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RESEARCH NOTE

Asymmetrical intermanual transfer of learning in a sensorimotor task

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Abstract We examined the influence of the hand employed in sensorimotor learning on the acquired sequence knowledge in a serial reaction time task. Right-handed subjects trained either with the dominant or with the nondominant hand sequences of finger postures in response to a corresponding stimulus sequence. In the course of training, they were repeatedly asked to switch to the opposite hand, either responding to the original stimulus sequence with nonhomologues fingers or to the mirror-ordered sequence of stimuli with homologues fingers. When the right hand was used at acquisition, transfer to the same stimulus sequence increased with practice. In contrast, when the left hand was trained, transfer to the homologues finger sequence increased with practice. The results indicate qualitative differences in the acquired sequence knowledge controlling the dominant and the nondominant arm systems.

Keywords SRT · Intermanual transfer · Sequence learning · Sensorimotor learning

Introduction

A remarkable characteristic of motor learning is that after practice with one limb subsequent performance of the same task with the untrained limb may be facilitated and such positive transfer effects have been reported for a wide variety of manual tasks, like for figure drawing (Halsband 1992), tapping (Laszlo et al. 1970), maze learning tasks (van Mier and Petersen 2006) sequential finger movements (Taylor and Heilman 1980), prism learning (Redding and Wallace 2008), and for force field adaptation settings (Criscimagna-Hemminger et al. 2003). Some results indicated better transfer from the dominant to the nondominant hand (e.g. Criscimagna-Hemminger et al. 2003; Halsband 1992; Redding and Wallace 2008), while other suggest better transfer from the nondominant to the dominant hand (e.g. Hicks 1974; Parlow and Kinsbourne 1990; Taylor and Heilman 1980). Still other studies reported similar transfer in both directions (e.g. van Mier and Petersen 2006) or transfer for some aspects in one direction and for other aspects of the same task in another direction (cf., Sainburg and Wang 2002; Parlow and Kinsbourne 1989; Thut et al. 1996). These directional effects have been linked to brain hemispheric specialization of function (e.g. Laszlo et al. 1970; Parlow and Kinsbourne 1989; Taylor and Heilman 1980) as well as to the nature of intermanual generalization (e.g. Criscimagna-Hemminger et al. 2003; Wang and Sainburg 2004).

In addition, the performance of the untrained limb may not only indicate the role of the hemispheres and of transfer related processes, but may also provide some insights into the nature of representation acquired during learning. In serial reaction time (SRT) tasks, e.g. in which participants respond to sequences of stimuli with sequences of responses, several learning mechanisms are discussed. There is evidence that associations are formed between successive stimuli (e.g. Clegg 2005; Remillard 2003) as well as between successive responses (e.g. Hoffmann et al. 2003; Nattkemper and Prinz 1997). Another related issue is to what extent motor learning is restricted to motor coordinates of specific effectors or involves a more abstract level, such as response selection or response locations (e.g. Keele

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et al. 1995; Willingham et al. 2000). The amount of effector-dependent learning can be estimated by the analysis of performance during a "mirror" transfer condition (e.g. Deroost et al. 2006; but see Grafton et al. 2002). After training of a repeating sequence with one hand, participants have typically to response with the opposite hand to a mirror-ordered sequence of stimuli. This leads to a response sequence that involves movements homologous to those used during training (e.g. the order of fingers does not change between the trained and the untrained hand). In contrast, responding to the same sequence of stimuli with the untrained hand (parallel transfer hereafter) is assumed to indicate an effector-independent component of learning (e.g. of perceptual learning or of learning of response locations), since the sequence of responses is changed in this condition, while the sequence of stimuli and of response locations remains the same. Thus, the amount of transfer in these conditions may allow conclusions about what kind of sequence knowledge is acquired during learning.

In the current experiment, we aimed to investigate the influence of the hand at acquisition on effector-dependence of learning by implementing mirror and parallel transfer conditions across the training in an SRT-like task. A similar approach has been previously used in two studies. Bapi et al. (2000) used a paradigm, in which a sequence of button presses was learned by trial and error. During different stages of training, two types of test blocks were used, in which the initial keypad and hand configurations were altered. In the visual condition, finger-keypad mapping was changed, while the keypad-display mapping was held constant (i.e. subjects responded to the original sequence of stimuli with the original sequences of button presses but with a changed sequence of finger movements). In the motor condition, the keypad-display mapping was changed resulting in the same sequence of finger movements as in the original learning condition. The authors observed that response times were comparable for these two conditions in the early stage of training. However, in the course of training, the response times in the motor condition became significantly shorter than in the visual condition. This result has been used as argument for the existence of effector-dependent learning that is relatively slow when compared with the development of effector-independent representations.

Chase and Seidler (2008) investigated the relationship between degree of handedness and transfer magnitude in an SRT-like task. After learning of a repeating sequence, participants had to response with the opposite hand either to the same sequence of stimuli or to a mirrored version of them. The influence of handedness on transfer was tested for left- and right-handed participants in both directions (i.e. from the dominant to the nondominant hand and vice versa). Right-handed participants showed a significant correlation between the degree of handedness and the magnitude of transfer to the motorically constant sequence indicating that involvement of the ipsilateral hemisphere during learning may influence intermanual transfer.

We applied a similar rationale like in these studies focusing however, mainly on learning-dependent changes within our transfer conditions. We assumed that the critical representation relating to sequence learning may be best observable in changes of transfer performance across the training, rather than in direct comparisons of performances at discrete learning stages.[1] If learning is primarily based on the acquisition of effector-independent knowledge, then the opposite hand should mainly profit in the parallel transfer conditions, where an increase in performance across the training may be expected. If effector-dependent learning takes place, the performance of the opposite hand in the mirror conditions should benefit more than in the parallel conditions.

Besides, the mentioned and rather inconsistent results regarding the intermanual transfer, there is a considerable evidence that motor control mechanisms of the dominant and the nondominant arm systems differ qualitatively in several respects (see e.g. Serrien et al. 2006 for a review). For instance, a recent hypothesis introduced by Sainburg et al. (e.g. Sainburg 2002; Sainburg and Kalakanis 2000; Sainburg and Schaefer 2004) postulates that the dominant limb system is specialized for controlling limb trajectory, whereas the nondominant system regulates limb position and posture. According to this one may assume that sensorimotor learning may involve different aspects of the same task dependent on the hand used during training. In particular, the nondominant arm system may be responsible for low-level processes, like for learning of sequences of arm postures, which takes place in an intrinsic, muscle-like coordinate system. In contrast, the dominant arm system may be associated with learning mechanisms, which are more abstract and effector independent (cf. e.g. Stoddard

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[1] Possible interactions between skillfulness, specific transfer conditions and expected differences in learning and motor control processes between two arm systems are a-priory difficult to predict without strict assumptions about the nature of interaction between the arm systems. For instance, the preferred hand is typically assumed to be more skillful. However, if this advantage is restricted to a special form of sensorimotor control, such as to effector-independent processes, performance differences between the parallel and mirror transfer conditions may already emerge at the beginning of training (if right hand is used in the transfer conditions). In this case these differences would not be directly related to learning of a sequence during experiment. Such an effect may not necessarily be expected, if the nondominant hand is used during transfer conditions and if it can be assumed to be less skillful in another form of control and/or learning. The impact of these or similar learning irrelevant interactions on the results may be, in our opinion, avoided, or at least reduced by focusing on learning-dependent changes in transfer performance within each type of transfer conditions.

and Vaid 1996; Ward et al. 1989). Accordingly, if the nondominant hand is used during training, an increase in performance across the mirror transfer conditions may be expected in the course of the experiment. Learning with the dominant hand, in contrast, should facilitate performance across the parallel transfer blocks.

Methods

Participants

Twelve students of the University of Würzburg participated in the present study. They gave their informed consent for the procedures and received an honorarium at the end of the experiment. The sample comprised 9 females and 3 males, with ages ranging from 21 to 29 years (mean age 23.8, SD = 3.01). All of them reported to be predominantly right-handed (i.e. they reported for each of the following tasks to typically perform it with their right hand: painting/drawing, throwing a ball at a target, using an eraser, dealing cards with the hand not holding the deck).

Task and apparatus

The visual stimuli were nine circles arranged as a 3 × 3 array and presented in gray on a white background at the center of a 17-in. monitor. The circles were 45 mm in diameter and were separated by 65 mm (i.e. from center to center). In each trial, 1–3 circles were filled indicating the current stimulus locations, to which participants had to response as fast and accurately as possible. The numerical keypad of a standard QWERTZ keyboard was used for responding. All other adjusted keys were removed from the keyboard and the keys of the numerical keypad were pasted over with an intransparent tape to occlude the vision of the digits. The circle locations were compatibly assigned to the keys (i.e. the upper row of circles corresponded to the keys “7”, “8” and “9”, the middle row to “4”, “5” and “6”, and the lower row to “1”, “2” and “3”). Moreover, participants were instructed to use their index, middle, and ring fingers, with the middle finger aligned to the middle column. The index and ring fingers were assigned to the outer columns. That means that when the right hand was used, participants responded to the circles appearing on the left side of the stimulus display by pressing the keys “1”, “4” or “7” with the index finger. When a circle was filled on the right side, the ring finger and the keys “9”, “6” and “3” had to be used. For the left hand, this finger keys assignment was reversed. We asked participants to perform responses as simultaneously as possible, if more than one target appeared.

Experimental procedure and design

The experiment consisted of 27 blocks with 23 sequence repetitions each. Twenty-one blocks were regular learning blocks, which were performed either with the right hand (RL condition hereafter) or with the left hand (LR condition hereafter). The remaining six blocks were transfer blocks, in which the opposite hand was used for responding.

During the learning blocks, a seven-element sequence was repeatedly presented (see Fig. 1). Participants were informed about the presence of sequence and were explicitly asked to learn it and to use this knowledge to optimize their responding.

The same stimulus sequence was also used in three of six transfer blocks (parallel transfer). For the residual transfer blocks, the original sequence was modified so that for each of the seven stimuli arrays the left and right targets were reversed around the vertical midline (mirror transfer).

Experiment comprised three transfer phases including a parallel and a mirror transfer block. These two blocks were always separated by a regular learning block to avoid a possible influence of the mirrored transfer on the parallel transfer blocks and vice versa. The first six blocks were always learning blocks. Starting with the sevens block a first transfer phase began. After the first transfer phase and after the next six consecutive learning blocks a second transfer phase with two transfer blocks and with an intermediate learning block was implemented. Subsequently, six learning blocks were again followed by two transfer blocks, which were separated by a learning block. The order of blocks was the same for the three transfer phases and one participant (either “parallel–learning–mirror” or “mirror–learning–parallel”), but was counterbalanced across participants.

The latency between the onset of the stimulus presentation and the last key press was defined as reaction time (RT). When one of the participant’s responses was incorrect, the German word for error appeared. At the end of each block, subjects received information about the mean RT as well as the number of errors of the previous responses.

Fig. 1 Sequence of stimuli used in the present experiment

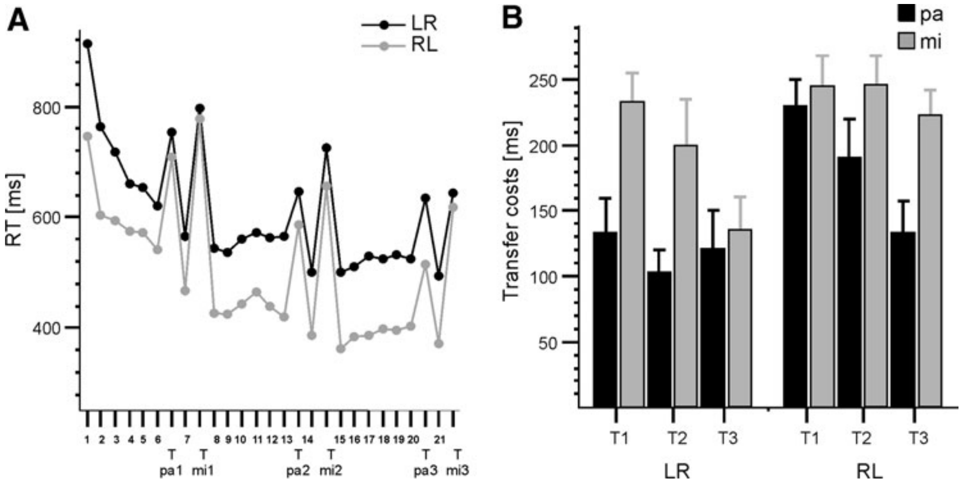

Fig. 2 **a** Mean reaction times (RT) per block of trials for both hand conditions. Note: for presentation purposes, parallel and mirror transfer blocks (T pa and T mi) are arbitrary ordered so that T pa blocks precede T mi blocks. In reality, the order of transfer blocks was counterbalanced across participants (see "Methods"). **b** Mean transfer costs (RT differences between learning and transfer blocks) according to the six types of transfer blocks, separated by hand condition. *Error bars* are standard errors

Data analysis

Reaction times averaged for each block of trials were considered for analysis. Transfer costs indicating the amount of intermanual transfer of sequence knowledge were defined as RT differences between the median RT in a transfer block and the median RT in learning block preceding this transfer block. We used this measure as an index for sequence learning similarly to the usage of RT costs typically computed between regular structure blocks and those, in which a random sequence of stimuli and responses is implemented (cf. e.g. Deroost et al. 2006). According to this, a decrease in transfer costs implies that sequence learning takes place. Unlike typical RT costs computed between blocks performed with the same hand, comparisons of intermanual transfer costs associated with responses of both hands allow only limited conclusions since they may contain hand differences, which are present prior to sequence learning (e.g. dominant hand may be expected to exhibit faster RTs than the nondominant hand). On this account, we mainly focused on possible changes in transfer costs in the course of training within each hand condition, which may be assumed to be independent from learning irrelevant effects. We assumed that the transfer costs in the mirror and parallel conditions would decrease in the course of training dependent on whether effector-dependent or effector-independent knowledge would be acquired.

Moreover, to analyze the effects of transfer blocks on performance in the training blocks, RT differences were computed between learning blocks preceding and following the transfer. This measure indicates the amount of consolidation of what has been learned in the training hand. We suppose that the 'consolidation gain' may depend on interactions between the type of the acquired sequence knowledge and the type of the required transfer. In particular, we expect that parallel transfer stronger interferes with the consolidation of effector independent, whereas mirror transfer stronger interferes with the consolidation of effector-dependent sequence knowledge because the transfer hand accesses at the, respectively, same representation. Thus, the impact of the transfer blocks on the consolidation gain possibly provides further insights into the respectively dominant type of acquired sequence knowledge.

The manipulation of the hand at acquisition, the non dominant left hand (LR) or the dominant right hand (RL) constituted a between-subject factor. Six participants each were randomly assigned to one of these two experimental conditions. The types of transfer as well as time of transfer were used as within-subjects factors.

Results

Reaction times from error trials were excluded from analyses (4.88%). Moreover, responses with a latency of more than 2,000 ms were considered as outliers and were also discarded from further analyses (0.51%). For the remaining trials, median RTs were computed for each subject and block of trials. The mean medians for each hand condition and learning block are shown in Fig. 2a).

The average RTs decreased in the course of training for both hand conditions. These learning-related changes in performance are substantiated by the results of an analysis of variance (ANOVA) with block as a within-subjects factor (21 levels) and hand condition as a between-subject factor (2 levels) indicating a highly significant main effect of block, F (20, 200) = 43.77, $P < 0.001$, partial $\eta^2 = 0.814$.[2] When the left hand was used for responding, the RTs were slower on average than when the right hand was used. However, neither a main effect hand condition nor a hand condition × block interaction reached the significance

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[2] Note: only the data of regular learning blocks were included in this analysis.

threshold, $F(1, 10) = 2.35$, $P = 0.156$, partial $\eta^2 = 0.190$ and $F(20, 200) = 0.59$, $P = 0.920$, partial $\eta^2 = 0.055$.

To assess the completeness of intermanual transfer, RT differences were computed between transfer blocks, in which the original sequence or its mirrored version were presented, and learning blocks, which directly preceded these transfer blocks. Figure 2b illustrates the corresponding transfer costs dependent on time and type of transfer as well as on hand condition. An ANOVA performed on these values with hand as between-subject factor, transfer type and time of transfer and as within-subjects factors revealed significant main effects for hand, $F(1, 10) = 6.16$, $P = 0.032$, partial $\eta^2 = 0.381$, transfer type, $F(1, 10) = 23.15$, $P = 0.001$, partial $\eta^2 = 0.698$, and for time of transfer, $F(2, 20) = 6.58$, $P = 0.006$, partial $\eta^2 = 0.397$, and more importantly, a significant hand × transfer type × time interaction, $F(2, 20) = 5.18$, $P = 0.015$, partial $\eta^2 = 0.341$.

When participants practiced with the right hand and responded to the same sequence of stimuli with their left hand (i.e. in the RL and parallel transfer condition), transfer costs decreased from the first to the third transfer block (see Fig. 2b). For the LR and parallel transfer condition, in contrast, such a time-dependent change of transfer costs is not observable. The results pattern associated with the mirror transfer are quite distinct. A decrease in transfer costs with practice was strongly pronounced in the LR condition, but seems to be absent in the RL condition. To substantiate this observation, four ANOVAs with the within-subjects factor time were performed for each hand condition and transfer type separately. Significant main effects of time were only evident in the analyses of the LR condition for the mirror transfer, $F(2, 10) = 5.40$, $P = 0.026$, partial $\eta^2 = 0.519$, and of the RL condition for the parallel transfer, $F(2, 10) = 7.43$, $P = 0.011$, partial $\eta^2 = 0.598$ [$F(2, 10) = 0.277$, $P = 0.763$, partial $\eta^2 = 0.053$ and $F(2, 10) = 0.908$, $P = 0.434$, partial $\eta^2 = 0.159$, for the RL & mirror transfer and LR & parallel transfer conditions respectively].

We also analyzed the influence of transfer blocks on performance in the neighboring training blocks. We aimed to delineate the amount of interference between the acquired representation and the processes accompanied the opposite hand performance, which may have been caused by hand switches. For this purpose, RT differences were computed between learning blocks preceding and following the transfer. Table 1 shows the according values.

Table 1 Mean RT differences (ms) between learning blocks following one of the transfer blocks and those learning blocks, which preceded the transfer blocks

Hand condition	Transfer type	Mean (SD)
RL	pa1	33.58 (46.85)
	mi1	80.17 (53.49)
	pa2	19.58 (49.34)
	mi2	35.75 (19.72)
	pa3	17.67 (35.88)
	mi3	43.67 (28.98)
LR	pa1	74.83 (52.05)
	mi1	0.33 (38.99)
	pa2	46.25 (53.30)
	mi2	19.50 (43.30)
	pa3	35.50 (22.79)
	mi3	26.33 (49.09)

The number of participants was 6 for the first two transfer phases, but was 3 for the last two transfer blocks

We performed an ANOVA to test the influence of the experimental conditions. Because the data of all subjects was only available for the first two transfer phases,[3] the included factor time contained only two levels in this analysis. A significant hand × transfer type interaction was observed, $F(1, 10) = 6.38$, $P = 0.030$, partial $\eta^2 = 0.389$, indicating a decrease in learning performance after parallel transfer blocks in the RL condition compared with the LR condition and conversely, a decrease in learning performance in the LR condition compared with the RL condition after mirror blocks. The same trend was also evident during the last transfer phase, which did not enter this analysis (see Table 1). This result indicates distinct effects of transfer blocks on learning, dependent on the hand used at acquisition as well as on the type of transfer. It also suggests that hand switches had a more detrimental effect on sequence learning in the RL and parallel transfer and in the LR and mirror transfer conditions as compared with both others.

Discussion

We investigated the nature of representation acquired during learning in a serial reaction time task. During training, participants responded to a repeating sequence of stimuli with either the dominant or the nondominant hand. Moreover, additional transfer blocks were implemented, in which responding with the opposite hand either to the same sequence of stimuli or to a mirrored version of stimuli triggering mirror movements of homologous fingers was required. We predicted that learning with the dominant hand would result in an increase in performance across the parallel transfer blocks, while training of the nondominant hand was assumed to facilitate the performance across the

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[3] Because the last block of the experiment was always a transfer block, its influence on learning performance could not be evaluated. However, due to the counterbalancing of blocks across participants, the last block was of the parallel type for one half and of the mirror type for the other half of subjects.

mirror transfer blocks. The results appear to confirm this hypothesis.

When the right/dominant hand was used during training, transfer costs substantially decreased with practice only for the responding to the same sequence of stimuli (i.e. only in the parallel transfer condition), whereas the other type of transfer (i.e. mirror transfer) was widely unaffected by the course of training. In contrast, when the left/nondominant hand received extensive training, an opposite results pattern was observed: transfer costs only decreased when the movements of the right hand mirrored those previously learned by the left hand, while the responding to the same sequence of stimuli / response locations did not change with practice. Comparable results have been previously reported by Ward et al. (1989) as well as by Stoddard and Vaid (1996). Using a finger maze learning task, the authors observed facilitated transfer to the mirror image maze, when the left hand was used in acquisition as compared with an identical maze. In contrast, right-hand acquisition enhanced opposite hand performance on an identical maze at transfer when compared with the mirror-reversed maze.[4]

According to the used rationale, this outcome indicates that sequence learning was related to different aspects of the sensorimotor performance depending on the practiced hand. Moreover, it suggests that learning occurred in an intrinsic and effector-dependent coordinate system for the nondominant/left hand, where only the mirror transfer was affected by training. In contrast, when the right/dominant hand was used during practice, participants seem to learn some more abstract aspects of the sequence, which are independent from the succession of the involved effectors. This would account for the observed enhancement of parallel transfer in the course of training. Both mechanisms may correspond to learning of sequences of arm/finger postures (cf. Rosenbaum et al. 1999) and to stimulus-based or response location-based learning, respectively (e.g. Clegg 2005; Willingham et al. 2000) and would fit well into recent findings suggesting a nonpreferred arm advantage in ability to utilize proprioceptive feedback and a dominant arm advantage for visual information processing (e.g. Goble and Brown 2008a, b).

This conclusion is supported by an additional analysis of the effect of transfer blocks on the subsequent training performance. After parallel transfer blocks a decrease of the consolidation gain was observed for the right training hand as compared with the left hand. In contrast, mirror transfer blocks led to a decrease in the consolidation gain for the left hand compared with the right hand. According to the literature on dual task effects (e.g. Navon and Gopher 1979; Norman and Bobrow 1975) such as selective consolidation reduction can be taken as a sign that two tasks compete for the same resources. Following the above-mentioned hypothesis, the results may be explained by the amount of the involved interference processes. In particular, if the nondominant arm system is specialized for low-level intrinsic processes, like for learning of sequences of arm postures, whereas the dominant arm system operates on a more abstract, effector-independent level, the observed interaction would be due to interference emerging in the left practiced hand and mirror transfer and in the right practiced hand and parallel transfer conditions as a result of similar cognitive resources shared by the two arm systems in these conditions. In other words, opposite hand performance may have impaired consolidation of the memory trace, when a critical representation of the trained arm system has been accessed.

Although these conclusions appear to be plausible they apparently seem to be inconsistent with findings of Chase and Seidler (2008) observed in a similar experimental setup (see "Introduction"). In that study, participants showed better transfer in the parallel condition than in the mirror condition and this difference was not dependent on the direction of transfer. However, participants received much less training prior to the transfer blocks as compared with our experiment. Effector specific (i.e. motor) representation has been shown to develop slowly and to affect the performance under conditions of extensive praxis (e.g. Bapi et al. 2000; Berner and Hoffmann 2008; Park and Shea 2003; see also below). Thus, the lack of the transfer type differences relating to the direction of transfer observed by Chase and Seidler and training dependent and transfer type specific changes found in the present experiment may possibly be attributed to different training intensities applied in both experiments. Moreover, since only one transfer phase was implemented in the study of Chase and Seidler (2008) and a different approach has been pursued a direct comparison of the results of both studies is difficult. On the other hand, the results appear to be comparable, if only the first or the second transfer phase of the present experiment is considered. At this stage of learning, parallel transfer proved to be better than mirror transfer for both hand conditions. However, this difference was more pronounced for the left training hand. The same trend is also evident in the data of Chase and Seidler (see Fig. 5 panel a). There are also other factors, such as inter-stimulus interval, which may account for partially divergent results and conclusions and further studies are needed to evaluate the validity of respective statements. In particular, it would be interesting to examine whether correlations between degree of handedness and magnitude of transfer reported by Chase and Seidler for the mirror condition are dependent on the direction of transfer and/or training intensity.

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[4] In the study of Ward et al (1989) this effect was only reported for left-handers.

The results of previous studies suggested that effector-dependent and effector-independent sequence knowledge are simultaneously acquired (Bapi et al. 2000; Hikosaka et al. 2002; Nakahara et al. 2001; Rand et al. 1998, 2000). However, the time course of development as well as neural substrates proved to be different for these two types of representations (cf. e.g. Bapi et al. 2000). An effector-dependent representation appears to be acquired slowly, while an effector-independent representation develops faster and seems to be used in the early stages of learning. Based on these findings, one may argue that learning differences between two hands observed in the present study are not absolute. Rather, the dominant and the nondominat arm systems may differ in the time course of development of both the effector-dependent and independent representations. If so, then the observed effects would emerge due to different speeds of both arm systems, at which effector-dependent and/or independent sequence learning progresses. Accordingly, the left hand may be associated with an earlier switch in processing mode (from an effector-independent to an effector-dependent representation) than the right hand, although both arm systems may simultaneously acquire representations in both coordinates. This may possibly explain why comparable difference patterns (i.e. differences between parallel and mirror transfer conditions) are present in the LR condition during the first transfer phase and in the RL condition during the last transfer phase of the present experiment.

A number of brain imaging studies of right-handed subjects performing SRT tasks with the dominant hand identified a network of areas in the contralateral left hemisphere including sensorimotor cortex, supplementary motor area (SMA), and premotor regions (PMC), the activity of which has been related to sequence acquisition (Grafton et al. 1995, 1998; Hazeltine et al. 1997). In a follow-up study, Grafton et al. (2002) examined the neural correlates of sequence learning with nondominant hand. The results indicated learning-related activity in the left PMC and left SMA, suggesting their role in acquisition of effector-independent knowledge. However, many additional brain areas also proved to contribute to left hand learning. Although the functional mechanisms underlying this results pattern are not well understood, the results point to dissociation between the two arm systems with respect to sequence learning processes. It is notable that in the study of Grafton et al. (2002) transfer of learning to the dominant hand has also been tested by mirror and parallel conditions. The intermanual transfer was significantly better in the parallel condition than in the mirror condition. However, as in the study of Chase and Seidler (2008), subjects received much less training prior to the transfer blocks than in the present experiment. Moreover, for the two initial transfer phases, our results are highly comparable with those reported by Grafton et al. (2002).

Our conclusions are, of course, tentative and should be considered with caution. For instance, the used paradigm of intermanual transfer has frequently been used for the investigation of interhemispheric communication, rather than of learning processes per se. Accordingly the results may indicate direction-related differences in the intermanual generalization, and not in sensorimotor learning. Moreover, the observed performance changes may have been arisen as a result of learning of the hand, which received much less training (i.e. of the untrained hand). If this would be the case, then the assignment of the assumed learning mechanisms to the dominant and nondominant arm systems would be different. Finally, we mainly focused on training-related changes in transfer costs, which, in our opinion, may be directly related to the processes of the involved learning mechanisms. If, however, transfer performances at discrete training phases are considered separately, another, alternative interpretations are possible.

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