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Behavioral/Systems/Cognitive

Is Interlimb Transfer of Force-Field Adaptation a Cognitive Response to the Sudden Introduction of Load?

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Recently, Criscimagna-Hemminger et al. (2003) reported a pattern of generalization of force-field adaptation between arms that differs from the pattern that occurs across different configurations of the same arm. Although the intralimb pattern of generalization points to an intrinsic encoding of dynamics, the interlimb transfer described by these authors indicates that information about force is represented in a frame of reference external to the body. In the present study, subjects adapted to a viscous curl-field in two experimental conditions. In one condition, the field was introduced suddenly and produced clear deviations in hand paths; in the second condition, the field was introduced gradually so that at no point during the adaptation process could subjects observe or did they have to correct for a substantial kinematic error. In the first case, a pattern of interlimb transfer consistent with Criscimagna-Hemminger et al. (2003) was observed, whereas no transfer of learning between limbs occurred in the second condition. The findings suggest that there is limited transfer of fine compensatory-force adjustment between limbs. Transfer, when it does occur, may be primarily the result of a cognitive strategy that arises as a result of the sudden introduction of load and associated kinematic error.

Key words: arm movement; motor learning; dynamics; force field; interlimb transfer; psychophysics

Introduction

Motor-learning studies have examined patterns of generalization as a means to identify the frame of reference for movement planning and control. In the context of studies of adaptation to new dynamics, conflicting results have been found. Although transfer of learning observed across configurations of the same limb has led to the conclusion that dynamics are encoded in an intrinsic joint- or muscle-based system of coordinates (Shadmehr and Mussa-Ivaldi, 1994; Ghez et al., 2000; Malfait et al., 2002), a recent study by Criscimagna-Hemminger et al. (2003) has reported a pattern of interlimb transfer that is consistent with an encoding of forces in extrinsic coordinates.

Numerous studies have examined the transfer of learning between limbs to explore the role of the hemispheres, as well as communication between hemispheres. In addition to the question of the direction of transfer (dominant to nondominant or vice versa), the issue of the pattern of synergies favored by the motor system (mirror symmetric synergies in intrinsic coordinates or synergies that preserve the extrinsic coordinate system of representation across hands) has been addressed in many contexts (for review, see Cardoso de Oliveira, 2002; Swinnen and Wenderoth, 2004). The variety of the results suggests that patterns of generalization are highly dependent on the task.

In the context of force-field adaptation, transfer of learning within a limb has been studied extensively, whereas interlimb transfer has been only recently assessed. Criscimagna-Hemminger et al. (2003) addressed three issues: the existence and the direction of transfer across arms, the dependence of this possible transfer on callossal connections, and the coordinate system encoding knowledge of dynamics that would transfer across limbs. Given their own previous results (Shadmehr and Mussa-Ivaldi, 1994; Shadmehr and Moussavi, 2000), they did not expect transfer of adaptation from the trained arm to the contralateral arm, or if transfer occurred, their expectation was that it would occur in intrinsic coordinates. Surprisingly, they found transfer from the dominant to nondominant arm that occurs in extrinsic coordinates.

The present study seeks to understand the conflicting results for the transfer of learning within and between limbs. Typically, in force-field adaptation studies, the sudden introduction of load induces a substantial kinematic error that provides multiple sources of information, heterogeneous in nature, that might involve different kinds and systems of representation. Also, patterns of generalization seem to be sensitive to subjects' awareness of the introduction of a perturbation (Baraduc and Wolpert, 2002). Here, we tested the idea that interlimb transfer in extrinsic coordinates arises from a response to the sudden introduction of load that is essentially cognitive in nature. We demonstrate that, when loads are introduced gradually, no transfer occurs between limbs. These same gradually applied loads produce typical patterns of intralimb transfer and associated aftereffects when the load is suddenly removed.

Materials and Methods

Experimental setup. Twenty-six right-handed adults (Edinburgh Inventory) (Oldfield, 1971), aged 22–31 years, participated in the study. Sub-

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Table 1. Experimental design

	First training		Second Training	
Group	Condition	Target	Condition	Target
1	Abrupt	1	Gradual	2
2	Gradual	2	Abrupt	1
3	Abrupt	2	Gradual	1
4	Gradual	1	Abrupt	2

Subjects were divided into two groups: six subjects first trained in the abrupt, and then in the gradual condition; the order of training was reversed for the other subjects. In each group, three subjects moved to target 1 in the abrupt training condition and to target 2 during the gradual training condition. Movement directions were reversed for the other subgroup.

jects were seated and held the handle of a two-link manipulandum (Interactive Motion, Cambridge, MA). They made horizontal arm movements with their right or left arm supported by an air sled. The shoulder was restrained and the wrist was braced. Subjects were instructed to move the handle of the manipulandum to targets that were mounted on a horizontal panel below the apparatus. Subjects could see their arm throughout the experiment.

Experimental procedures. Subjects made 12 cm point-to-point movements to 1 cm diameter targets. They were trained to produce movements of 500 ± 50 msec. Two sets of targets were defined, one set for each hand (see Fig. 1*A*). Both arms had the same configuration; initial elbow angles were set at 90°, and shoulder angles were ~50°. For each arm, target 1 corresponded to a movement away from the body, and target 2 corresponded to a movement toward the body. The robot produced a force field in which the force f was a function of the velocity of the hand v; specifically, $f = Bv$, where $B = \{0, -\alpha; \alpha, 0\}$ $N \cdot sec \cdot m^{-1}$, with $0 < \alpha \leq 15$. At the end of each movement, the subject's hand was brought back to the start position by the robot.

Subjects were trained to move in the force-field environment with their right hand and were tested for transfer of adaptation to their left hand. The following two training conditions were defined: an "abrupt training," in which the load was introduced suddenly, and a "gradual training," in which it was smoothly introduced. The abrupt training consisted of a single set of 30 trials. The gradual training extended over four sets of 40 trials each—160 trials in total. In the abrupt-training condition, after 15 movements were performed with the motors of the robot turned off ("null field"), the force field was unexpectedly and abruptly turned on; that is, the value of α flipped from 0 to 15 $N \cdot sec \cdot m^{-1}$ between the 15th and the 16th trial and remained at this value for the last 15 movements. In contrast, in the gradual-training condition, the force field was gradually increased; the value of α changed smoothly from 0 to 15 $N \cdot sec \cdot m^{-1}$ over the first 145 trials. Specifically, the change in α was nonlinear: $\alpha = n^x$, with n = trial number and $x = \log(15)/\log(145)$, to obtain $\alpha = 145^{\{\log(15)/\log(145)\}} = 15\ N \cdot sec \cdot m^{-1}$ on the 145th trial. As in the abrupt-training condition, the amplitude of the field remained constant for the final 15 trials.

It will be noted that subjects performed an unequal number of trials in the two training conditions. Subjects received more training in the gradual condition than in the abrupt condition. These differences should favor transfer of learning in the gradual-training condition.

Each subject trained in both abrupt and gradual conditions and was tested twice, once after each training was completed. Twelve subjects were divided into two groups as follows: six subjects first experienced the abrupt training, and then the gradual training; the other subjects were trained in the reverse order. Each group was further divided as follows: three subjects moved to target 1 during the abrupt training and to target 2 in the gradual training, whereas targets were reversed for the other subgroup (Table 1).

For all of the subjects, the detailed sequence of testing was as follows. First, during a familiarization phase, subjects made movements with the left hand—40 trials performed to target 1 or 2—in the null field. Two "force-field catch trials," pseudorandomly selected trials during which the motors of the robot were turned on, were introduced to evaluate the effect of the force field before any learning. Second, subjects trained to reach with the right hand in the force field in either the abrupt or gradual condition to target 1 or 2. Third, they were tested for transfer of learning to the left hand, making movements in the same direction as in the training trials, performing 15 movements in the force field with $\alpha = 15$ $N \cdot sec \cdot m^{-1}$. For each subject, these three phases were then repeated, changing training condition and movement direction.

Six additional subjects were tested in a condition that assessed performance with the left hand in the absence of any training with the right. As above, the testing began with a familiarization phase that included force-field catch trials. "Naive" performance of the left hand in the force field was then assessed, that is, without any previous training with the right hand. Three subjects in this naive condition moved first to target 1 and then to target 2. Three other subjects were tested in the opposite order. Subjects in the naive condition completed one block of 15 trials in each movement direction.

Control 1. A control study was conducted to ensure that, in the gradual-training condition, adaptation involved the development of anticipatory changes to the underlying control rather than a strategy of muscle cocontraction. Four subjects trained in the gradual condition only, making movements to target 1. Two null-field catch trials were interspersed in each training set (eight in total), to follow the development of aftereffects. After adaptation with the right arm, transfer of aftereffects to the left arm was assessed in a transfer test performed in the null field. This final test was motivated by the idea that, if there was interlimb transfer, it should be reflected in a transfer of aftereffects.

Control 2. In a control study, we assessed generalization of adaptation in the gradual condition across different configurations of the same arm. Four subjects trained with the right hand in the gradual condition, as described above. Two subjects trained with target 1, and the other two trained with target 2. In the training configuration, the initial shoulder angle was set at 45°. Subjects were tested for transfer to two different configurations of the same limb in which initial shoulder angles were 0 and 90°, respectively. The initial elbow angle was held constant at 90° in all three—training and transfer—configurations. For each transfer test, a set of targets was defined such that joint displacements were identical with those in the central position (see Fig. 3).

The familiarization phases—one in each of the two transfer workspace locations—and the gradual training were as in the main experiment. Each subject was then tested for transfer twice, once in each transfer configuration. Order of testing was balanced across subjects. Subjects were not retrained in the central position between the two transfer tests. Subjects were moved with respect to the robot for movements in the different parts of the workspace.

Data analysis. Hand positions and forces were sampled at 200 Hz. Position measurements were obtained using encoders in the robot arm. Forces were measured with a force–torque sensor that was mounted above the handle of the manipulandum. The signals were low-pass Butterworth-filtered at 20 Hz and numerically differentiated. The start and end of movement were defined by 5% of the maximum tangential velocity. Adaptation and transfer of learning were assessed quantitatively in terms of "initial direction error" (Sainburg et al., 1999), the angular distance between the vector from the start position to the target and the vector from the start to the position of the hand at peak of tangential hand velocity. We also computed the maximum perpendicular displacement of the hand path from a straight line to the target and obtained qualitatively similar results. Statistical analyses were conducted using repeated-measure ANOVAs that included time (familiarization, training, testing phases for each condition), movement direction, and order of training (Table 1). Tukey's honestly significant difference criterion was used for *post hoc* pairwise comparisons, after a significant ANOVA. Analyses involving the naive group were run separately and focused specifically on comparing the naive group with performance in the gradual condition; *t* tests were used for this purpose.

Results

Each subject was trained with the right hand in the two conditions: an abrupt condition, in which the force field was turned on suddenly, and a gradual condition, in which the forces were smoothly increased. Figure 1, *B* and *C*, show the initial angular deviation averaged across subjects, as well as illustrative hand paths by single subjects for both conditions. The vectors plotted along the hand paths show the forces applied in the horizontal plane by the hand of the subject. In Figure 1*B*, it can be seen that, in the abrupt condition, the sudden introduction of the force field initially produced a clear hand-path deviation, but by the end of 15 movements in this new dynamic environment, hand kinematics approached those in the null field. In contrast, in Figure 1*C*, when the force gradually increased, from the beginning to the end of training, kinematics were similar to those in the null field.

We quantified the effects of learning in the abrupt condition using measures of position error. In the gradual condition, because there was no substantial change to the movement trajectory over the course of training, adaptation was quantified in terms of the aftereffect observed in null-field catch trials, that is, in trials in which the field was unexpectedly removed (control 1). In the abrupt condition, we averaged the error measures obtained in the last three trials in the null field, the first three movements made in the force field and the error measures in the very last three trials at the end of training. *Post hoc* comparison confirmed a significant effect of the sudden introduction of the field (error was larger in the first trials in the force field than in those performed before its introduction; $p < 0.01$). When the field was introduced abruptly, a significant effect of learning could be observed (error was smaller in the last force-field trials than in the first ones; $p < 0.01$). By the end of the training, movements were not different from those under null-field conditions ($p > 0.05$). In the gradual condition (see Fig. 3*A*), a comparison of the aftereffect deviation observed in the first and the last null-field catch trials (trials 10 and 159, respectively) showed that subjects developed anticipatory responses in proportion to the increase in force applied by the robot (error was larger in the last null-field catch trial than in the first one; $p < 0.01$). Levels of adaptation achieved by the end of the two training schemes were comparable ($p > 0.05$).

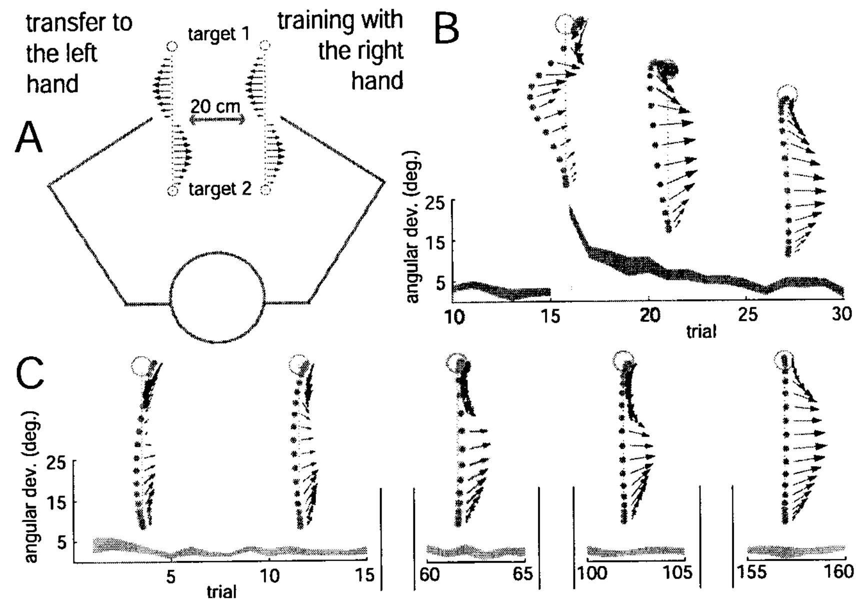

Figure 1. *A*, Subjects were trained with their right hand to move in a force-field environment and were tested for transfer of learning to their left hand. *B*, Abrupt-training condition in which the load was introduced suddenly (after 15 null-field trials). *C*, Gradual-training condition in which the force field was smoothly introduced. *B*, *C*, The initial angular deviation (mean ± 1 SE) is shown over the course of training for the right hand. Representative hand paths and compensatory forces for single subjects are shown. The dots show positions of the hand during movement and the vectors represent forces applied by the hand of the subject. deg.,Degree; dev., deviation.

After subjects trained in the gradual or abrupt condition with the right hand, they were tested for transfer of learning with the left. Transfer tests consisted of 15 movements with the force field at full amplitude: $B = \{0, -15; 15, 0\}$ N · sec · m^{-1}. Figure 2*A* shows hand paths with the left hand by single subjects representative of each experimental group; s1 to s4 were from groups 1 to 4, respectively (Table 1). The dashed lines show hand paths recorded in force-field catch trials introduced during the familiarization phase. Hand paths plotted in solid lines show the very first trial of the transfer tests. It can be seen that there was no transfer of learning after the gradual training; movement paths were similar for prelearning catch trials and transfer trials in this condition. (Similar patterns were observed for all of the subjects.) In contrast, transfer of learning was observed with the sudden introduction of the load; when subjects trained in the abrupt condition, there was a substantial reduction of the effect of the field. Statistical analysis confirmed these observations. For each subject, we took the mean of the deviations observed in the two prelearning force-field catch trials, and the error in the first trial of each transfer test. Learning in the gradual condition did not lead to any improvement in the transfer task relative to unexpected and sudden load introduction during the familiarization phase ($p > 0.05$). In contrast, the abrupt-training condition produced a significant reduction in kinematic error for transfer trials ($p < 0.01$). Interactions attributable to direction and order (Table 1) were tested; none was significant ($p > 0.05$), indicating that there was no reliable effect attributable to the specific sequence of training.

Figure 2*B* shows means across subjects for the initial angular deviation in each trial of the transfer tests. (Performance for naive subjects is also shown.) For statistical analysis, we averaged over the deviations in the first three and last three trials of each test. As described above, learning to compensate for a suddenly introduced load with the right hand improved subjects' performance with the left hand. Thus, in the abrupt condition, subjects' hand paths were less deviated than those observed after gradual training ($p < 0.01$). In both conditions (abrupt and gradual), subjects improved their performance throughout the test (hand paths were straighter in the last than in the first trials for both tests; $p < 0.01$) and achieved comparable levels of adaptation by the end of the test ($p > 0.05$). Again, interactions attributable to direction and order were not significant ($p > 0.05$).

A comparison of performance in the gradual condition with the performance of naive subjects showed no measurable interlimb transfer (Fig. 2*B*, inset). Indeed, hand paths in the gradual condition were no less deviated in the first trial of the transfer test than those observed in the initial trials of the naive group ($p > 0.05$). One may also note the overlap of the learning curves for subjects in the gradual and naive conditions (Fig. 2*B*). This similarity underscores that training in the gradual condition did not facilitate learning in the transfer test.

In addition to the absence of interlimb transfer in the gradual condition, no transfer of aftereffects was observed in control 1. As

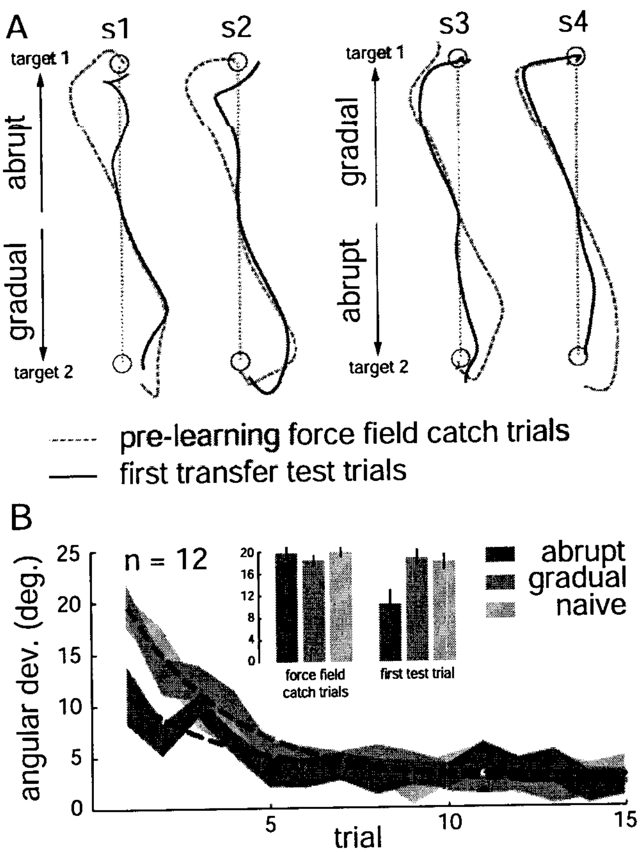

Figure 2. Transfer of learning to the left hand is not observed when the load is applied gradually. There is partial transfer of learning in the abrupt condition. *A*, Movements of the left hand for single subjects. Dashed lines show hand paths for force-field catch trials that were interspersed during the familiarization phase before training. Solid lines show hand paths in the first trial of the transfer tests. Subjects s1 to s4 were from groups 1 to 4 (Table 1). *B*, Initial angular deviation averaged (mean ± 1 SE) in each trial of the transfer tests. The bar plots show the mean over subjects of the two force-field catch trials that were introduced during the familiarization phase and the mean (±1 SE) of the first test trials. The plot gives the first trial of the transfer test for the experimental group and, for the group of naive subjects, the first test trial with the left hand in the force field. deg., Degree; dev., deviation.

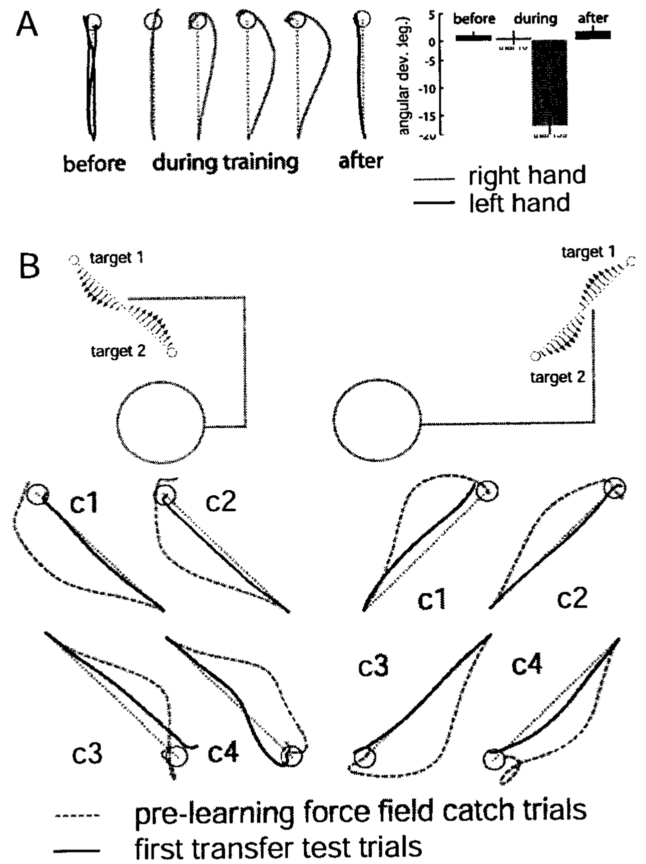

Figure 3. *A*, Control 1. Trials performed in the null-field condition. From left to right, end of familiarization with the left hand (before), null-field catch trials over the course of learning with the right hand in the gradual-training condition (during training), and first trial to test for transfer of aftereffect to the left hand (after). One sees that aftereffects develop during training with the right hand that do not transfer to the left hand. The bar plot shows the mean initial angular deviation across subjects (±1 SE). *B*, Control 2. Intralimb transfer of learning is observed in the gradual-training condition. The figure shows limb configurations and movement directions that were used in the two intralimb transfer tests, along with hand paths for each of the four control subjects (c1 to c4). Dashed lines show hand paths that correspond to force-field catch trials during the familiarization phase; solid lines show the first trial of each intralimb transfer test.

illustrated by the hand path labeled "after" in Figure 3*A*, the first movement performed in the null field with the left hand was as straight as those executed with the same hand at the end of the familiarization phase ($p > 0.05$). Thus, when training is gradual, neither learning nor aftereffects transfer between arms. Note that lack of transfer of the aftereffect does not preclude transfer of learning (Wang and Sainburg, 2003).

These findings are in striking contrast to the results of control 2. Indeed, for the same gradual-training condition, excellent generalization across different configurations of the same arm was found. As can be seen in Figure 3*B*, adaptation to the gradually introduced field in the central workspace location dramatically improved performance in the other two positions. In this figure, individual hand paths for each of the four control subjects are plotted. The dashed lines show the hand paths that correspond to force-field catch trials that were recorded during the familiarization phase at each of the transfer locations. Hand paths plotted in solid lines show the very first trial of each transfer test. For both transfer configurations, hand paths in the first transfer trial were straighter than in the prelearning force-field catch trials ($p < 0.01$). Moreover, hand paths in the first transfer trials did not differ from those at the end of the familiarization (mean of the last three trials) in the null field ($p > 0.05$). There is thus a clear difference in the pattern of interlimb and intralimb generalization for the same gradual-training condition (Fig. 2*A*), in agreement with findings on transfer of visuomotor adaptation (Wang and Sainburg, 2004a).

We also evaluated interlimb transfer in the abrupt condition by directly comparing the level of adaptation exhibited by the right hand during the training phase, and the performance of the left hand in the transfer test. [For these comparisons, as a preliminary step, we assessed for each arm the effect of the field before adaptation. For the left hand, as previously described, we considered the mean of the two prelearning force field catch trials. For the right arm, the first perturbed trial of the abrupt training provided an analogous estimate. For the two target directions, prelearning hand-path deviations were comparable across hands ($p < 0.05$). One should note that the field had a comparable effect, as can be seen by comparing Figures 1*B* and 2*B*, for both arms given the specific limb configurations and movement directions that were chosen in the present experiment; such symmetry is not observed in general (Bagesteiro and Sainburg, 2002).] Consistent with the fact that transfer across limbs was observed in the abrupt condition, subjects exhibited better performance in the first transfer trials, with the left hand, than in the first training trials, with the right hand ($p < 0.01$). However, they did not perform as well in the transfer task as they did at the end of the training ($p < 0.01$). In addition, as mentioned above, performance substantially improved in the course of the transfer test (deviation in the last three transfer trials was smaller than in the first three transfer trials; $p < 0.01$). This seems to indicate that, even in the abrupt-training condition, there is incomplete transfer of learning between arms.

Discussion

The experimental paradigm that is often used to examine learning of new dynamics involves the sudden introduction of a load that initially produces a marked kinematic error, which subjects can readily perceive. Adaptation under these conditions may involve both gradual changes to motor commands and higher-level, possibly conscious, error correction strategies. These distinct and complementary adaptation processes might use different kinds of information that is represented in different reference frames.

Our idea was that the interlimb transfer reported by Criscimagna-Hemminger et al. (2003) might rely substantially on the use of high-level information about the effects of the force field. This kind of information may be mostly independent of that which underlies predictive changes observed in patterns of muscle activity that are developed by a trained arm. We hypothesized that by limiting kinematic error and, as a consequence, the amount of visual and kinesthetic input arising from the perturbation, information available for cognitive strategies would be reduced and this would impair generalization across arms.

To test this hypothesis, we designed a training condition in which the external forces were introduced gradually, so that subjects could not at any point during learning consciously notice a clear discrepancy between their intended and their actual movements. In this adaptation condition, subjects could easily, by small adjustments to their motor commands, maintain a constant hand path despite the alteration of the dynamic environment. We compared interlimb transfer after this training condition (gradual training) with the generalization across limbs that occurred when subjects had learned to correct for the effects of a force field that was suddenly introduced (abrupt training).

As expected, when subjects trained in the gradual condition, no measurable generalization across arms could be observed; subjects in the gradual condition performed no better in the transfer test than naive subjects. Moreover, subjects did not benefit from a more extensive exposure to the field provided in the gradual condition, relative to the fairly short experience that was offered by the abrupt training. The same conclusion, that there is little interlimb transfer of sensorimotor learning, was also reached in control 1, in which no interlimb transfer of aftereffects could be observed for subjects who trained in the gradual condition. The findings of control 1 also ruled out the possibility that the learning that was observed in the gradual-training condition might be a consequence of a cocontraction strategy, because subjects developed, during learning, the usual aftereffects, indicative of anticipatory mechanisms. It should be noted that the learning that occurred in the gradual condition is characteristic of that observed in other force-field adaptation studies. Specifically, as shown in control 2, there is intralimb generalization after gradual training, a finding that points to the effectiveness of this procedure in producing both force-field learning and generalization.

In the abrupt condition, performance at the beginning of the transfer task was worse than at the end of the training task. Because the effect of the field was similar for the left and right hands, this shows that transfer was incomplete in this condition. It is as if subjects in the abrupt condition had acquired information about the effect of the field and on this basis were capable of predicting the direction of the load (Flanagan et al., 2003). However, this awareness alone was not sufficient for a precise compensatory-force adjustment to occur. Indeed, several studies seem to indicate that these kinds of fine adjustments are mediated by implicit processes unavailable to consciousness (Gentile, 1998). They appear to develop in an effector-specific way, and seem to be used subsequently only if the effector–environment interface remains unchanged (Salimi et al., 2000). In the present study, such invariance held only in the intralimb case of control study 2 (Thoroughman and Shadmehr, 1999).

Criscimagna-Hemminger et al. (2003) point to the fact that the interlimb transfer in extrinsic coordinates they observed occurred for movements performed, with each arm, near the midline of the body. They suggest that a more complex pattern of transfer would probably occur if, at the same time as a translation to the contralateral arm, the transfer test involved a change of the workspace location, that is, a combination of interlimb and intralimb transfer. The midsagittal plane of the body, which is the plane of bilateral body symmetry, appears indeed to be a fundamental reference in spatial perception and orientation (Ventre et al., 1984). However, in the present case, because the pattern of generalization (in the abrupt-training condition) reflects an extrinsic frame of reference rather than mirror image symmetry, it would seem that transfer might be more related to bimanual coordination. Indeed, interlimb generalization in extrinsic coordinates might be related to the activation of motor schemes involved in bimanual interactions with the environment, which may involve representations in object-centered extrinsic coordinates rather than representation in joint- or muscle-based intrinsic coordinates (Diedrichsen et al., 2004).

In the present study, we have not addressed issues related to the direction of interlimb transfer that bear on the role of cognition in the transfer process. Criscimagna-Hemminger et al. (2003) observed no transfer from nondominant to dominant despite sudden introduction of the force field. One might speculate that differences in the resources involved in learning the task with the dominant versus the nondominant arm may explain this result; additional demands imposed by the use of the nondominant arm might be associated with a lower level of awareness, and consequently reduce the amount of transfer. Quantification of the resources (cognitive and noncognitive) involved in the task when performed with the dominant versus the nondominant arm would be needed to go beyond conjectures relative to the role played by cognition in the transfer observed in the present study and by Criscimagna-Hemminger et al. (2003). Recent results that show different directions of transfer for adaptation to novel inertial dynamics and adaptation to visuomotor rotation (Wang and Sainburg, 2004a,b) also provide information directly relevant to this question.

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