motorically constant sequence. This raises the possibility that degree of handedness does not necessarily modulate the transfer effect per se, but rather modulates the amount of learning that occurs. Participants who exhibit better learning would have more knowledge available to transfer. We do not think that this wholly

explains the relationship between degree of handedness and transfer, however. The relationship between amount of learning and magnitude of transfer existed for all participants (both right and left handed) and for both types of sequence transfer (motorically constant and spatially constant), while the degree of handedness effect was specific to right handers transferring to the motorically constant sequence.

Sainburg and colleagues have conducted extensive experiments on intermanual transfer of sensorimotor adaptation (Sainburg 2002, 2005; Sainburg and Wang 2002; Wang and Sainburg 2004). They have found that NON arm adaptation to a visuomotor rotation improves trajectory control of the DOM arm, while DOM arm adaptation improves endpoint control of the NON arm. Our data replicate some aspects of their results, but differ in other ways that are worthy of discussion. First, the right handers in the current investigation showed better transfer of DE (trajectory measure) from the NON to the DOM hand (as opposed to from DOM to NON), similar to the results of Sainburg et al. However, our right handed participants showed better transfer of IEE (endpoint measure) from the NON to the DOM hand (opposite direction of Sainburg studies). The left handers in the current study showed positive and equal transfer for both measures in both directions. Wang and Sainburg (2006) also tested their paradigm with left handed participants. They found that left handers showed greater transfer of DE from the NON to the DOM arm, but also found some positive transfer of DE from the DOM to the NON arm when DE was calculated at the time of peak tangential velocity (the method used in the current investigation). They found asymmetrical transfer of endpoint accuracy for left handers, with greater transfer from the DOM to the NON arm. Thus, for their investigations, they found that performance for left handers mirrored the pattern that they reported for right handers. The discrepancies between the current data set and their studies may be attributable to a few key methodological differences. First, we specifically recruited individuals across a broad range of handedness scores in order to investigate effects related to degree of handedness, while their studies report on consistent right and left handers. Our finding that degree of handedness modulates the magnitude of intermanual transfer for left handers may have contributed to differences between our study and their report of left handers (Wang and Sainburg 2006). Second, our sensorimotor adaptation paradigm requires participants to make movements with the hand and fingers, while their participants employ whole arm movements. They have demonstrated that the DOM arm uses interaction torques more efficiently than the NON arm (Bagesteiro and Sainburg 2002), which may play a reduced role in moving smaller effectors. It remains to be seen whether the dynamic dominance hypothesis (Sainburg

2002) applies specifically to arm movements, or also is applicable to more fine motor control behaviors achieved with the hand and fingers.

Despite some discrepancies between the current pattern of results and Sainburg's model of intermanual transfer (Sainburg 2002), our data are more compatible with this model than with the proficiency (Laszlo et al. 1970) or cross-activation (Parlow and Kinsbourne 1989) models outlined in the introduction, which predict that transfer will only occur from the DOM to the NON hand. These latter two models make predictions based on the superiority of the dominant limb/hemisphere. However, the Sainburg studies have shown that the NON limb is specialized for endpoint control, and recent work demonstrates NON arm advantages in processing of proprioceptive information (Goble and Brown 2008a, b). Our findings of symmetrical transfer in the left handed participants support the notion that the NON limb has control advantages too.

In conclusion, our data demonstrate that degree of handedness has an impact on the amount of motor learning that occurs, and on the magnitude of intermanual transfer for both sequence learning and sensorimotor adaptation tasks. We found that degree of handedness was related to intermanual transfer of sensorimotor adaptation in left handed participants, while degree of handedness was related to intermanual transfer of sequence learning in right handed participants. The findings suggest that involvement of the ipsilateral hemisphere during learning may influence intermanual transfer magnitude. Moreover, the results underscore the importance of considering both direction and degree of handedness in studies of lateralization and intermanual transfer, and re-emphasize that handedness should be viewed as a continuous, rather than discrete, variable.

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