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Transfer of short-term motor learning across the lower limbs as a function of task conception and practice order

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ABSTRACT

Interlimb transfer of motor learning, indicating an improvement in performance with one limb following training with the other, often occurs asymmetrically (i.e., from non-dominant to dominant limb or vice versa, but not both). In the present study, we examined whether interlimb transfer of the same motor task could occur asymmetrically and in opposite directions (i.e., from right to left leg vs. left to right leg) depending on individuals' conception of the task. Two experimental conditions were tested: In a dynamic control condition, the process of learning was facilitated by providing the subjects with a type of information that forced them to focus on dynamic features of a given task (force impulse); and in a spatial control condition, it was done with another type of information that forced them to focus on visuomotor features of the same task (distance). Both conditions employed the same leg extension task. In addition, a fully-crossed transfer paradigm was used in which one group of subjects initially practiced with the right leg and were tested with the left leg for a transfer test, while the other group used the two legs in the opposite order. The results showed that the direction of interlimb transfer varied depending on the condition, such that the right and the left leg benefited from initial training with the opposite leg only in the spatial and the dynamic condition, respectively. Our finding suggests that manipulating the conception of a leg extension task has a substantial influence on the pattern of interlimb transfer in such a way that the direction of transfer can even be opposite depending on whether the task is conceived as a dynamic or spatial control task.

1. Introduction

The fact that practicing with one hand influences subsequent performance with the untrained hand surprised scientists from different fields as early as the middle of the 19th century. A German physiologist Ernst Heinrich Weber wrote in his letter to Gustav Theodor Fechner, a German physicist, that his children were able to write mirror-inverted letters with their left hand without any practice with that hand before (see Fechner, 1858). Within a self-experiment, Fechner (1858) made the same observation in recording measured data, where he sometimes spontaneously used his left hand and wrote the measured numbers mirror-inverted without much decrement in performance compared to right hand writing. Today, the aforementioned effect is known as interlimb (e.g. Sainburg & Wang, 2002; Malfait & Ostry, 2004), intermanual (e.g. Birbaumer, 2007; Perez et al., 2007b), contralateral (e.g. Harris & Diamond, 2000; Vangheluwe, Wenderoth, & Swinnen, 2005), interlateral (e.g. Teixeira, 2006) or bilateral transfer (e.g. Inui, 2005; Teixeira, 2000), and also as cross-education (e.g. Farthing, 2009; Gabriel, Kamen, & Frost, 2006) or contralateral strength training effect (e.g. Carroll, Herbert, Munn, Lee, & Gandevia, 2006). One reason for these different denotations of the same effect is that the transfer paradigms are used to investigate different research questions from various research areas including physiology, cognitive and neural sciences, in which the transfer effect is investigated to understand a general mechanism of motor control at a higher level in the central nervous system and/or at a lower level in the neuromuscular system, as well as sports and health sciences, in which the effect may be used to optimize learning or rehabilitation processes.

The pattern of interlimb transfer, whose neural correlates are thought to involve the supplementary motor area, ventrolateral thalamic nucleus and cerebellum (Perez et al., 2007b; Seidler, 2010), seems to be strongly influenced by the way the two brain hemispheres are specialized (Birbaumer, 2007; Serrien, Ivry, & Swinnen, 2006). Studies suggest that various aspects of movement control are differentially mediated by the right and the left cerebral hemispheres (e.g. Brown & Kosslyn, 1993; Corballis, 1991; Serrien

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et al., 2006; Stöckel & Weigelt, 2011; Wang & Sainburg, 2007a). While the left hemisphere is often suggested to be specialized for fine motor skills and simultaneous actions, as well as sequential and dynamic control of movements (Corballis, 1991; Goodale, 1990; Harrington & Haaland, 1991; Jeannerod, 1986), the right hemisphere is characterized as being holistic and intuitional, and also specialized for visuo-spatial control of movements (Ghilardi et al., 2000; Goodale, 1990; Previc, 1991). For example, Roy and MacKenzie (1978) provided evidence for a predominance of the left-hand–right-hemisphere system for spatial tasks, while Peters (1980) as well as others (i.e. Annett, Annett, Hudson, & Turner, 1979; Todor & Doane, 1978) have shown an advantage of the right-hand–left-hemisphere system for fast sequential and dynamic movements. These findings are in agreement with Sainburg's *dynamic dominance hypothesis* (2002), which posits that the essential factor that distinguishes dominant from non-dominant arm performance is the facility governing the control of limb dynamics. According to this hypothesis, the two limb/hemisphere systems are specialized for controlling different features of movement in such a way that the dominant system is specialized for controlling dynamic features of movement, and the non-dominant system for controlling spatial features of movement. This hypothesis received support from interlimb transfer studies which demonstrated that dynamic features of reaching movement (e.g., initial direction information) following adaptation to a novel visuomotor condition transfers primarily from the non-dominant to dominant arm, and spatial features (e.g., final position information) from the dominant to non-dominant arm in both right- and left-handers (Sainburg & Wang, 2002; Wang & Sainburg, 2003, 2006). However, it has also been demonstrated that adaptation to a novel dynamic condition during targeted reaching transfers from the dominant to non-dominant arm (Sainburg & Wang, 2002; Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Wang & Sainburg, 2004a, 2004b, 2006; Galea, Miall, & Woolley, 2007), which is opposite to the direction of transfer observed following visuomotor adaptation. Based on these findings, Wang and Sainburg (2004a,b, 2007a; Sainburg & Wang, 2002) further suggested that the dominant system learning leads to the development of a neural representation of a dynamic task, which can be used by the non-dominant system to facilitate non-dominant performance, whereas the non-dominant system learning does not.

While most previous studies employed laboratory tasks to study interlimb transfer, Stöckel and colleagues attempted to test this phenomenon in more ecological settings by investigating the pattern of interlimb transfer following the acquisition of various sport skills, such as basketball throwing and dribbling (Senff & Weigelt, 2011; Stöckel, Hartmann, & Weigelt, 2007; Stöckel, Weigelt, & Krug, 2011; Stöckel & Weigelt, 2011). These studies showed that initial practice with the right hand led to an improvement in subsequent performance with the untrained left hand, as compared to its naïve performance, when the tasks required a high demand on the generation of maximum forces (Stöckel & Weigelt, 2011). Additionally, the opposite pattern (i.e., transfer from the left to the right hand) was observed for the tasks with high visuomotor demands (Senff & Weigelt, 2011; Stöckel et al., 2011). These results are in agreement with the findings stated in the previous paragraph that the direction of interlimb transfer can be influenced by the type of motor tasks employed (Sainburg & Wang, 2002; Criscimagna-Hemminger et al., 2003; Wang & Sainburg, 2004a, 2004b, 2006; Galea et al., 2007).

Here, it is important to note that certain tasks can be performed with more emphasis placed on either their dynamic or visuomotor demands depending on the way an individual views the tasks. When throwing a dart, for example, one might focus more on dynamic features of the task (e.g., generation and dissipation of forces required for the arm movement) for optimal performance, whereas another might focus more on its visuomotor features (e.g., position and/or distance of the target relative to her body position). That is, the same motor task can be performed, or learned, differently depending on whether an individual conceives it as a task with high demands on force control or as one with high visual–spatial demands.

In the present study, thus, we examine the effect of task conception on the pattern of interlimb transfer by directing individuals' attention to specific task demands. We investigated the skill acquisition process of an optimization task in a fully crossed transfer paradigm with two groups of subjects practicing in an opposite order with respect to the leg used (i.e., the left leg used first and then the right leg used, or vice versa). The physical nature of the task was essentially the same for all participants, which was to perform single leg extensions on a horizontal swing to reach a predefined force impulse (dynamic) or pendulum distance (spatial). Participants were, however, forced to focus either on the dynamic features or on the spatial features of the task based on the type of feedback provided (i.e., force impulse vs. distance). We hypothesized that the pattern of interlimb transfer would vary depending on the conceived task demands. It should be noted here that most previous findings on interlimb transfer were based on the upper limb movements. It is reasonable to think that previous findings from the upper limb transfer studies would be generalized to the lower limb tasks employed in the present study, because both the upper and the lower limbs on the same side are thought to be controlled mainly by their contralateral brain hemisphere (e.g., Amunts et al., 1996; Aramaki, Honda, & Sadato, 2006; Brodmann, 1906; Penfield & Jasper, 1954; Perez, Wise, Willingham, & Cohen, 2007a).[1] It has also been suggested that the right (dominant) and the left (non-dominant) legs contribute more to the task of forward propulsion and postural control in walking respectively (Clifford & Holder-Powell, 2010; Sadeghi, Allard, Prince, & Labelle, 2000), which is in accordance with the dynamic dominance hypothesis. Thus, we predicted that interlimb transfer from the trained to the untrained leg would occur asymmetrically (e.g., from the left to the right leg, but not vice versa), and also that the direction of transfer would depend on the type of movement information provided. If this were not the case (i.e., transfer direction is the same between the two feedback conditions), it would indicate that the conception of a given motor task regarding its specific demands does not matter in determining the pattern of interlimb transfer.

2. Methods

2.1. Participants

Sixty-seven university students volunteered in this study and practiced the task under one of two different information conditions. Prior to the experiment, thirty-four of them were randomly assigned to the "spatial control" condition and thirty-three to the "dynamic control" condition. Informed consent was solicited prior to participation. Hand preference was detected by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were right-handed. The mean laterality index of our subjects was 92.2.

2.2. Apparatus and task

Participants were required to perform a leg extension task by pushing against a dynamometric platform while lying in the supine position on a horizontal swing (Fig. 1). To achieve a comparable

[1] The aforementioned statement may need to be interpreted with caution, because other studies (e.g., Chapman, Chapman, & Allen, 1987; Coren, 1993; Coren & Porac, 1978) have suggested that the hand-foot concordance is only seen in 85–94% of the individuals.

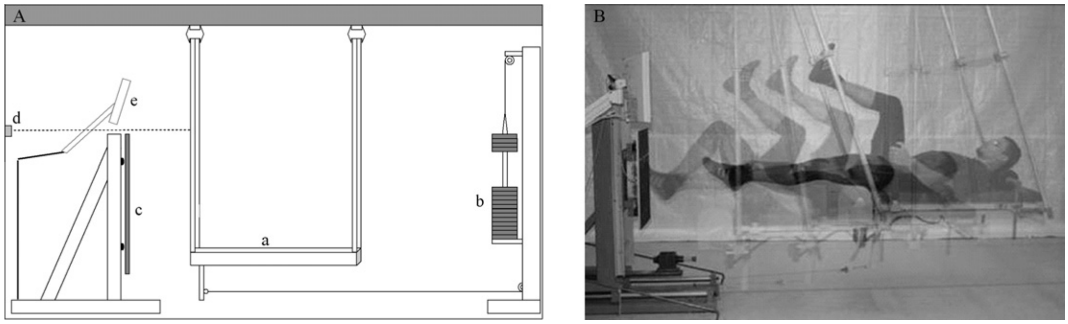

Fig. 1. Set-up of the "horizontal swing" measurement system (A) with the swing, where the participants were placed in supine position (a), the balancing weight (b), the dynamometric platform (c), the distance measuring unit (d), and the feedback screen (e). On the right side, (B) a dynamic depiction of the leg extension task from the initial contact at the platform until the maximum deflection is illustrated.

posture across participants, we measured their femoral length, according to which we adjusted the starting position of the swing (Fig. 1A). The height of the swing always remained the same across subjects. A balancing weight connected to the swing (Fig. 1A, b) required the subjects to perform pushing movements with some physical strain. The weight of the swing itself was completely compensated so that the participants only had to set their own body weight in motion by pushing against the platform.

Our integrated measuring system, which consists of a distance measuring unit, a potentiometer, a dynamometric platform and a desktop computer, captured movement parameters, such as force (N), contact time at the force plate (ms), and spatial deflection of the horizontal swing (mm). Spatial deflection, which is the covered distance of the swing, was assessed by a precision potentiometer connected to the swing over a wire rope (Fig. 1A, d; Posiwire, ASM®) with a sensitivity of 8 V/m and a measuring range of 1250 mm. Changes in voltage measured by the potentiometer were digitized using an isolated USB data acquisition module (DT9800, Data Translation GmbH, Germany), transmitted to the computer and converted into a length unit (mm) by our software (Delphi programming-based software that was custom developed in cooperation with the Institute of Applied Training Science, Germany). A dynamometric platform (Fig. 1A, c; KAM®, AST GmbH, Germany) was used to capture the force information of a pushing movement, as well as contact time (i.e., time between initial contact with the platform and departure from it), with a sampling rate of 1000 Hz. Signals, filtered with a cut-off-frequency of 50 Hz (Bessel low-pass filter, Robotron, Germany), were digitized, transmitted to the computer and converted by the software (using a predefined calibration factor) into a force unit (N). The absolute force and contact time data were used to compute force impulse (i.e., integral of the force over the period of time during which subjects stayed in contact with the force plate), which were then used along with spatial deflection to compute the deviation between a target value (i.e., 80% of maximum force impulse or maximum spatial deflection; more information provided in the following paragraphs) and an actually attained value in each movement trial. Using this deviation information, offline visual feedback indicating the outcome of the subjects' performance (termed 'feedback' hereafter) was presented on a monitor (Fig. 1A, e) immediately following each trial, in the form of a coloured arrow. The colour of the arrow was determined in such a way that three yellow lights with different shades represented three different ranges of the attained values that were lower than the target value (in steps of 5%), while three differently shaded red lights represented those higher than the target value (Fig. 2). Presentation of this feedback challenged our participants to optimize their performance.

All our participants performed the same leg extension task regardless of the condition. At the beginning of each trial, the swing was fixed in a standardized rest position with the participant belted in the supine position with one foot softly in contact with the platform and the other foot resting on the horizontal bar that connects the two vertical poles of the swing (see Fig. 1B). To adjust the participants' position on the swing, they first brought their legs to a position in which the angle between their bent thigh and the bottom of the swing was 90°. Then, they were moved to the point at which the backside of the thigh (i.e. hamstring) was flush with the edge of the swing (see Fig. 1B). In that position, they were fastened with one belt at the hip and another at the chest, along with a head support. To perform a trial, the participants were required to push against, and lose contact with, the platform by fully extending the leg that was in contact with the platform (see Fig. 1B). Although the physical properties of the task were the same between the two information conditions, the two conditions were different in that the targeted value for each subject, along with the type of feedback presented on the monitor, were defined differently, as described below.

(a) '*Spatial control*' condition – The participants were instructed to achieve the target value, which represented 80% of the maximum spatial deflection that was specifically determined for each participant prior to the training period, in

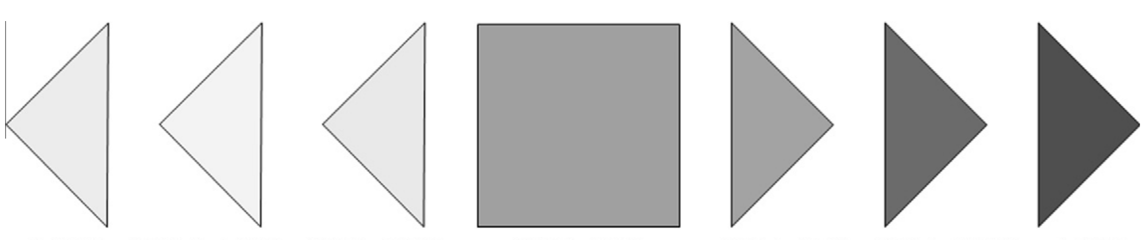

Fig. 2. Depiction of the light display that provided subjects with information regarding their performance after each trial. One of the three triangles with different shades of colour (yellow for the triangles on the left, red for the ones on the right side) flashed when the normalized performance error with a sign from a given trial fell within the range shown under each triangle. The flashed triangle retained its colour until the completion of the next trial. The colour of the rectangle in the middle was always green.

each trial as precisely as possible. Accordingly, the participants only received the feedback pertaining to the spatial aspect of the task.

(b) '*Dynamic control*' condition – The participants were instructed to achieve the target value, which represented 80% of the maximum force impulse specifically determined for each participant, in each trial as precisely as possible. Accordingly, the participants only received the feedback pertaining to the dynamic aspect of the task.

2.3. Procedure

Prior to the experiment, each participant was randomly assigned to one of two information conditions ('spatial control' vs. 'dynamic control'), and then to one of two experimental groups in each information condition. One experimental group used the right leg during the learning period (Rtrain group); and the other group used the left leg for training (Ltrain group). Post-training performance was assessed in the trained and untrained leg, where we were particularly interested in the transfer effects (i.e., the post-training performance in the non-trained leg). In the spatial control condition, 17 subjects (13 male and 4 female, 22.7 ± 3.6 years of age) were assigned to the Rtrain group and 17 subjects (10 male and 7 female, 21.6 ± 1.9 years of age) to the Ltrain group. In the dynamic control condition, 17 subjects (10 male and 7 female, 23.0 ± 4.9 years of age) were tested in the Rtrain group and 16 subjects (13 male and 3 female, 23.1 ± 2.9 years of age) in the Ltrain group. (Our post-experiment analysis confirmed that subjects' performance was not different between males and females.) Because the procedure was the same for all participants, the following depiction will be independent of participant's group and condition affiliation.

The experiment consisted of four parts: a classification period, a PRE test, a learning period and a POST test. Conducting all these parts lasted approximately two hours. During the *classification period*, personal information (e.g., age, sex) and anthropometric data (e.g., body weight, femoral size) were obtained, based on which the balancing weight and the distance between the swing and the platform appropriate for each participant were determined. Then, the participants performed a maximum leg extension (instruction: to achieve a maximum spatial deflection or maximum force impulse, depending on the information condition) for three times with each leg. The highest value out of these three trials was assumed to be the participant's maximum for the given leg, 80% of which was determined as the participant's individual target value. These values were automatically computed and stored by our software, and were also used to calculate a normalized performance error (i.e., |target value − attained value|/target value). This error was also used, after being added with a sign (+ indicating an overshoot, − indicating an undershoot), to provide the feedback following completion of each trial. At the beginning of the *PRE test*, the participants received specific instructions and explanations in a written form regarding their information condition and experimental group that they belonged to.[2] Then, they started the PRE test, during which they performed six trials of the leg extension task, first with the leg that would be used during the POST test, then with the other leg (e.g., six trials with the left leg, then six trials with the right leg for the Rtrain group). They were instructed to minimize the deviation between the attained value and the target value in each trial by utilizing the feedback received from the previous trial. During the *learning period*, the participants continued to perform the leg extension task with only one leg (the left leg for the Ltrain, the right leg for the Rtrain group) in eight blocks of six trials. After each block, participants received a rest for about one minute (and about 15 s in between trials). Following the learning period, the participants performed the *POST test,* whose procedure was the same as that in the PRE test, except that the trained leg was tested first, and then the untrained leg.

2.4. Data analyses

Performance error, the difference between the target value and the attained value in terms of spatial deflection (for the spatial control condition) or force impulse (for the dynamic control condition), was first measured in each trial for each participant. This error was used as a primary measure in this study because it is analogous to 'final position error,' which has been frequently used in previous inter-arm transfer studies and shown to be differentially influenced by the sensorimotor nature of given motor tasks (i.e., dynamic vs. visuospatial) (Sainburg & Wang, 2002; Wang & Sainburg, 2003, 2004b; Wang and Sainburg, 2007a). Performance error was then divided by the target value, which provided a normalized measure that allowed us to compare between the two types of errors regardless of units (i.e., mm vs. N). This normalized performance error (NPE) served as the main dependent measure in the present study.

To ensure that the leg extension task was equivalent between the two information conditions regardless of how it was conceived, both types of target values (i.e., one measured in distance (mm), the other in impulse (N s)) were computed in each of the two conditions, and subjected to a repeated-measures ANOVA with Information (dynamic, spatial) as a between-group factor and Leg (trained, untrained) as a within-group factor for each type of target values separately.

To examine the change of performance with time in each leg, two repeated-measures ANOVA's were conducted: one to assess whether performance with the trained leg improved over time (i.e., whether learning occurred), and the other to assess whether performance with the untrained leg changed over time, from PRE to POST test (i.e., whether the training with the opposite leg influenced the untrained leg performance). For the former analysis, data from the trained leg were subjected to an ANOVA with Information (dynamic, spatial) and Group (Ltrain, Rtrain) as two between-group factors, and Block (PRE, 1–8 from the learning period, POST) as a within-group factor; and for the latter, data from the untrained leg to an ANOVA with Information and Group as two between-group factors, and Time (PRE, POST) as a within-group factor.

Bonferroni corrections were made to adjust the alpha level for conducting three ANOVA's (i.e., alpha = .05/3 = .017). For any significant main or interaction effects, post hoc pairwise comparisons using the Sidak adjustment were performed between any two given conditions (e.g., between PRE and POST tests for the Rtrain group).

3. Results

Table 1 shows the mean target values, as well as the mean PRE and POST test results, for both trained and untrained legs of each subject group in each information condition. The target values were not statistically different between the two legs or between the two subject groups within each information condition

[2] Excerpt from the instruction participants of the spatial condition received prior to the leg extension task (translation from German): "Now, you are required to push with your right/left foot against the platform to constantly realize 80% (i.e. your individual target deflection) of the distance you covered with the swing in the trial for maximum deflection. Each of the training and test blocks consists of six single trials (with a short rest between each trial), where you are required to minimize the deviation between your attained deflection and your individual target deflection. After each trial you will be visually informed (PC screen) about this deviation for immediate corrections." The instruction for the dynamic condition was almost the same, but focusing at the force impulse that had to be produced.

Table 1
Target values and normalized performance errors (NPE) for two subject groups in each information condition. The values in shaded areas indicate an improvement in performance with the untrained leg following opposite leg training.

	Spatial control condition				Dynamic control condition			
	Rtrain group (n = 17)		Ltrain group (n = 17)		Rtrain group (n = 17)		Ltrain group (n = 16)	
	R	*L*	*L*	*R*	*R*	*L*	*L*	*R*
Target value (mm or Ns, ± SE)	*684.6* *(14.4)*	*692.5* *(16.9)*	*667.2* *(18.2)*	*683.9* *(20.2)*	*317.5* *(12.3)*	*327.2* *(18.3)*	*354.7* *(17.3)*	*352.6* *(18.0)*
NPE during PRE test (% ± SE)	3.19 *(0.34)*	3.04 *(0.27)*	3.96 *(0.49)*	3.64 *(0.53)*	6.14 *(0.59)*	7.57 *(1.13)*	7.54 *(0.73)*	6.82 *(0.76)*
NPE during POST test (% ± SE)	1.82 *(0.23)*	3.72 *(0.48)*	1.71 *(0.21)*	2.59 *(0.34)*	4.88 *(0.47)*	5.53 *(0.50)*	5.43 *(0.67)*	7.26 *(0.98)*

(p > .05 using paired t-tests and independent t-tests, respectively). The table also indicates an improvement in performance from the PRE to POST test in many conditions, not only for the trained, but also for the untrained leg.

3.1. Target values of the leg extension task in the two information conditions

As described in the data analyses section, the two types of target values (one measured in N s, the other in mm) were computed for both the trained and the untrained legs in each of the two information conditions. These target values, illustrated in Fig. 3, were subjected to a repeated-measures ANOVA with Information (dynamic, spatial) and Leg (trained, untrained), which did not show any significant effect (neither interaction nor main effect) for either type of target values. This indicates that the leg extension task per se was equivalent between the two information conditions, as well as between the two legs, regardless of how the task was conceived (i.e., either as a dynamic or as a spatial control task).

We further examined whether the pattern of change in performance of the trained leg over time (from the PRE to the POST test) would differ depending on how the NPE was computed (i.e., using the performance errors expressed either in mm or in N s). Our post hoc analyses indicated that the NPE was not significantly different between the two information conditions at the PRE test, regardless of how it was computed (4.51% and 3.58% in the dynamic and the spatial condition, respectively, using performance errors expressed in mm; 6.82% and 7.52% in the dynamic and the spatial condition, respectively, using performance errors expressed in N s). However, the pattern of change in performance during the training was dependent on the type of performance errors, such that the NPE computed using the performance errors expressed in mm, but not those expressed in Ns, decreased steadily in the spatial control condition (from Block 1: 2.50% to POST test: 1.7%, p < .05), and vice versa in the dynamic control condition (from Block 1: 6.15% to POST test: 5.15%, p < .05). This suggests that the effect of training on a performance improvement in the two information conditions was only associated with the specific type of information provided in each condition.

3.2. Changes in performance with the trained leg

Figs. 4 and 5 illustrate the changes in performance for both Ltrain and Rtrain groups in the two information conditions throughout the three experimental periods: PRE test, learning period and POST test. In both conditions, the normalized performance error decreased steadily from the PRE test to the POST test, indicating a training effect. Our repeated-measures ANOVA with Information (dynamic, spatial), Group (Ltrain, Rtrain) and Block (PRE, 1–8 from the learning period, POST) revealed a significant main effect of Block, $F(9, 567) = 8.95$, p < .001. Post hoc pairwise comparisons indicated a significant improvement in performance from the PRE to the POST test for both legs (p < .05). Significant improvements were observed in pairwise comparisons between some other blocks as well, including those between the PRE test and blocks 3–8, and between block 1 and the POST test (p < .05). This clearly indicates that learning of the leg extension task occurred throughout the blocks, regardless of the conditions and groups. A significant main effect was also observed for Information, $F(1, 63) = 84.96$, p < .001, indicating that the mean NPE obtained in the spatial control condition was significantly lower than that obtained in the dynamic condition. No other factors had significant main or interaction effects.

3.3. Changes in performance with the untrained leg

Performances with the untrained leg during the PRE and the POST test are also illustrated in Figs. 4 and 5. Our ANOVA revealed a significant three-way interaction effect among Information (dynamic, spatial), Group (Ltrain, Rtrain) and Time (PRE, POST), $F(1, 63) = 8.81$, p = .004, indicating that the difference between the two groups in terms of the amount of change in performance from

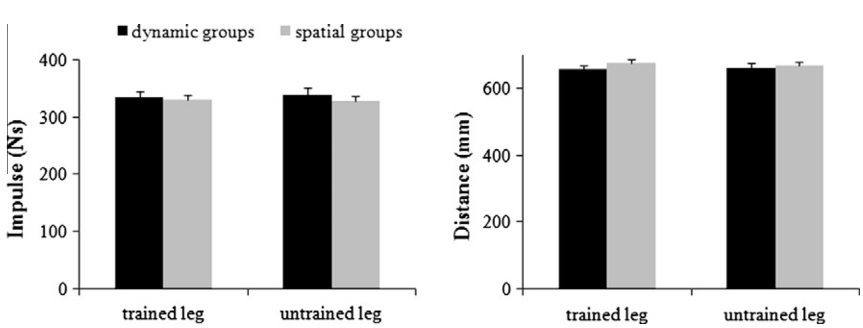

Fig. 3. Target values (measured in Ns and mm) at the PRE test for both the trained and the untrained legs in each of the two information conditions. Error bars indicate standard errors.

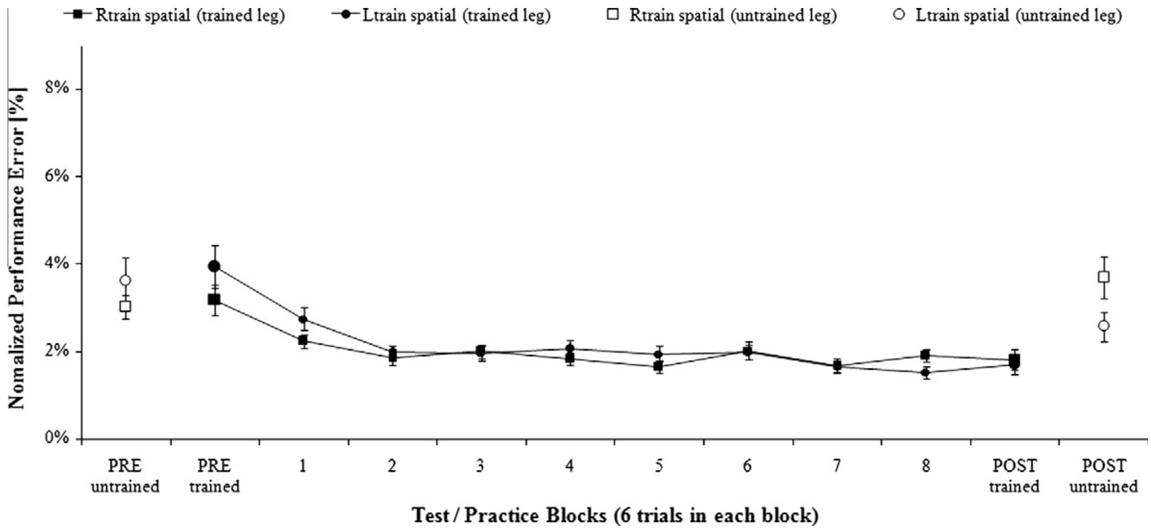

Fig. 4. Learning data in the spatial control condition. Changes in performance with the untrained (open symbols) and the trained (closed symbols) legs of the Rtrain (rectangles) and the Ltrain (circles) groups across blocks are illustrated. Error bars indicate standard errors.

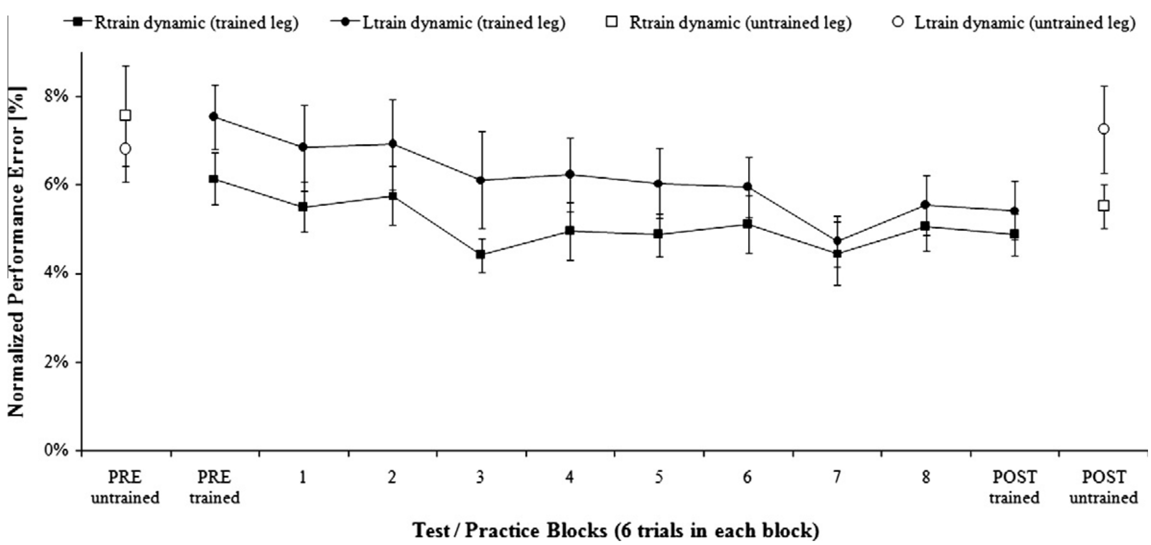

Fig. 5. Learning data in the dynamic control condition. Changes in performance with the untrained (open symbols) and the trained (closed symbols) legs of the Rtrain (rectangles) and the Ltrain groups (circles) across blocks are illustrated. Error bars indicate standard errors.

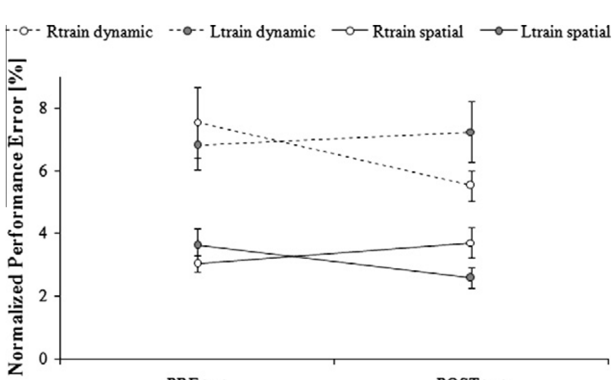

Fig. 6. Changes in performance with the untrained leg from PRE to POST test for Rtrain (open circles) and Ltrain (closed circles) groups are compared between the spatial (solid line) and the dynamic (dotted line) control condition. Error bars indicate standard errors.

PRE to POST tests varied depending on the information condition. This interaction effect is also illustrated in Fig. 6. According to the post hoc pairwise comparisons, the change in performance from the PRE to POST test was statistically significant only for the Ltrain group in the spatial condition, and only for the Rtrain group in the dynamic condition ($p < .05$). These results indicate that the training with the left leg improved subsequent performance with the right leg, as compared to the right leg performance prior to the training, but not vice versa, in the spatial information condition. In contrast, the training with the right leg improved subsequent performance with the left leg, but not vice versa, in the dynamic information condition. The amount of improvement observed in performance with the left leg of the Rtrain group from the PRE to POST test in the dynamic condition (PRE: 7.57% to POST: 5.53%) was as large as that observed in performance with the left leg of the Ltrain group due to training (PRE: 7.54% to POST: 5.43%). The performances observed in the other two groups (i.e., Rtrain and Ltrain groups in spatial and dynamic conditions, respectively) were not statistically significant ($p = .17$ and $p = .62$, respectively).

To examine whether the asymmetrical pattern of interlimb transfer was also specifically associated with the type of information provided in each information condition, NPE's for the untrained leg were computed again using the performance errors expressed in distance and in impulse in the dynamic and the spatial control conditions respectively, and subjected to further analyses. Surprisingly, our data showed that the significant interaction effect observed in the spatial condition (shown in the lower half of Fig. 6), indicating asymmetrical transfer, was also observed when the NPE was computed using the performance errors expressed in N s (a significant interaction between Group and Time at $p < .001$). The asymmetrical transfer effect observed in the dynamic condition (shown in the upper half of Fig. 6) was also present when the NPE was measured using the performance errors expressed in mm (a significant interaction between Group and Time at $p = .007$). However, the improvement in performance from the PRE to the POST test in the dynamic condition, which was significant when the NPE was computed using the performance errors expressed in Ns, failed to reach the significance level in this case (PRE: 5.91% to POST: 5.54%, $p = .09$). These data, collectively, indicate that the asymmetrical pattern of interlimb transfer observed in the present study may not be exclusively associated with the specific type of information provided in each information condition (i.e., the same pattern of interlimb transfer generalized across different performance measures, at least in the spatial condition).

4. Discussion

Magill (2001) described transfer of learning as "*the influence of having previously practiced or performed a skill or skills on the learning of a new skill*" (p. 205). If this occurs between two limbs for the same skill, it can be referred to as interlimb transfer. The direction of interlimb transfer, which is often asymmetric (i.e., greater transfer from one side to the other than vice versa), varies across studies, in that while some researchers demonstrated greater transfer following initial practice with the (dominant) right arm (e.g. Criscimagna-Hemminger et al., 2003; Farthing, 2009; Teixeira, 2000), others reported greater transfer following initial practice with its counterpart (e.g. Morris, Newby, Wininger, & Craelius, 2009; Senff & Weigelt, 2011; Stöckel et al., 2011). Although a number of factors have been identified to play a role in determining the direction, such as the type of movement parameters examined (e.g., movement direction vs. endpoint accuracy), the nature of sensorimotor transformations underlying given tasks (e.g., visuomotor vs. dynamic) and the location of workspace in which each arm performed the tasks (Wang & Sainburg, 2004a, 2004b, 2006), the main source of inconsistency regarding the direction of transfer across studies remains to be further investigated.

Another important factor that can influence the direction of transfer is the conception of a given motor task, which may vary across individuals or depending on instructions given to them. In the present study, we hypothesized that the pattern of interlimb transfer would vary depending on whether the leg extension task is conceived as a dynamic or a spatial control task, based on which we predicted that interlimb transfer from the trained to the untrained leg would occur asymmetrically depending on the nature of task demands that were emphasized (i.e., feedback of performance expressed in the form of either force impulse or spatial deflection). The current results provide support to our hypothesis by demonstrating asymmetrical transfer, whose direction differed between the two task conditions. That is, the untrained right leg performance of the subjects who focused on meeting the spatial demands (i.e., deflection) substantially benefited from the initial training with the left leg, and the untrained left leg performance of those who focused on meeting the dynamic demands (i.e., force impulse) from that with the right leg, but not vice versa. This indicates that the learning of the leg extension task that was physically equivalent between the two information conditions transferred in opposite directions (i.e., right to left leg or vice versa) depending on the type of visual feedback the subjects received, which forced them to conceive the task differently (as either a visuomotor or a dynamic task). This finding is in agreement with the notion that the two brain hemispheres serve different functions in the interpretation of visual information (Springer & Deutsch, 1998). The directions of transfer observed in the present study are also in line with other previous findings from the upper limb studies, which demonstrated different directions of transfer depending on certain features of the tasks employed (e.g., Stöckel & Weigelt, 2011; Teixeira, 2000; Wang & Sainburg, 2004b), as well as those from a lower limb study, which demonstrated asymmetrical transfer only from the left to the right leg when visual–spatial information was provided for learning specific ankle movements (Morris et al., 2009).

With regard to the changes in performance observed during the training session, our data indicated that the performance of the trained leg improved at a faster rate and also more steadily in the spatial information condition than in the dynamic condition. This finding can be viewed in the light of research on the influence of the learner's focus of attention, induced by instructions or feedback, on motor learning. It has been suggested that motor learning can be facilitated more effectively when performers direct their attention to external factors (e.g., effects of their movement), as compared to internal ones (e.g., their own movement), as well as to distal events, as compared to proximal ones (Bell & Hardy, 2009; Wulf & Prinz, 2001). While all the participants in the present study were required to focus on the effect of their movement (i.e., having an external focus), they might have been required to direct their attention differentially depending on the condition they belonged to, that is, either to distal or to proximal aspects of the leg extension task. Those in the spatial condition, who utilized the amplitude-based information, might have directed their attention to the required distal event (i.e., meeting the specific displacement requirement per se), whereas those in the dynamic condition, who utilized the impulse-based information, might have focused rather on a proximal event (i.e., intersegmental coordination). Our finding (i.e., better performance improvement in the spatial condition), thus, seems to be in accord with the idea of facilitative effects of directing an attentional focus on distal events (cf. Bell & Hardy, 2009). Along the finding that the direction of interlimb transfer varied between the two information conditions, it further suggests that the pattern of interlimb transfer might also be influenced depending on whether individuals focus their attention on the distal or proximal aspects of a given motor task.

Our current findings are also in line with some other previous findings, which demonstrated that the pattern of interlimb transfer could be influenced by perceptual factors as well. Wang and Sainburg (2007b) reported that when the two arms performed a novel visuomotor adaptation task at lateral workspaces that were not shared by the arms, interlimb transfer of initial direction information of reaching movement occurred symmetrically (i.e., from the right to the left arm, and vice versa). However, this type of information has been shown to transfer asymmetrically when the two arms performed the same task at a shared, midline workspace (Sainburg & Wang, 2002). This indicates that the perception of the subjects regarding the workspace locations in which the two arms perform a task can substantially change the direction of interlimb transfer. More recently, Wang (2008) conducted a similar study in which the perception of workspace locations was manipulated by dissociating visual workspace from motor workspace. Some subjects performed a novel visuomotor adaptation task with the two arms (one at a time) at two lateral workspaces that were not overlapped while the visual display of the task performance was presented at a shared, midline workspace. Others performed the same task with the two arms at a shared, midline workspace while the visual display was presented at two separate, lateral workspaces. The results showed that despite substantial adaptation to a novel visuomotor rotation with each arm, no transfer occurred when the visual and motor workspaces were dissociated in space. The aforementioned study, thus, demonstrated that the misperception of workspace locations due to dissociation between visual and motor workspaces could result in a lack of transfer across the limbs. Our current results are also in accordance with previous findings from bilateral coordination studies, which demonstrated that whereas bilateral movements that are inconsistent in joint space are usually hard to be performed, they can be performed easily by changing their visual feedback to make them appear consistent (Bogaerts, Buekers, Zaal, & Swinnen, 2003; Mechsner, Kerzel, Knoblich, & Prinz, 2001). Collectively, thus, these findings unambiguously indicate that the pattern of interlimb transfer can be influenced not only by varying specific (and physical) features of a given motor task, but also by manipulating simply the cognitive (i.e., conceptual or perceptual) information that is inherent to those specific features of the task.

5. Conclusion

Studies of interlimb transfer provide information about higher-level processes of human motor control, which can be directly used to optimize motor learning processes. In sport practice, findings from interlimb transfer studies can be useful for improving training techniques and/or schedules for specific sport skills (Stöckel et al., 2007, 2011; Stöckel & Weigelt, 2011). In rehabilitation settings (e.g., after stroke), interlimb transfer effects may help to improve or keep up the capabilities of the injured limb by including a practice session with the intact hand or foot. Previous studies of interlimb transfer repeatedly indicated that the pattern of interlimb transfer can be substantially influenced by manipulating various physical aspects of a given motor task. The present study adds to the literature by demonstrating that interlimb transfer of motor learning could occur in opposite directions (i.e., right to left leg or vice versa), even if it involved learning a physically equivalent motor task, depending on the type of movement information provided during the learning process. In this study, the type of information influenced individuals' conception of a given motor task in such a way that one type of information stressing the dynamic aspect of the task caused the transfer to occur from the right to the left leg, whereas another type of information stressing the visuomotor features caused it to occur from the left to the right leg. These findings clearly suggest that the pattern of interlimb transfer can be influenced not only by varying specific (and physical) features of a given motor task, but also by manipulating the conception information inherent to those specific features of the task. Because the pattern of transfer between the legs observed in this study is similar to that between the arms reported in previous studies, we also suggest that the idea of hemispheric specialization of motor control suggested by others (e.g., Birbaumer, 2007; Sainburg, 2002; Serrien et al., 2006) applies to both upper and lower extremities. However, given that the degree of learning observed with the particular task employed in the present study was relatively small, other motor tasks that could show greater learning might result in a different pattern, or extent, of transfer across the extremities.

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