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Learned Dynamics of Reaching Movements Generalize From Dominant to Nondominant Arm

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Criscimagna-Hemminger, Sarah E., Opher Donchin, Michael S. Gazzaniga, and Reza Shadmehr. Learned dynamics of reaching movements generalize from dominant to nondominant arm. *J Neurophysiol* 89: 168–176, 2003. First published October 10, 2002; 10.1152/jn.00622.2002. Accurate performance of reaching movements depends on adaptable neural circuitry that learns to predict forces and compensate for limb dynamics. In earlier experiments, we quantified generalization from training at one arm position to another position. The generalization patterns suggested that neural elements learning to predict forces coded a limb's state in an intrinsic, muscle-like coordinate system. Here, we test the sensitivity of these elements to the other arm by quantifying inter-arm generalization. We considered two possible coordinate systems: an intrinsic (joint) representation should generalize with mirror symmetry reflecting the joint's symmetry and an extrinsic representation should preserve the task's structure in extrinsic coordinates. Both coordinate systems of generalization were compared with a naïve control group. We tested transfer in right-handed subjects both from dominant to nondominant arm (D→ND) and vice versa (ND→D). This led to a 2 × 3 experimental design matrix: transfer direction (D→ND/ND→D) by coordinate system (extrinsic, intrinsic, control). Generalization occurred only from dominant to nondominant arm and only in extrinsic coordinates. To assess the dependence of generalization on callosal inter-hemispheric communication, we tested commissurotomy patient *JW*. *JW* showed generalization from dominant to nondominant arm in extrinsic coordinates. The results suggest that when the dominant right arm is used in learning dynamics, the information could be represented in the left hemisphere with neural elements tuned to both the right arm and the left arm. In contrast, learning with the nondominant arm seems to rely on the elements in the nondominant hemisphere tuned only to movements of that arm.

INTRODUCTION

Generalization is the process by which knowledge gained through training in one situation changes performance in a different situation. The ability to generalize motor skills is of practical importance for developing training methods and rehabilitation techniques. It is also of theoretical interest because generalization is a powerful tool that can be used to uncover tuning properties of elements of neural computation (Poggio 1990; Thoroughman and Shadmehr 2000). For instance, in the motor system, patterns of generalization of force as a function of direction of reaching movements have been used to argue for a bimodal tuning of the computational elements with respect to movement direction (Donchin 2002). Patterns of generalization in terms of spatial configuration of the arm have been used to argue for a very wide global tuning of the computational elements with respect to the static position of the hand (Shadmehr and Moussavi 2000). Lack of generalization in training with time-dependent force patterns (rather than state-dependent ones) has been used to argue that the computational elements are strongly tuned to the sensory state of the movement and may have no tuning with respect to time at which that state was visited (Conditt and Mussa-Ivaldi 1999). While these findings have provided significant information on the nature of computation that is performed by the brain in learning to compensate for forces with the trained arm, we do not know if force compensation generalizes to the contralateral limb. In effect, we do not know if the computational elements are tuned to movements of both arms. If they are, then learning with one arm should generalize to the other arm.

Transfer of a skill learned in one hand to the other hand has been used as evidence for the role of the hemispheres in controlling that skill. Transfer from the dominant to the nondominant arm (D→ND), which is the direction most often reported, has been interpreted as evidence for the ability of a representation formed in the dominant hemisphere during training with the dominant hand to influence the performance of the nondominant hand (Laszlo et al. 1970). This may be through two mechanisms: either through callossal connections or through ipsilateral projections. It has also been proposed that transfer in the opposite direction reflects a dominance of the right hemisphere (in right-handers) for some aspects of motor control, so both directions of transfer may be explained with a single model where direction of transfer identifies the hemisphere of representation (Thut et al. 1996).

In general, these arguments say very little about the possibility of the involvement of subcortical areas—including basal ganglia, cerebellum, red nucleus, and spinal cord—in the process of learning motor control. In part, this is because little is known about lateralization in these subcortical structures, although some recent work has indicated that they probably play a significant role (Day and Brown 2001). While it is possible to

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get some indication of the role of the cerebral hemispheres themselves through the study of subjects with a sectioned corpus callosum, this has rarely been pursued in the case of motor learning and transfer.

When asking whether prediction of force dynamics generalizes from one arm to another, we must also be concerned about the coordinate systems of the transfer. For example, generalization of force fields in the trained limb occurs in an intrinsic coordinate system (Shadmehr and Moussavi 2000), suggesting that interlimb transfer of these tasks might also be in an intrinsic coordinate system. On the other hand, generalization of visuomotor rotations occurs in an extrinsic coordinate system (Krakauer et al. 1999). This observation suggests that for the simple task of making a reaching movement, maps that compute kinematic variables (for example, target location) engage different parts of the motor system than maps that transform those kinematic variables to forces (Ghez et al. 2000; Shadmehr and Mussa-Ivaldi 1994).

In the current study, we asked whether learning a force field with one arm generalizes to the other arm. Because we had previously observed that learning generalizes in a muscle-like, intrinsic coordinate system for the trained arm, we had little expectation that there would be generalization to the contralateral arm. We found the very surprising result that there was not only strong generalization, but also that it seemed to be with respect to an extrinsic coordinate. To investigate the neural basis of this generalization, we examined an individual who had undergone a complete section of the corpus callosum. Our results provide a significant challenge to current models of how the brain learns reaching movements.

The results presented in this paper are part of an undergraduate research report submitted by Sarah Criscimagna-Hemminger to Johns Hopkins Biomedical Engineering, and have been presented in abstract form.

METHODS

Subjects

Thirty-six (13 female and 23 male) neurologically intact subjects, aged 18–40 yr (mean = 22), participated in the experiment. Handedness was assessed using the Edinburgh Inventory (Oldfield 1971). The Johns Hopkins University Joint Committee on Clinical Investigation approved the protocol, and all subjects signed a consent form.

We also tested a split-brain patient to assess whether the inter-limb transfer of the force field depended on the inter-hemispheric connections via the corpus callosum. *JW*, a right-handed, 48-yr-old male, had a two-stage commissurotomy in 1979 that resulted in complete resection of the corpus callosum but spared the anterior commissures (Gazzaniga et al. 1984). The surgeries were undertaken to treat pharmacologically intractable epilepsy that began after a closed head injury at age 13. *JW*'s right hemisphere can successfully process simple verbal commands, and his case has been characterized in previous reports (Gazzaniga et al. 1985). Eight months after the second stage of surgery, his neurological examination was unremarkable with the exception of typical split-brain phenomena. *JW*'s daily activities suggest that his sensory and motor abilities continue to be normal: He is a licensed automobile operator and constructs elaborate miniature models in his spare time. We tested *JW* on the current experiment by taking the robot to Dartmouth University.

Behavioral task

We used the curl-field motor learning paradigm that has been described elsewhere (Shadmehr and Brashers-Krug 1997). Subjects held the handle of a two link robotic manipulandum and were asked to make point-to-point reaching movements. Motion of the manipulandum was restricted to the horizontal plane, and the subject's arm was supported in the horizontal plane using a sling. One-centimeter-square targets appeared at 10 cm in one of six directions (Fig. 1*C*) in a pseudorandom out-and-back pattern. The order of the target directions was the same for all subjects. The computer provided positive reinforcement in the form of a target explosion if the movement was completed within a certain window around 0.5 s. The window was initially 140 ms and was reduced slightly after every success and enlarged slightly after every failure. In-house software on a PC controlled the behavioral task and recorded position, velocity, and force at the handle at 100 Hz.

The robot produced forces that depended linearly on instantaneous hand velocity: $F = \beta\dot{x}$, where β was a curl matrix that resulted in forces that were perpendicular to the motion of the hand. Two different force fields were used (Fig. 1, *A* and *B*). These force fields changed the dynamics of the arm, significantly distorting previously straight hand paths. With practice, the hand paths tended to become straight again. Previous studies of this simple paradigm suggested that the improvement in performance is due to the construction of an internal model of the force field by the brain (Conditt and Mussa-Ivaldi 1999; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 2000). An important piece of evidence for this conjecture is the fact that if the force field is unexpectedly removed (i.e., returned to null), the movements exhibit aftereffects. In an aftereffect, the movement trajectory seems to be a mirror image of the distorted trials induced by initial exposure to the force field. A movement where the force field is removed is called a catch trial. One in six targets were pseudorandomly selected to serve as catch trials.

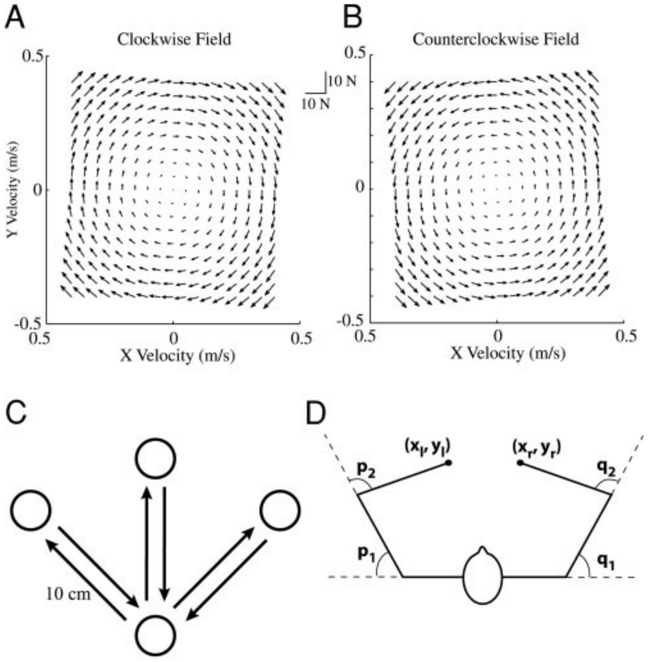

FIG. 1. Target layout and velocity-dependent curl fields. *A*: forces exerted by the robot in the clockwise field (CW) as a function of the velocity of the subject's instantaneous movement. *B*: forces exerted by the counterclockwise field (CCW). *C*: 4 targets were used in an out-and-back pattern such that each movement out to a target was followed by a movement back in toward the center. In this way, subjects moved in six possible directions. *D*: a schematic showing the labels used to describe transfer in extrinsic and intrinsic coordinates.

Coordinate systems of transfer

Assume a subject learned a counter clockwise (CW) curl field with his right hand. If the subject then switched to using the left hand, it is possible that no transfer at all would occur, and the subject would behave as though the field had never been learned (that is, like a naïve subject). However, if transfer does occur, the characteristics should depend on the subject's internal representation of the field. We present two hypotheses for how this transfer may occur.

Hypothesis 1: inter-limb generalization occurs in extrinsic coordinates

This kind of generalization suggests that for a given hand velocity, the forces on the left and right hands should be the same. We tested subjects for the possibility that the field was represented in extrinsic coordinates by testing transfer from the CW field in one arm to the same CW field in the other arm.

Hypothesis 2: inter-limb generalization occurs in intrinsic coordinates

If the internal representation of the field is in intrinsic joint-like coordinates, then the situation is more complicated. To give an intuitive example of this, consider the following. If with her right arm a subject learned to strongly activate biceps to displace the hand in a given direction (direction being defined in terms of displacement in joint configuration of the current arm), this hypothesis predicts that she would expect to also strongly activate biceps on the left arm to displace the hand in the same direction (direction again being defined in terms of displacement in joint configuration of the current arm).

In the example of the subject learning the CW curl field with the right arm, the robot produces a field $F = \beta_r \dot{x}$, where $\beta_r = [0\ 13; -13\ 0]$ N.s/m and $\dot{x}$ is hand velocity. The field is a transformation from velocity of the hand to forces on the hand. Its coordinate system is Cartesian. If, however, the subject formed a representation of the field not in terms of a map from hand velocity to hand force, but in terms of a map from joint velocity to joint torques, we can use the coordinate system described in Fig. 1*D* to write the field as

$$\tau_r = J_r^T \beta_r \dot{x} = J_r^T \beta_r J_r \dot{q} \qquad (1)$$

Here, the forces have been transformed into torques and hand velocity has been transformed to joint velocity using the Jacobian, $J_r^T = (\partial x_r / \partial q)$. The generalization patterns seen in earlier experiments suggest that this is a good approximation of what subjects actually learn (Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994). Mathematically, the hypothesis on inter-limb generalization in intrinsic coordinates claims that the subject expects that the torque fields on each arm should be equal when joint velocities for each arm are equal

$$\tau_r(\dot{q}) = \tau_l(\dot{p})$$

If the force field on the left hand is defined as: $F_l = \beta_l \dot{x}$, then the preceding equation can be rewritten as

$$J_r^T \beta_r \dot{x} = J_l^T \beta_l \dot{x}$$

$$J_r^T \beta_r J_r^T \dot{q} = J_l^T \beta_l J_l^T \dot{p} \qquad (2)$$

If two movements are the same in terms of their joint velocities, i.e., $\dot{q} = \dot{p}$, then

$$\beta_l = (J_l^T)^{-1} J_r^T \beta_r J_r J_l^{-1} \qquad (3)$$

If we assume that the link lengths of the two arms are similar, that is, the left arm has link lengths that are equal to the links of the right arm, and further assume that the workspace for this task is such that $q \approx p$, that is, the hand is on or near the midline, then the Jacobians in *Eq. 3* acquire a special property. If $\beta_r = [a\ b; c\ d]$, the Jacobians transform this matrix into $\beta_l = [a\ -b; -c\ d]$. This means that if the subject trains in field β_r on the right hand, and that field describes a CW curl pattern such that $\beta_r = [0\ 13; -13\ 0]$, then according to the hypothesis, on the left hand, the field should generalize to a counter clockwise pattern described by

$$\beta_l = -\beta_r$$

In summary, a joint coordinate generalization from the right arm to the left arm means that if the workspace is near the midline, then a CW curl field on the right arm should be generalized to a counter clockwise (CCW) pattern on the left arm. This is the familiar mirror transformation of the forces about the midline.

It is noteworthy that the transformation that we just described is mirror only when the two hands are at the same physical location. In our current experiment, this condition is true. In other experiments where the two hand positions may not be the same, a joint-based transfer of forces will not, in principle, imply a mirror transformation.

Experimental procedures

The sequence of trials experienced by each subject is described in Table 1. Subjects were randomly divided into six groups in a 3x2 factorial design (Table 2). The D→ND (dominant to nondominant) subjects were first trained on their right hand (training hand) and then tested on their left hand (testing hand). The ND→D subjects experienced the reverse. For subjects in the intrinsic group, the training field was a clockwise field (CW). They were then tested on a counterclockwise field (CCW) so that when they switched hands, they also switched to a mirror image of the field they hand learned. Subjects in the extrinsic group switched hands but were trained and tested on the same, CCW, field. The control group consisted of subjects who were only exposed to a null field in their training hand. They were, however, tested on the CCW field on their "test" hand.

Before any exposure to the force fields, all subjects were familiarized with the apparatus by performing 300 movements with each hand in the null field. During these familiarization trials, the robot did not apply perturbing force fields, and the manipulandum remained passive under the subject's control. Following familiarization trials, all subjects trained for 450 movements (3 sets of 150 trials with short breaks in between) on their training hand in the trained field (see Table 2). After training, subjects changed hands and performed 300 movements with the testing hand in the CCW field. During both training and testing, catch trials were interspersed pseudorandomly.

Protocol for the split-brain subject

We had the opportunity to also test a split-brain subject, *JW*, on this paradigm. As in other subjects, he was first familiarized with the task in baseline trails where he trained with the right and left arms in the null field. We then asked *JW* to use his right (dominant) hand for 450 movements and train in a CCW curl field. He was then asked to switch

TABLE 1. *Experimental procedures*

	Familiarization			
	1	2	Train	Test
Movements	300	300	300/450	300
Hand	Test hand	Train hand	Train hand	Test hand
Field	Null	Null	Train field	Test field

Each subject went through the same sequence shown in the table above, but for each subject, the train and test hand and the train and test field could be different (Table 2). After being familiarized on the apparatus with both hands while the robot was passive, subjects were trained on 1 hand in one field and then tested on the other hand in a potentially different field.

TABLE 2. *Experimental groups*

	Train		Test	
	Hand	Field	Hand	Field
Dominant to non-dominant (D → ND)				
Intrinsic	Right	CW	Left	CCW
Extrinsic	Right	CCW	Left	CCW
Control	Right	Null	Left	CCW
Non-dominant to dominant (ND → D)				
Intrinsic	Left	CW	Right	CCW
Extrinsic	Left	CCW	Right	CCW
Control	Left	Null	Right	CCW

Thirty-six subjects were divided into six groups as per the 3 × 2 factorial design shown (intrinsic/extrinsic/control × D → ND/ND → D). Each subject trained in 1 field—clockwise (CW), counterclockwise (CCW), or null—on 1 hand, and then switched hands. All subjects were tested on the CCW field on their "test" hand.

to his left hand. We tested for extrinsic coordinate system transfer using a CCW curl field for 75 movements (to prevent excessive familiarity with the field). The subject then took a 3-h break. After the break, the subject trained for 395 movements on a CW curl field with his dominant hand. We tested for an intrinsic coordinate system transfer for 150 movements using a CCW curl field on the left hand.

Data analysis

Data analysis was performed using Matlab (Mathworks, Natick, MA). Movement onset was determined off-line as the point at which velocity crossed 15% of the peak velocity on each movement. The end of movement was determined as the point at which velocity crossed below the 15% threshold. We assessed the error on each movement by comparing it with average performance of the same subject near the end of the baseline familiarization trials. To compute this error, we initially computed the perpendicular displacement (PD) for the last 75 movements in the familiarization set of each arm (when no forces were imposed on the hand). PD is the perpendicular distance between the line connecting movement onset and target to hand position at 300 ms after movement onset. This is typically the point for which movement errors are largest. We then computed PD for the movements in the training and test sets, and subtracted from this, the PD that we had recorded in the same subject in the baseline trials with the same arm. Therefore the result was a measure of within subject change in performance in the training and test trials with respect to the baseline trials.

During training, PDs should decrease in fielded trials but increase in catch trials, as has been previously shown (Shadmehr and Mussa-Ivaldi 1994). To combine the information given by the fielded and catch trials, we computed a adaptation index (AI)

$$\mathrm{AI} = \frac{|\mathrm{PD}_{\mathrm{CatchTrial}}|}{|\mathrm{PD}_{\mathrm{CatchTrial}}| + |\mathrm{PD}_{\mathrm{FieldedTrial}}|}$$

If subjects in a group that learned a field showed an AI after switching hands significantly greater than the AI found in the null group, then that would demonstrate transfer of learning. The adaptation index used PDs averaged over a bin size of 15 movements for the first bin and 25 movements for each bin after that. We discarded the last 10 movements, so there were six bins for each set. This allowed us to emphasize the behavior on the first trials of the set (which was important for determining the immediate effects of transfer) but ensured at least two catch trials in each bin.

Differences in AI of the different groups were tested using a repeated-measures ANOVA, which included the direction of transfer (D→ND and ND→D), the coordinate system of transfer (intrinsic, null, extrinsic), the interaction of these two factors, and time (the 6 movement bins listed in the preceding text). The design was a repeated measures design over time (because each subject provided a data point at each time bin, but subjects only appeared in 1 group). Tukey's honestly significant difference criterion was used to further pinpoint the differences that were causing effects in the ANOVA.

RESULTS

Figure 2 illustrates typical movement trajectories for fielded trials during different phases of training and testing for one subject in each of the three groups: intrinsic, extrinsic, and control. These three subjects from the D→ND group were initially trained with their dominant (right) hand and then tested with the nondominant hand (left). All movements have been shifted and rotated so that the initial target locations overlap and the final target locations overlap. Figure 2, *A–C*, show the first 10 training movements (performed with the right hand) for each of these three subjects. Noticeable displacement from a straight trajectory can be observed in the extrinsic and intrinsic subjects because subjects have not yet learned the curl field. The subjects from the control group, of course, do not suffer these perturbations. The last 10 movements in the training sets, immediately before transfer is tested, show a different picture. Now all subjects are able to make relatively straight movements in the field (Fig. 2, *D* and *F*). This indicates that the subjects have adapted to the appropriate curl field with their right arm. The final row of the figure (*G–I*) shows the first 10 fielded movement of the first test set, performed with the left

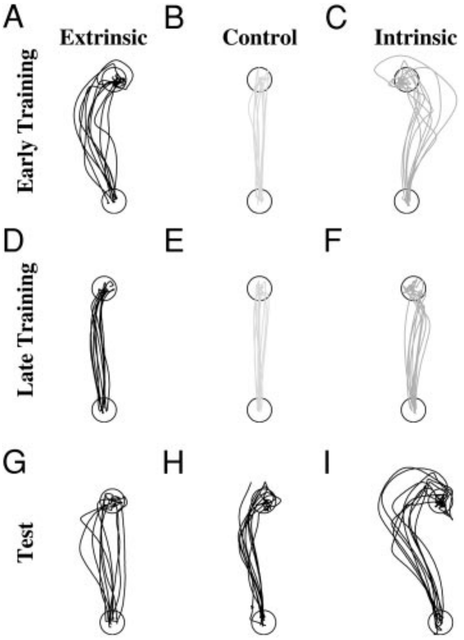

FIG. 2. Movement traces during training and testing. Examples of movement made by 3 representative subjects who were all in D→ND groups. Movements in the 6 different directions have been rotated so that they are shown going from the bottom toward the top of the page. The initial (*bottom*) and final (*top*) targets are shown. They are separated by 10 cm, providing a scale for the figure. Traces in black were made in the CCW field (*A, D, G, H,* and *I*). Traces in the intermediate gray were made in the CW field (*C* and *F*). Traces in the lightest gray were made in the null field and no external forces were applied (*B* and *E*). *Top*: the 1st 10 movements in the training field. *Middle*: the last 10 movements in the training field. *Bottom*: the 1st 10 movements in the test field (always a CCW field). All data in the column marked extrinsic (*A, D,* and *G*) are from 1 subject. Similarly, data in columns marked null and intrinsic are each from 1 subject.

hand, immediately after subjects transfer to a CCW curl field. This row allows an evaluation of transfer in each of these subjects. Note that, as portrayed in this figure, the field pushes to the left, so its effect can be assessed as a leftward tendency in the movements. Clearly, the intrinsic subject's movements (Fig. 2*I*) are more affected than the control subject's movements (Fig. 2*H*), and these are more affected than the extrinsic subject's movements (Fig. 2*G*).

The impression given by these typical subjects is that knowledge of the field transferred in an extrinsic coordinate system. When the field applied to the left hand was the same in extrinsic coordinates, performance was better than control. When the field applied to the left hand was the same in intrinsic coordinates, performance was worse than control.

This impression is reinforced by looking at the population averages. Figure 3 shows the average perpendicular displacement across subjects ($n = 6$ for each group) during training and testing sessions for the D→ND group. The error in the fielded trials of the extrinsic group (Fig. 3*A*) continues to decrease despite changing hands, indicating that the subjects were able to use their prior knowledge of the field. However, the error for the control group (Fig. 3*B*) and, even more so, the intrinsic group (Fig. 3*C*) increases when changing hands. That the intrinsic subjects perform, on average, worse than the control subjects reinforces the idea that the intrinsic group suffered interference from the previous training.

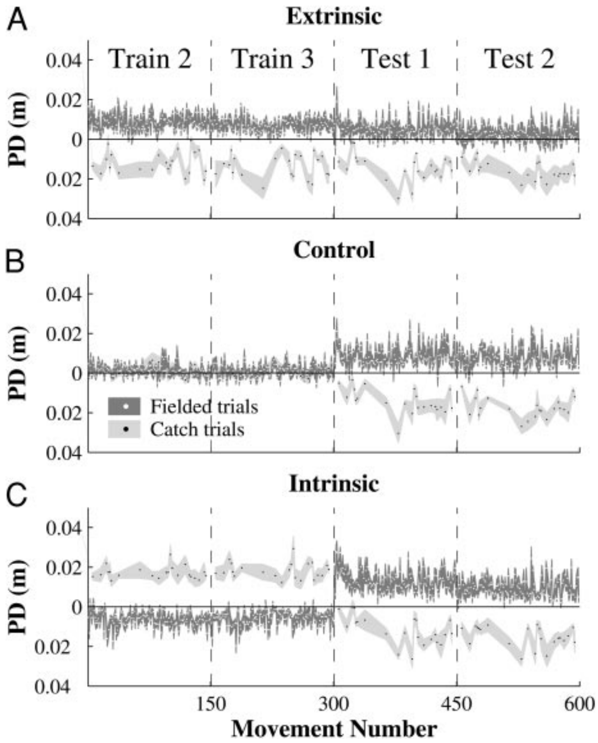

FIG. 3. Average perpendicular displacement for transfer to nondominant hand. Dots show the mean PD for subjects in the D→ND group for the last 2 training sets and the 2 test sets. Subjects switch hands between the train 2 and test 1 data sets. Subjects in the extrinsic group (*A*) have been training on a CCW field on their right hand (so fielded errors are positive) and switch to a CCW field with their left hand. Subjects in the null group (*B*) have been training in their right hand with no field (so both fielded and catch movement errors are nearly 0). Subjects in the intrinsic group (*C*) have trained their right hand on a CW curl field and now switch to a CCW curl field with their left hand. The colored patches behind the dots indicate ± SE.

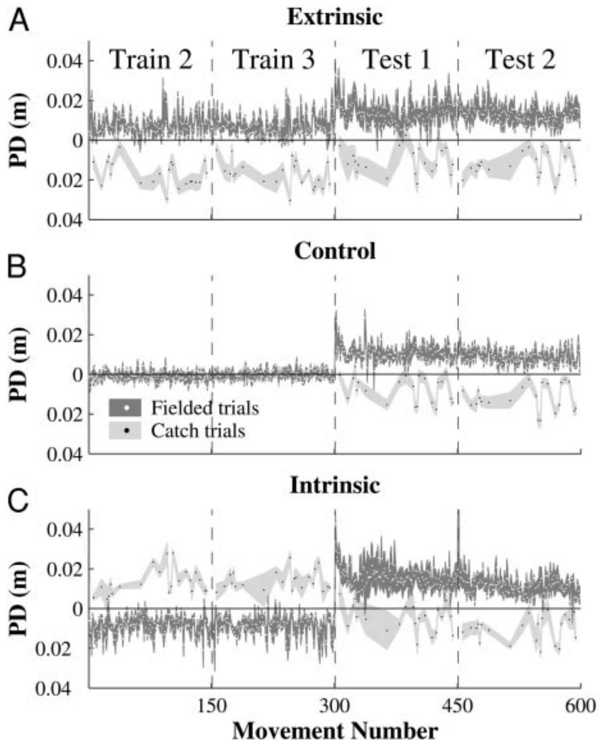

FIG. 4. Average perpendicular displacement for transfer to dominant hand. Format as in Fig. 3, but this time mean and SE of ND→D subjects is shown.

We next tested whether the pattern of generalization shown in Figs. 2 and 3 was duplicated in the subjects who initially trained on the nondominant (left) hand and were then tested on the right hand (i.e., the ND→D group). Figure 4 shows the averaged perpendicular displacement data for these subjects. In contrast with D→ND subjects, ND→D subjects showed no effect from having learned the field previously. No clear difference between the control group and the extrinsic or intrinsic groups can be discerned after transfer. This suggests that the ability to learn to predict forces during reaching movements transfers asymmetrically, from the dominant to the nondominant hand, but not vice versa.

Because the PD in the fielded trials and the catch trials provides two independent measures of the same effect (the amount of learning), we generated an index that combines these two methods and called it the AI (see METHODS). This index should grow close to 1 as the catch trials increase and as the size of error in fielded trials decrease. The AI for the first set after transferring to the untrained hand is shown for all groups in Fig. 5. Figure 5A shows the index for the D→ND groups and Fig. 5*B* shows the index for the ND→D groups. In Fig. 5*A*, it is even clearer than before that the extrinsic group consistently performs better than the control group, indicating transfer of learning, and that the intrinsic group performs worse, indicating interference. While a slight trend for extrinsic to be better than null, and null better than intrinsic can be seen in Fig. 5*B*, this difference does not approach significance (as discussed in the following text), and we conclude that the transfer is asymmetrical.

We tested the statistical significance of our findings using a repeated-measure ANOVA. The results showed a significant effect of the direction of transfer (D→ND and ND→D, $F = 154$, $P < 0.001$), for the coordinate system of transfer (extrin-

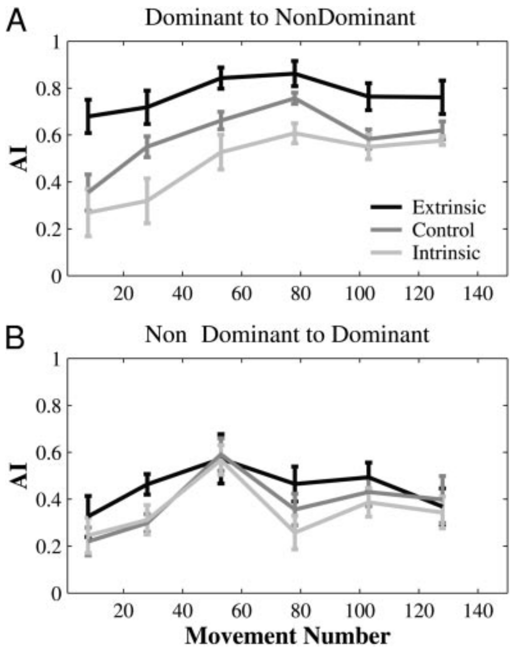

FIG. 5. Adaptation index (AI) for first transfer set. Mean (± SE) for the AI for the 1st test set for all 6 groups. Note that there are differences between the D→ND groups: extrinsic subjects perform better after transfer than null subjects who perform better than intrinsic subjects. In the ND→D groups, there are no such differences. The uneven spacing along the *x* axis is the result of having fewer trials in the first bin (see METHODS).

sic intrinsic and null, $F = 43$, $P < 0.001$), and for the interaction between them ($F = 11$, $P < 0.001$). Time was also a significant factor in the ANOVA. Post hoc analysis of the differences showed, as expected, that the control D→ND group was significantly better than the intrinsic D→ND group ($P < 0.01$) and significantly worse than the extrinsic D→ND group ($P < 0.001$). In contrast, the control ND→D group was not significantly different from either the intrinsic or extrinsic ND→D groups ($P > 0.2$).

We followed up our study of generalization in neurologically intact subjects with a test of a split-brain patient. Our goal was to assess whether the inter-limb transfer of the force field depended on the inter-hemispheric connections via the corpus callosum. *Patient JW* is a right-handed male who had an operation in 1979 that resulted in complete resection of the callosal fibers (Gazzaniga et al. 1984). We took the robot to Dartmouth University and trained *JW* in the baseline task (null field) first with the left arm and then the right arm. He then trained with the right arm in a counter clockwise curl field. His performance in terms of error (perpendicular displacement) in the fielded trials was quite comparable with our normal subjects and his movements in catch trials displayed aftereffects (Fig. 6*A*, *top*). We next tested for generalization of learning from the trained right arm to the left arm in extrinsic coordinates. We found little or no decrement in performance when he switched from the right to the left arm (Fig. 6*A*, *top*).

To confirm that *JW* was, in fact, generalizing from one arm to the other, we decided to test a second field. We asked him to return about 3 h later, and in this session, he initially trained with the right arm in the clockwise field and was then tested again with the left arm in the counter clockwise field. If there is generalization in extrinsic coordinates, we should now see interference. Remarkably, despite the fact that the left arm experienced the same field as earlier in the day, performance after transfer was significantly affected (Fig. 6*A*, *bottom*). This contrast is underlined by the AI in Fig. 6*B*. Therefore similar to our neurologically normal volunteers, *JW* exhibited generalization from right to left in extrinsic coordinates.

DISCUSSION

This study has produced three main findings. First, learning to compensate for dynamics of reaching movements in right-handed individuals generalizes from dominant arm to the nondominant arm (D→ND) but not vice versa. Second, D→ND generalization in the workspace that we tested (near the midline) is in an extrinsic, Cartesian-like coordinate system. Third, generalization of this motor skill does not depend on transfer of information between the hemispheres via the corpus callosum.

Hemispheric localization of adaptation

Many studies have reported transfer exclusively from the dominant to the nondominant hand and vice versa, and there are also studies that show transfer in both directions or in neither. For instance, in different paradigms, researchers have uncovered skills that transfer from the dominant to the nondominant arm (Ammons 1958; Gordon et al. 1994; Halsband 1992; Parlow and Dewey 1991; Teixeira 2000) and from the nondominant to the dominant arm (Hicks 1974; Parlow and Kinsbourne 1990; Taylor and Heilman 1980) as well as skills

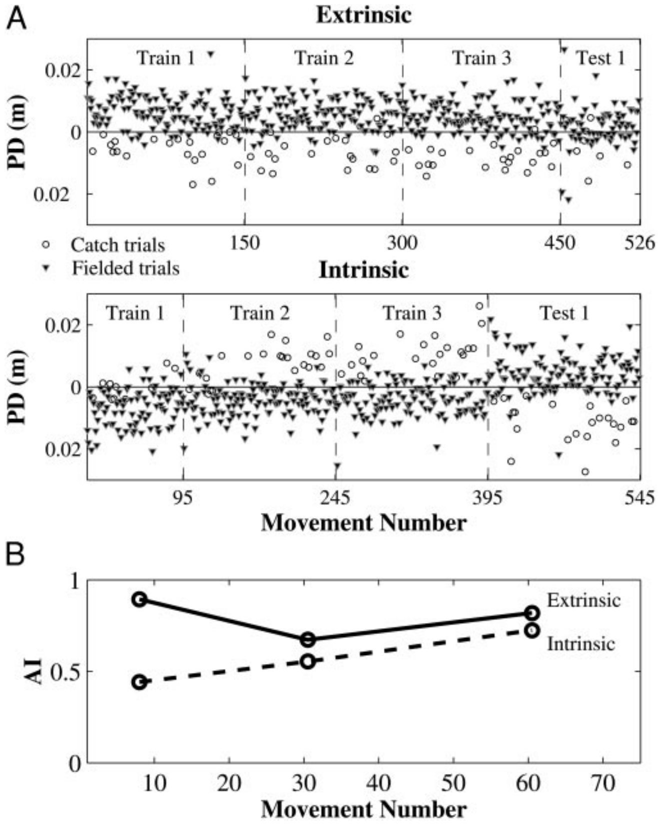

FIG. 6. Transfer in a split brain subject. Data from a single split brain subject. *A*: Perpendicular displacement of fielded trials and catch trials during D→ND transfer in extrinsic coordinates (*top*) and intrinsic coordinates (*bottom*). *B*: AI calculated on the 1st 75 movements of the test set for the data shown in *A*.

that transfer both directions (Morton et al. 2001) and skills that do not transfer in either direction (Baizer et al. 1999; Kitazawa et al. 1997; Rand et al. 1998; Teixeira 1993). Consistent with this variety of results, there have also been reports of one direction of transfer for some aspects of a task and another direction of transfer for other aspects of the same task (Parlow and Kinsbourne 1989; Sainburg and Wang 2002; Thut et al. 1996). This implies that patterns of generalization strongly depend on the task.

In adapting to dynamics of reaching movements, we observed that information acquired during training with the dominant right arm generalizes to the control of the left arm. Other motor tasks that display the same direction of transfer include inverted-reversed printing (Parlow and Kinsbourne 1989), mirror drawing (Ewert 1926; Thut et al. 1996), figure drawing (Halsband 1992), precision grip (Gordon et al. 1994), rotary pursuit (Ammons 1958), and tapping skill (Laszlo et al. 1970; Parlow and Dewey 1991; Teixeira 2000).

One proposed framework that attempts to explain D→ND transfer in different tasks is the dynamic dominance hypothesis proposed by Sainburg and colleagues (Sainburg 2002; Sainburg and Wang 2002). Under this hypothesis, following Taylor and Heilman (1980), D→ND transfer in right-handed individuals implies that the nondominant hemisphere is somehow trained during the time that the dominant hand is being exposed to the task. This could be through callosol connections. However, our current finding that transfer is normal in a split-brain patient makes this interpretation less likely.

We favor another interpretation. It is possible that the hemisphere that was used in learning the task during movements with the contralateral arm can also control the ipsilateral arm. While each hemisphere is specialized in representing movements of the contralateral hand, the degree of ipsilateral control may not be equal for the dominant and nondominant hemispheres. It has been suggested that the dominant hemisphere can effectively control the nondominant arm but not vice versa. For instance, in callosotomy patients, when visual information is restricted to one hemisphere, that hemisphere can produce a reaching movement with the ipsilateral arm (Gazzaniga 2000). This is because a small but significant number of corticospinal projections to the proximal muscles of the arm are from the ipsilateral hemisphere (Galea and Darian-Smith 1997). When the callosotomy patients are asked to point toward a visually presented target, if the visual information is presented to the left hemisphere, reaching with the ipsilateral arm is highly accurate (Gazzaniga et al. 1967). However, if the target is presented to the right hemisphere, reaching with the ipsilateral arm is only moderately accurate. Indeed, lines of converging evidence (reviewed in Haaland and Harrington 1996) indicate that the dominant hemisphere may have a significant role in controlling the nondominant arm via ipsilateral projections but not vice versa.

This consideration raises the possibility that when the dominant arm is first used in learning the dynamics of reaching movements, adaptation is primarily in the dominant hemisphere, which can later assist in performing the task with the nondominant arm. Alternatively, when the nondominant arm is first used in learning the task, adaptation in the nondominant hemisphere cannot be brought to bear on movements of the dominant hand, preventing generalization of the skill. This explanation does not depend on transfer of information through the corpus callosum because either hemisphere can guide and control ipsilateral movements involving the more proximal muscles of the shoulder and elbow. This is consistent with our finding that a split-brain subject also showed transfer of the skill from right arm to the left arm.

Of course, alternative explanations may be possible if one assumes that the internal model is developed subcortically rather than cortically. However, little is known about lateralization in subcortical structures, and an elaborate theory in this case would be pure conjecture.

Coordinate system of force generalization

Let us now turn to the result that the coordinate system of transfer was extrinsic. One of the first examples of transfer in the scientific literature involved a scientist who had to write the digit "9" many times with his left hand and then found, when returning to the right hand, a tendency to invert that digit (Fechner 1858; reviewed in Davis 1898). This is an example of mirror symmetric transfer. However, despite the extensive literature on bilateral transfer, the issue of coordinate systems has hardly been considered. In some cases, authors have implicitly assumed through the structure of the task that some skills will transfer in extrinsic coordinates and others in intrinsic coordinates. For instance, when Hicks tested inverted-mirror printing, it was assumed that generalization would be in extrinsic coordinates (Hicks 1974), but, in a later experiment using a typing task, generalization was assumed to be in mirror-symmetric coordinates (Hicks et al. 1982). One study (Salimi et al. 2000) did test for both intrinsic symmetric and extrinsic transfer in a precision grip task, but they did not find transfer in either condition (perhaps because very few training trials were used). Finally, bimanual synergies that are mirror symmetric across the midline are more stable and natural than synergies that preserve the extrinsic coordinate system across the hands (Swinnen et al. 1997). Thus the literature seems to imply that if there is transfer, mirror symmetric (intrinsic coordinate) transfer is likely.

There is one study, however, whose results anticipates ours and is particularly relevant because the task also involved learning dynamics of reaching movements. DiZio and Lackner (1995) used a rotating room to apply coriolis forces to the arm during free reaching movements. In their task, as in ours, there is gradual accommodation to the forces that can be measured by the perturbation of the arms trajectory during the reach. They trained subjects to make straight movements with their right arms during the rotation, then stopped the rotation and tested the subjects first on their left arm and then on their right arm. Their results are consistent with ours: subjects had aftereffects with their left arms, indicating transfer from the right arm to the left. Now after a number of movements with the left arm in the "null" field, the aftereffects wash out and movements become straight again. However, when subjects now were asked to make movements with their right arm (again in the null field), they still had aftereffects of the original training. This suggests no transfer from the left arm to the right. DiZio and Lackner (1995) do not mention whether their subjects were all right handed, but it is probably safe to assume that on average they were. Just as important is the fact that the initial perturbations of the postrotation left arm movements were consistent with an internal representation in extrinsic coordinates: the direction of error was the same as in subjects whose initial postrotation movements were performed with the right arm. Therefore these results are consistent with ours in that when the left and right hands are near the midline, transfer is in extrinsic coordinates and only from right to left.

This pattern of generalization between arms contrasts with the pattern of generalization within the same arm. When a subject is trained to compensate for forces by performing reaching movements in a small workspace, the result is a rotation in the preferred direction (that is, the direction of movement that evokes maximal activation) of arm muscles (Thoroughman and Shadmehr 1999). If the configuration of the arm is changed and the subject is tested for reaching movements in a new workspace, the motor system expects the change in the preferred direction of muscles to be maintained (Shadmehr and Moussavi 2000). The result strongly implies generalization of the force patterns in intrinsic coordinates as a function of position of the trained arm. This suggests that the neural system that transforms a desired movement vector into motor commands relies on elements that encode spatial position of the limb very broadly and encode direction of movement in terms of changes in an intrinsic coordinate.

How could learning in this task generalize within the same arm in intrinsic coordinates but across arms in extrinsic coordinates? In the primary motor cortex (M1), and other motor cortices, neurons are activated most strongly during movement to a particularly preferred direction. The preferred direction of many cells change when the animal is exposed to a force field (Li et al. 2001). The magnitude and direction of these changes is comparable to the changes observed in the primary direction of activation in muscles. Studies of primary motor cortex (M1) neural activity as a function of arm posture in grasping (Kakei et al. 1999), reaching (Caminiti et al. 1990; Scott and Kalaska 1997), and force control tasks (Scott et al. 2001; Sergio and Kalaska 1997) show that many of the task related cells are sensitive to pattern of forces and posture of the limb. This makes cells in M1 reasonable candidates for the computational elements of learning in the case where training and tests of generalization are confined to one arm.

However, neurophysiological evidence suggests that during adaptation, changes are not confined to M1, and similar changes in preferred directions can be seen in the premotor cortex (PM) and the supplementary motor area (Schioppa et al. 2002). Recent observations indicated that some cells in M1 (Steinberg et al. 2002) and dorsal PM (Kalaska et al. 2001) that are tuned for reaching movements in one arm are also tuned for reaching movements of the other arm. Particularly in PM and to a lesser extent in M1, preferred direction of neurons is similar whether the contralateral or ipsilateral arm is reaching. If some of these cells change their preferred direction, the effect would be a generalization to the other arm in extrinsic coordinates.

Our prediction then, is that the learning in this task depends on a group of cells that have the following tuning properties: each neuron's preferred direction rotates with the configuration of the arm, in particular the position of the shoulder, but when the workspace for the reaching movements is directly on the midline, the preferred direction remains invariant to whether the contralateral or the ipsilateral arm is used. The fact that the transfer is from dominant to the nondominant arm but not vice versa suggests that the cells in the nondominant hemisphere that participate in learning in this task are not tuned to movements with the ipsilateral arm. Indeed, our prediction differs from the Taylor and Heilman callosal access model in that the neurophysiology we describe should not depend on an intact collosum. The crucial behavioral prediction of this model is that if the curl field is transferred from the right hand to the left hand and at the same time to a different part of the workspace, then the field should undergo rotation just as it does when generalization is tested across the workspace without switching hands.

An alternative explanation follows the logic of Ahissar and Hochstein (1997) in suggesting that different kinds of generalization may by facilitated by different neural representations. Thus in our case, it may be possible that interlimb transfer is facilitated by one neural network, where movements are coded in extrinsic coordinates, whereas intralimb transfer is facilitated by a different network, coding in intrinsic coordinates. This idea gains credibility with a recent demonstration that the premotor representation of movements is more likely to be in extrinsic coordinates while representation in the primary motor area is more likely to be in intrinsic coordinates (Kakei et al. 1999, 2001). This explanation could be distinguished from the one given above by testing for generalization under conditions where transfer is tested simultaneously going from one arm to another and from one part of the workspace to another.

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