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Generalization of Motor Learning Based on Multiple Field Exposures and Local Adaptation

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Malfait, Nicole, Paul L. Gribble, and David J. Ostry. Generalization of motor learning based on multiple field exposures and local adaptation. *J Neurophysiol* 93: 3327–3338, 2005. First published January 19, 2005; doi:10.1152/jn.00883.2004. Previous studies have used transfer of learning over workspace locations as a means to determine whether subjects code information about dynamics in extrinsic or intrinsic coordinates. Transfer has been observed when the torque associated with joint displacement is similar between workspace locations—rather than when the mapping between hand displacement and force is preserved—which is consistent with muscle- or joint-based encoding. In the present study, we address the generality of an intrinsic coding of dynamics and examine how generalization occurs when the pattern of torques varies over the workspace. In two initial experiments, we examined transfer of learning when the direction of a force field was fixed relative to an external frame of reference. While there were no beneficial effects of transfer after training at a single location (*experiments 1* and *2*), excellent performance was observed at the center of the workspace after training at two lateral locations (*experiment 2*). *Experiment 3* and associated simulations assessed the characteristics of this generalization. In these studies, we examined the patterns of transfer observed after adaptation to force fields that were composed of two subfields that acted in opposite directions. The experimental and simulated data are consistent with the idea that information about dynamics is encoded in intrinsic coordinates. The nervous system generalizes dynamics learning by interpolating between sets of control signals, each locally adapted to different patterns of torques.

INTRODUCTION

Psychophysical and neurophysiological studies have analyzed patterns of generalization to identify the variables used by the nervous system for movement planning and control (Imamizu et al. 1995). The encoding of information about dynamics has been studied by examining transfer of learning across differences in movement direction (Gandolfo et al. 1996; Sainburg et al. 1999; Thoroughman and Shadmehr 2000), amplitude and duration (Goodbody and Wolpert 1998), and movement path (Conditt et al. 1999). Generalization has also been examined across different configurations of the same arm (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994) and across limbs (Criscimagna-Hemminger et al. 2003; DiZio and Lackner 1995; Malfait and Ostry 2004; Wang and Sainburg 2004).

Studies that have examined transfer of learning within the same arm have provided evidence consistent with the idea that information about dynamics is represented in muscle- or joint-based coordinates. Specifically, transfer occurs when the relation between joint displacement and experienced torque remains unchanged over different workspace locations rather than when the mapping between hand displacement and force is preserved (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994). Work to date has not explained how generalization occurs when the pattern of torques changes with the configuration of the arm as is the case simply when forces have constant direction relative to an external frame of reference (but see Hwang et al. 2003). Moreover, other studies, notably work on interlimb transfer, indicate that patterns of generalization can be highly dependent on the nature of the task (Cardoso de Oliveira 2002; Malfait and Ostry 2004; Swinnen and Wenderoth 2004) and that information about dynamics may be represented in extrinsic coordinates (Criscimagna-Hemminger et al. 2003; DiZio and Lackner 1995).

In the present paper, we have used a viscous force field that acts in a fixed direction relative to an external frame of reference (Fig. 1*A*)—this defines a mapping between joint displacement and torque that varies with the configuration of the arm. The aim was to assess the generality of intrinsic coding of dynamics and determine how generalization occurs when the pattern of torques changes over the workspace. We test the idea that the nervous system interpolates between control signals that are locally adapted to different torque patterns to achieve generalization. In *experiment 1*, we examined transfer of learning across two sides of the workspace (left and right). In *experiment 2*, we assessed how learning at two lateral locations (left and right) generalizes to a third intermediate arm configuration (center). In *experiment 3* and associated simulations, we used several different composite force fields to compare the patterns of generalization for purposes of determining the system of coordinates in which these fields are learned and the specificity of the learning.

METHODS

Experimental setup

Twenty eight right-handed adults (Edinburgh Inventory) (Oldfield 1971), aged 21–33 yr, participated in the experiments. Subjects were seated and held the handle of a two-link manipulandum (Interactive Motion, Cambridge, MA). They made horizontal arm movements with their right 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 8-mm-diam targets that were

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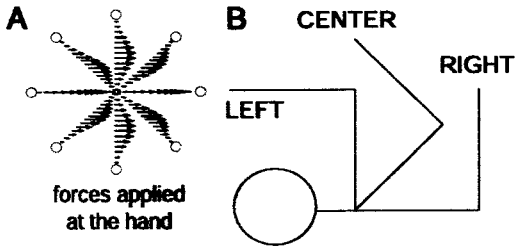

FIG. 1. *A*: subjects made center-out movements to 8 targets. Forces were applied at the hand in proportion to hand speed and always acted parallel to the frontal plane. *B*: 3 different arm configurations were used: left, right, and center. In *experiment 1*, subjects adapted to the force field at the left or the right and were then tested for transfer at the opposite location. In *experiments 2* and *3*, subjects learned the field at both the left and the right and were tested for transfer at the center.

mounted on a horizontal panel below the apparatus. Subjects could see their arm throughout the experiment.

Experimental procedures

Subjects made 12-cm center-out movements in eight different directions. In *experiments 1* and *2*, movement directions were 0, 45, . . . , 315° relative to the frontal plane. In *experiment 3*, movement directions were 22.5, 67.5, . . . , 337.5°. Participants were trained to produce movements of 500 ± 50 ms. Movements were performed in three different arm configurations: at the left, center, and right of the workspace (Fig. 1*B*). In all three configurations, the initial elbow angle was 90°, whereas the initial shoulder angle was 90° at the left, 45° at the center, and 0° at the right (shoulder angle was measured relative to the frontal plane and elbow angle was measured relative to the upper arm). The robot produced a force field in which the force f acted parallel to subjects' frontal plane—along the Cartesian x axis—and was proportional to the speed of the hand. Specifically, the forces applied at the hand were $f_x = \alpha\sqrt{(v_x^2 + v_y^2)}$ and $f_y = 0$, where f_x, f_y, v_x, and v_y are respectively the forces (N) and hand velocities (m/s) along the Cartesian axes. In *experiments 1* and *2*, the forces were always to the right, specifically, we used $\alpha = +20\ \mathrm{N \cdot s \cdot m^{-1}}$. In *experiment 3*, we used composite force fields in which forces were to the right for some movement directions—$\alpha = +20\ \mathrm{N \cdot s \cdot m^{-1}}$—and to the left for others—$\alpha = -20\ \mathrm{N \cdot s \cdot m^{-1}}$. Subjects made movements in a counterclockwise order, performing cycles of eight movements each. Forces were experienced only during movement to the target; at the end of each trial, the hand was brought back by the robot. To hold inertia constant, subjects were moved relative to the robot for movements in different workspace locations.

When forces act in a constant direction (Fig. 1*A*), the associated pattern of torques varies over the workspace. Using: $x = l_1 \cos\theta_1 + l_2 \cos(\theta_1 + \theta_2)$, $y = l_1 \sin\theta_1 + l_2 \sin(\theta_1 + \theta_2)$, where θ_1 and θ_2 are, respectively, shoulder and elbow angle, and l_1 and l_2 are lengths of upper and forearm, the transformation from endpoint force to joint torque is: $T = J^t F$, where $J = [-l_1 \sin\theta_1 - l_2 \sin(\theta_1 + \theta_2), -l_2 \sin(\theta_1 + \theta_2); l_1 \cos\theta_1 + l_2 \cos(\theta_1 + \theta_2), l_2 \cos(\theta_1 + \theta_2)]$ is the configuration-dependent differential transformation matrix—Jacobian matrix. Figure 2 illustrates the correspondence between forces and torques over the workspace. In Fig. 2, *A* and *B*, the workspace of the hand is represented in Cartesian space. In Fig. 2*A*, for each hand position, vectors represent forces and have components f_x and f_y. In Fig. 2*B*, for each hand position, vectors represent torques the components of which are the torque at the shoulder and torque at the elbow. The length of the vectors gives the amplitude of the torques, and their orientation indicates the distribution of torques between the shoulder and elbow. One sees that a constant direction force field corresponds to a torque field that varies across the workspace. Thus if subjects learn a force field the direction of which is constant—relative to an external frame of reference—at two different locations this requires adaptation to two different pattern of torques.

Experiment 1

We first used a procedure previously employed by Shadmehr and Moussavi (2000) and Malfait et al. (2002) to test whether training in a single area of the workspace would be sufficient to produce transfer of learning under conditions in which force direction was constant in an external frame of reference. Eight subjects were divided into two groups. Each group learned the force field shown in Fig. 1*A* at one side of the workspace and was then tested for transfer at the opposite location. Subjects in *group L* learned the field at the left and were then tested for transfer at the right; locations were reversed for *group R*. The experiment consisted of four phases: two familiarization phases (1 in each location), a training period, and a test for transfer, all performed within a single day. During the familiarization phases, subjects learned the task under "null field" conditions (4 blocks of 5 cycles of movements at each location). The training consisted of 10 blocks of five cycles each (400 movements in total, 50 in each direction). Subjects were tested for transfer across arm configurations. The transfer test consisted of one block of five cycles at the opposite location using the same force field as in training. The end of the training and the transfer test were separated by ~2 min.

Experiment 2

Generalization across workspace locations has been observed when the pattern of torques remains constant (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994). When the torque field varies with the arm configuration, training in a single location may not provide a basis for generalization elsewhere. In this study, we tested the idea that subjects can generalize learning about a constant force direction (in extrinsic coordinates) when they are provided with multiple exposure locations. Four subjects participated in the second experiment. The experiment involved training at both the left and the right followed by a transfer test in the center. The force field for all three locations was the same as in *experiment* 1 (see Figs. 1*A* and 3*A*). The experiment consisted of four sessions each on a different day. On the first day, subjects trained under "null field" conditions at each location (3 blocks of 5 cycles). On the next two days, subjects trained in the force field at the left and right, respectively. Two subjects trained at the right on the first day and two trained at the left. In each training session, subjects did five

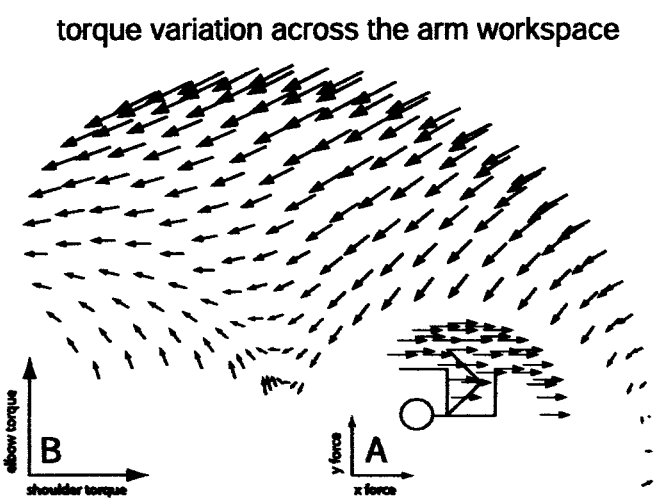

FIG. 2. Torque variation across the workspace of the limb. The figure shows the region that may be reached by the hand, represented in Cartesian space. *A*: for each hand position in the smaller plot, each vector has components f_x and f_y and represents the force applied at the hand. *B*: for each hand position in the larger torque plot, the components of each vector are the torque at the shoulder and the elbow (counterclockwise moments are considered positive).

blocks of 10 cycles in the force field (400 movements in total, 50 in each direction). On the fourth day, subjects first performed three blocks of 10 cycles at each of the lateral locations and were then tested for transfer at the center using the same force field as in the training conditions (1 block of 10 cycles). The end of the training and the transfer test were separated by ~2 min.

Experiment 3

The purpose was two-fold. It was to identify the coordinate system in which the transfer of learning observed in *experiment 2* occurs—that is, when the pattern of torque changes with the configuration of the limb. It was also to test the idea that generalization involves interpolation between the control signals associated with different patterns of torques—each learned in a different workspace location. To test this idea, we compared the patterns of generalization induced by two different training conditions. Sixteen subjects participated in the third experiment. As in *experiment 2*, subjects trained at the left and the right and were then tested for transfer at the center. Subjects were divided into two groups. Subjects of *group E* learned the same force field at both locations; subjects of *group I* adapted to a different force field in each arm configuration (E and I refer to extrinsic and intrinsic, respectively). The force fields that were used are shown in Fig. 4, *A* and *B* (*boxes 1* and *2*). As in *experiments 1* and *2*, forces always acted parallel to the frontal plane, but this time each force field was divided into two subfields: for four movement directions the forces were to the right—$\alpha = +20\ \mathrm{N \cdot s \cdot m^{-1}}$—whereas for the other directions, the hand was pushed left—$\alpha = -20\ \mathrm{N \cdot s \cdot m^{-1}}$. All subjects were tested at the center with the same field (Fig. 4*C*). The organization of the experimental sessions was the same as in *experiment 2* except that during the familiarization phase (1st day) "force-field catch trials" were introduced to assess the effect of the field before any learning.

Data analysis

Hand positions were sampled at 200 Hz, low-pass Butterworth filtered at 20 Hz, and numerically differentiated. Because the fields had perturbing effects that differed depending on the direction of the movement, we used three distinct measures of kinematic error: the initial angular deviation (IAD), the path length (PL), and the tangential velocity variation (TV). The initial angular deviation was defined as the angular distance between the vector from the center to the target and the vector from the center to the position of the hand at peak tangential velocity (Sainburg et al. 1999). The length of the hand path in Cartesian space was computed, after re-sampling the position curves to 101 time points, as $\Sigma\, ds_i$, where $ds_i = \sqrt{[(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2]}$, with the index over time $i = 1, \ldots, 100$. To compute variation in the velocity profile, we compared the tangential velocity curves observed in the transfer tests, tv_o, with a tangential velocity template tv_t obtained, for each subject, by averaging the tangential velocity curves (re-sampled to 101 points) of the last five cycles of the familiarization phase—while no forces were applied by the robot; specifically: $\Sigma\, (tv_{oi} - tv_{ti})^2$, with the index over time $i = 1, \ldots, 101$. The start and end of movement were defined by 5 or 10% of maximum tangential velocity depending of the error index that was computed; 5% was used for the positional indices, and 10% was used for the velocity profile index.

SAS GLM and MIXED procedures were used to run multi- and univariate repeated measures analyses of variance. Training condition (E vs. I), order of training, and initial movement direction in the transfer test were between subjects factors, and movement direction, workspace location, and sets of trials (initial and final training and transfer) were within subject variables. For post hoc comparisons, *P* values were compared with α levels adjusted by using a Bonferroni-Holm sequential procedure. In the following, main effects and interactions that are not reported were not significant at $\alpha = 0.05$.

Predicted patterns of generalization in experiment 2

This study tests whether transfer will be observed if subjects are given multiple exposures (in different locations) to force fields that are constant in direction in extrinsic coordinates. Transfer of learning is predicted by both extrinsic and intrinsic coding hypotheses (see Fig. 3). If the nervous system "switches" to an extrinsic system of reference to encode the direction of the force field, subjects should expect the same force field at the center as at the sides. Under the hypothesis of intrinsic coding, subjects would expect a specific pattern of torque—rather than a specific force field. The expected pattern of torques is found by considering the correspondence between forces and torques. For each configuration—left, right, and center—Fig. 3*A* illustrates the forces that are associated with the different center-out movements. Figure 3*B* gives the torques associated with shoulder and elbow displacement for the same set of movements. In this figure, a joint path that involves primarily elbow flexion is highlighted. When we zoom in on this movement (below), it may be seen that the torques associated with this joint path act primarily about the shoulder at the left, whereas at the right the torques are more equally distributed to both joints. At the center the torque vectors have an intermediate orientation. The exact relationship between torques at the left, right and center is as follows.

In general, for a force field in which no forces are applied along the *y*-Cartesian axis, that is $f_y = 0$, the torques at the shoulder and at the elbow are $\tau_1 = -l_1 \sin\theta_1 - l_2 \sin(\theta_1 + \theta_2) f_x$ and $\tau_2 = l_1 \cos\theta_1 + l_2 \cos(\theta_1 + \theta_2) f_x$, respectively. If we set $f_x = 1$, and define θ_1 and θ_2 as joint angles for movements at the right, we then have at the right

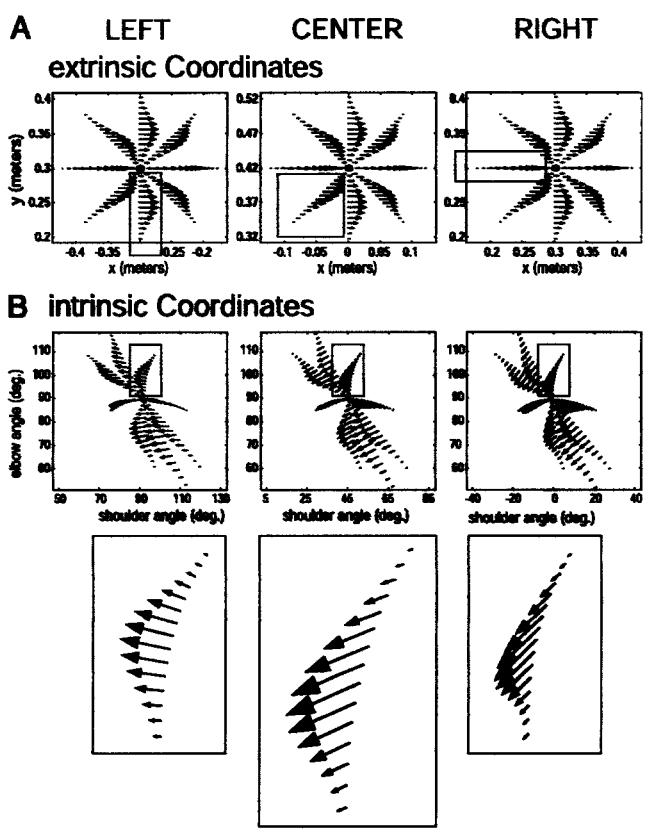

FIG. 3. While the force field is identical at the left, right, and center, the pattern of torque changes with the configuration of the arm. The figure shows motion paths and associated forces and torques at the left, right, and center. *A*: hand positions and associated forces in Cartesian space for movements with straight hand paths and bell-shaped velocity profiles. *B*: corresponding patterns of torque associated with joint rotations, represented in joint space. Note that joint paths that are identical in the different arm configurations correspond to different hand paths in each location of the workspace (highlighted in *A* and *B*).

$$\tau_{R1} = -l_1 \sin\theta_1 - l_2 \sin(\theta_1 + \theta_2)$$

$$\tau_{R2} = l_1 \cos\theta_1 + l_2 \cos(\theta_1 + \theta_2)$$

at the left

$$\tau_{L1} = -l_1 \sin(\theta_1 + \pi/2) - l_2 \sin(\theta_1 + \pi/2 + \theta_2) = -l_1 \cos\theta_1 - l_2 \cos(\theta_1 + \theta_2)$$

$$\tau_{L2} = l_1 \cos(\theta_1 + \pi/2) + l_2 \cos(\theta_1 + \pi/2 + \theta_2) = -l_1 \sin\theta_1 - l_2 \sin(\theta_1 + \theta_2)$$

and at the center

$$\tau_{C1} = -l_1 \sin(\theta_1 + \pi/4) - l_2 \sin(\theta_1 + \pi/4 + \theta_2)$$

$$= -l_1[\sin\theta_1 \cos\pi/4 + \cos\theta_1 \sin\pi/4] - l_2[\sin(\theta_1 + \theta_2)\cos\pi/4 + \cos(\theta_1 + \theta_2)\sin\pi/4]$$

$$= \sqrt{2/2}\{-l_1[\sin\theta_1 + \cos\theta_1] - l_2[\sin(\theta_1 + \theta_2) + \cos(\theta_1 + \theta_2)]\}$$

$$\tau_{C2} = l_1 \cos(\theta_1 + \pi/4) + l_2 \cos(\theta_1 + \pi/4 + \theta_2)$$

$$= l_1[\cos\theta_1 \cos\pi/4 - \sin\theta_1 \sin\pi/4] + l_2[\cos(\theta_1 + \theta_2)\cos\pi/4 - \sin(\theta_1 + \theta_2)\sin\pi/4]$$

$$= \sqrt{2/2}\{l_1[\cos\theta_1 - \sin\theta_1] + l_2[\cos(\theta_1 + \theta_2) - \sin(\theta_1 + \theta_2)]\}$$

By substitution and reordering, we have: $\tau_{C1} = \sqrt{2/2}(\tau_{R1} + \tau_{L1})$ and $\tau_{C2} = \sqrt{2/2}(\tau_{R2} + \tau_{L2})$; that is, the torque vector at the center is $T_C = \sqrt{2/2}(T_R + T_L)$.

Thus on the assumption that dynamics learning and generalization occur in intrinsic coordinates, one would predict that subjects who learn two distinct torque fields, at the left and the right, would perform well in a transfer test at the center because they would be expecting a pattern of torques intermediate to those experienced during training.

Patterns of generalization permit a dissociation of extrinsic versus intrinsic coding in experiment 3

Figure 4, *A* and *B*, shows the force fields (*1* and *2*) that were used to train subjects in *groups E* and *I*, respectively. *Boxes 3* and *4* give the associated patterns of torques. Learning in extrinsic versus intrinsic coordinates should result in different patterns of transfer. If learning occurs in extrinsic coordinates, subjects of *group E* (Fig. 4*A*) should be well prepared for the transfer test at the center because the force field at the left (*box 1*) and the right (*box 2*) are identical to that in the center (box in Fig. 4*C*). With extrinsic coding, subjects of *group I* (Fig. 4*B*) would be expected to perform well for movement directions 3, 4, 7, and 8 in which the forces have same orientation at both training locations (*boxes 1* and *2*). For the other directions—1, 2, 5, and 6—little transfer to the intermediate position would be expected.

To understand the predictions for intrinsic coding, one has to consider the representations in joint space. In Fig. 4, *A* and *B*, *3* and *4* show the torque fields at the left and at the right, respectively. The pattern of torques that subjects might expect at the center can be found

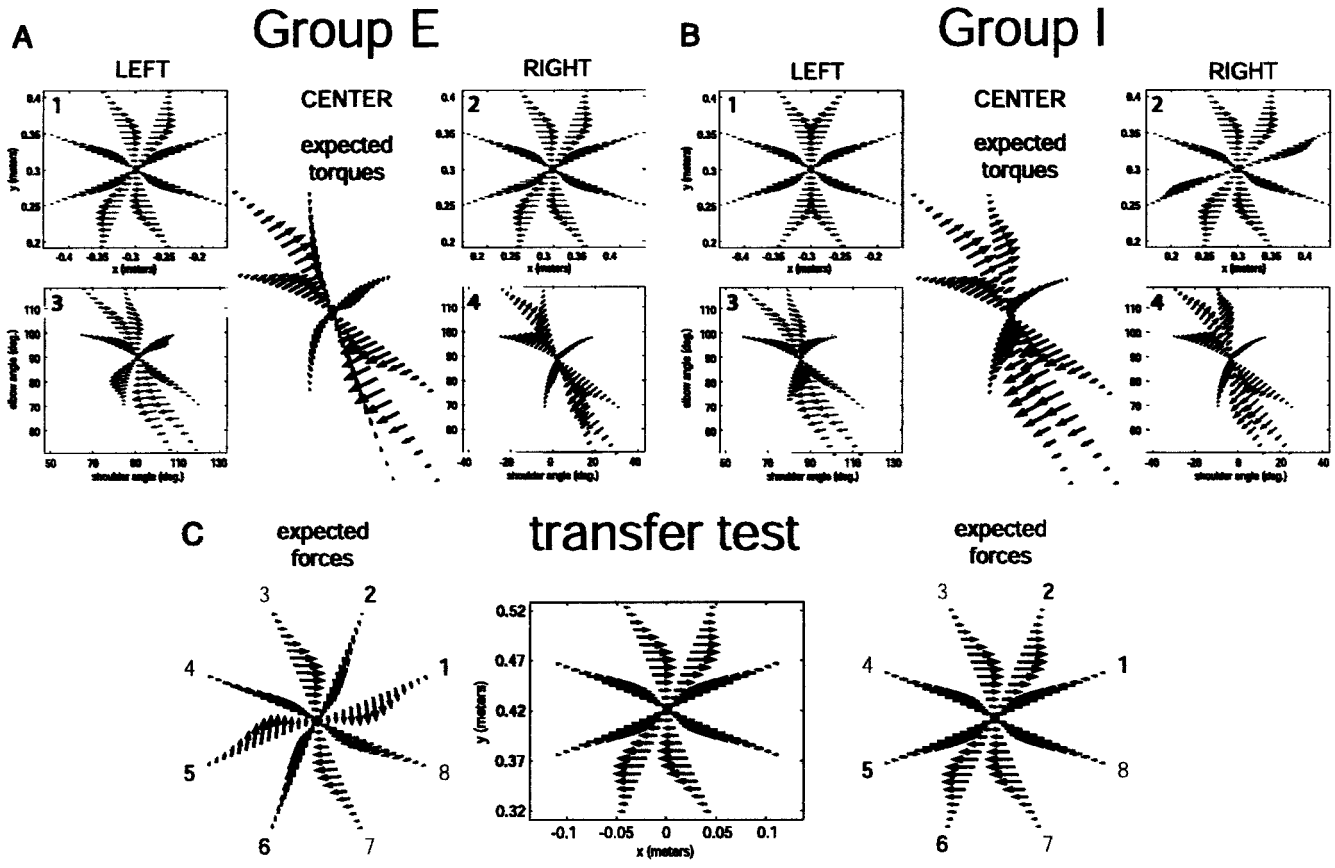

FIG. 4. Subjects were divided into 2 groups: *groups E* and *I*. All subjects were tested for transfer of learning at the center of the workspace. In all panels, conditions that were actually experienced by the subjects are plotted in boxes, whereas the plots labeled "expected" forces and torques were not actually experienced but correspond to patterns predicted on the assumption that learning occurred in intrinsic coordinates. *Boxes 1* and *2* present the patterns of forces applied at the hand. *Boxes 3* and *4* show the associated patterns of joint torque. *A*: subjects of *group E* learned the same force field at the left (*1*) and the right (*2*). *B*: subjects of *group I* adapted to different force fields at the left (*1*) and the right (*2*). *C*: the box shows the force field used for the transfer test at the center.

as in the preceding text. The "expected torques" can be converted into "expected forces." These are shown in Fig. 4*C* for both training conditions. One can see that, for *group I*, expected forces at the center (Fig. 4*C*, *right*) are identical to the force field that is actually used in the transfer test. Thus if adaptation and generalization occur in intrinsic coordinates, good performance would be expected in all directions. In contrast, for *group E*, the conversion of expected torques to expected forces (Fig. 4*C*, *left*) gives a pattern that is similar to the transfer test for directions 3, 4, 7, and 8 but different for directions 1, 2, 5, and 6.

In summary, if learning occurs in extrinsic coordinates, subjects of *group E* should do better on the transfer test whereas if learning occurs in intrinsic coordinates, subjects of *group I* should do better.

Simulation of experiment 3

We tested the idea that generalization involves an interpolation between control signals by comparing empirical data from *experiment 3* with simulated patterns of generalization. We simulated center-out movements (12 cm in length and 500 ms in duration) that were performed under the same conditions as in *experiment 3*. For the simulations, we used a model of two-joint planar arm movement in which the control signals are based on the λ version of the equilibrium-point hypothesis (Feldman 1986; Feldman et al. 1990). According to the model, muscle force depends on the difference between muscles' actual length and centrally specified threshold lengths λ for motoneuron activation as well as on length- and velocity-dependent afferent feedback and reflex delays. Continuous time-varying shifts in joint equilibrium angles produce the simulated movements. Force-field learning was simulated as an iterative procedure that consists of trial-by-trial adjustments to the values of individual muscles λs on the basis of the difference between desired kinematics and actual joint displacements (see Gribble and Ostry 2000 for a detailed description of the learning algorithm).

Six muscle groups were modeled: single-joint elbow and shoulder flexors and extensors (biceps long head and triceps lateral head and pectoralis and deltoid), and a double-joint flexor and extensor (biceps short head and triceps long head). Musculo-skeletal geometry was estimated from anatomic sources (An et al. 1981, 1989; Winters and Woo 1990). Muscle-force-generating ability varied with estimates of physiological cross-sectional area (Winters and Woo 1990). Equations of motion relating accelerations to joint torques were obtained using Lagrangian methods (Hollerbach and Flash 1982). The muscle model was a variant of that described by Zajac (1989); it included activation and contraction dynamics and passive muscle stiffness. For each muscle, it also included modeled neural inputs (λs), length- and velocity-dependent afferent feedback, and reflex delays. The model also included an independent co-contraction command for changes in impedance at a given position or during movement (see Gribble et al. 1998 for details).

Preliminary simulations were run in the absence of external forces with the arm model positioned at the left and the right. This generated modeled control signals that compensated for the mechanical behavior of the limb under no-load conditions and for each movement direction resulted in a vector of modeled muscle commands (λs) that yielded straight-line movements in the absence of load.

The arm model then learned the force field at the left or the right of the workspace. We used as an initial motor command the time-varying vector of λs that resulted from "null field" training. After each simulated movement, the vector of λs was updated in proportion to the difference between desired and actual muscle lengths. This procedure resulted in a set of modified λ vectors that produced adapted movements in the presence of load.

This was followed by a second training session at the opposite location. The second training started using the final values of commands from the other side of the workspace. In other words, we assumed that new learning starts by using the λ vectors appropriate to the most recent training. A set of adaptation trials was then undertaken in which, once again, the vector of motor commands was updated in proportion to the error in λ (muscle command) coordinates. We produced simulated movements in the center of the workspace by using the vector average of the two sets of commands that produced adapted movement at the left and at the right, respectively.

In all simulations, we used a co-contraction command of 35 N for the simulation of movements made in the absence of force and a co-contraction level of 40 N for the training trials. As in Gribble et al. (1998), the cocontraction command was initially defined in force space and hence has units in Newton. A corresponding vector in λ space that resulted in this change in muscle force was computed and served as the actual cocontraction command. It should be noted that commands of this magnitude produce empirically observed values for stiffness during multi-joint movement (Gribble et al. 1998). We found that 15 iterations were sufficient to produce adapted movement for all directions in all force fields and workspace locations.

Figure 5 illustrates the adaptation and interpolation procedures using actual conditions from *experiment 3*. Figure 5, *A–C*, shows simulated movements at the right, left, and center, where in all cases forces move the hand to the left. Simulated hand path (dots) and corresponding joint displacements (solid lines) are shown together with joint equilibrium trajectories (dashed lines). In Fig. 5, *A* and *B*, the hand path in gray corresponds to the first simulated movement performed in the field and the trace in black shows the last adapted training trial. In the joint displacement graphs, solid lines show the simulated shoulder and elbow trajectories for the last training trial. The dashed lines show the joint equilibrium angles corresponding to the time varying λ vector that produce this adapted movement. The hand path in Fig. 5*C* corresponds to the first trial in the field at the center using as a command the average of λ vectors generated by iterations at the right and the left. Note that we use the vector average on the assumption that the command is computed on the basis of afferent information about the configuration of the limb, which in this case, based on the shoulder angle, lies midway between the left and right configurations.

RESULTS

Experiment 1

In this experiment, we asked if subjects who trained at one side of the workspace would do better in a transfer test at the other side, than subjects who were in the field for the first time. Two groups of subjects trained at the left (*group L*) or the right (*group R*) and were then tested for transfer at the opposite side. To assess transfer, we compared performance of subjects of *group L* in the transfer test at the right with the performance of subjects of *group R* at the start of training at the right. A similar comparison was carried out for subjects who trained at the right and were then tested for transfer at the left.

Figure 6 shows hand paths for all subjects. The *top row* shows subjects in *group L*, the *bottom row* is for *group R*. Hand paths are shown for the first and the last trials of the training phase and for the first trials of the transfer test. One sees that all subjects performed poorly on initial exposure to the field. By the end of training, hand paths become fairly straight. It can be seen that subjects of *group L* did not perform substantially better in the transfer test at the right (Fig. 6*C*) than subjects of *group R* at the beginning of training (*D*). Subjects of *group R* showed some benefit in the transfer test at the left as a result of their previous experience with the field; their hand paths were in general less perturbed during the transfer test (*F*) than those produced by the subjects of *group L* (*A*).

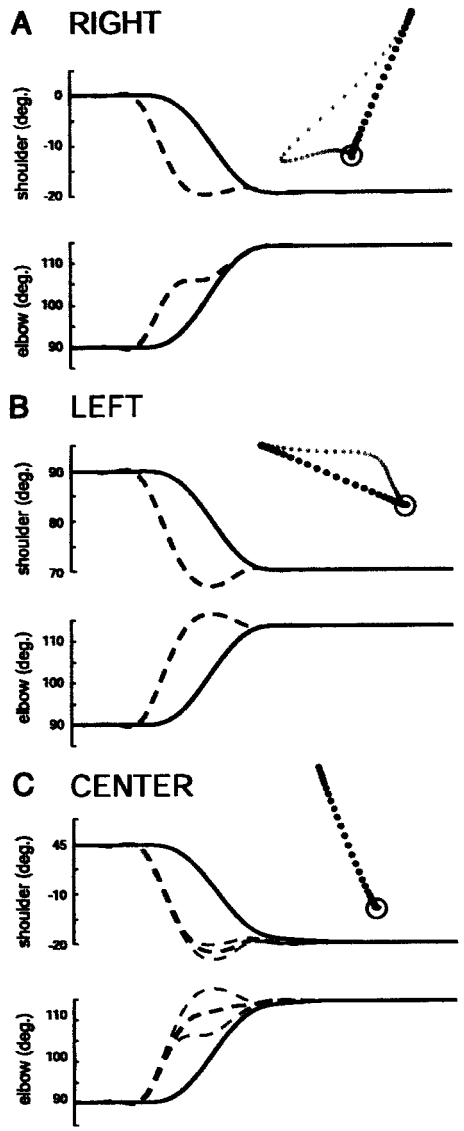

FIG. 5. *A–C*: simulated movements involving the same joint displacements at the right, left, and center. In all cases, forces push the hand to the left. Simulated hand paths in Cartesian space (dots) and corresponding joint displacements (solid line) are shown along with joint equilibrium trajectories (dashed line). *A* and *B*: the hand path in gray corresponds to the 1st simulated movement performed in the field and the trace in black shows the last adapted training trial. In the joint displacement graphs, the solid lines show the "actual" shoulder and elbow trajectories for the last training trial. The dashed lines show the joint equilibrium angles that produce this last adapted movement. *C*: the hand path corresponds to the 1st trial performed in the field at the center using as a command the average of the "adapted" λ vectors from right and the left. In the joint displacement graphs, the equilibrium joint trajectories are shown as dark dashed lines. The corresponding equilibrium trajectories from the right and the left are translated by 45 and −45° and shown with lighter dashed lines.

For statistical analysis, we computed means for the first and last three training cycles and for the first three transfer cycles. We obtained global error indices by averaging over directions. Figure 7, *A–C*, shows the means (±SE) across subjects for the three measures: initial angular deviation (IAD), length of the path (PL) and variation in the tangential velocity profile (TV), respectively; □ are for *group L*, ▨ are for *group R*.

We ran three separate repeated-measures ANOVAS (univariate) with training condition (left vs. right) and initial movement direction as between subjects factors and trials (initial, final, transfer) as a within-subjects factor. For all three error measures, a significant main effect of trials was observed [$F(2,12) = 20.85$, $P < 0.001$; $F(2,12) = 12.57$, $P < 0.01$; $F(2,12) = 29.21$, $P < 0.0001$, for IAD, PL, and TV, respectively]. Significant, or close to significant, interactions between training conditions and trials were also observed [$F(2,12) = 4.28$, $P < 0.05$; $F(2,12) = 3.35$, $P < 0.07$; and $F(2,12) = 8.78$, $P < 0.01$, for IAD, PL, and TV].

Post hoc comparisons revealed a significant effect of learning. For all three measures of kinematic error, initial training trials were more perturbed than final ones ($P < 0.01$). The force field was found to have comparable effects at initial exposure on path lengths and velocity profiles at both locations ($P > 0.05$ for both). However, the field induced larger initial angular deviation at the right than at the left ($P < 0.01$). Accordingly we assessed transfer of learning separately for each group. We show this set of contrasts with square brackets in Fig. 7. For subjects of *group R*, velocity profiles in the transfer test at the left were less perturbed than those of *group L* at the beginning of training ($P < 0.01$). However, initial angular deviations and path lengths were comparable for the two groups ($P > 0.05$ for both). For *group L*, initial angular deviation in the transfer test was less than in the initial training trials of *group R* ($P < 0.05$). There were no differences in path lengths or velocity profiles ($P > 0.05$ in both cases).

Experiment 2

Four subjects trained at the left and the right and were then tested for transfer in the center. In Fig. 8*A*, hand paths for individual trials are plotted for two subjects who trained first at the left. Figure 8*B* shows trials for two other subjects who trained first at the right. Both panels show the first and last training trials and the first transfer trials at the center.

Performance at the start of the transfer test was comparable to that at the end of training. This was quantified by computing a global index of positional error by averaging over the eight movement directions. The excellent transfer that was observed is illustrated in Fig. 9, which shows values of IAD for the first and the last 10 training cycles along with means for the 10

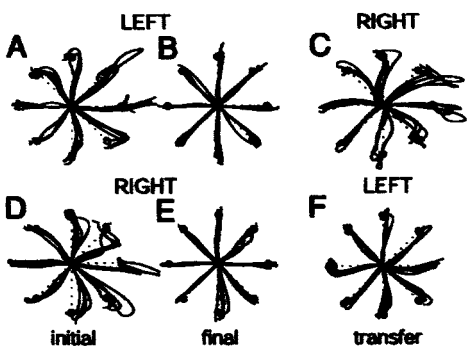

FIG. 6. Hand paths for individual trials by all subjects in *experiment 1*. *Top*: data for subjects who learned the field at the left and were tested for transfer at the right (*group L*). *Bottom*: subjects who trained at the right and tested at the left (*group R*).

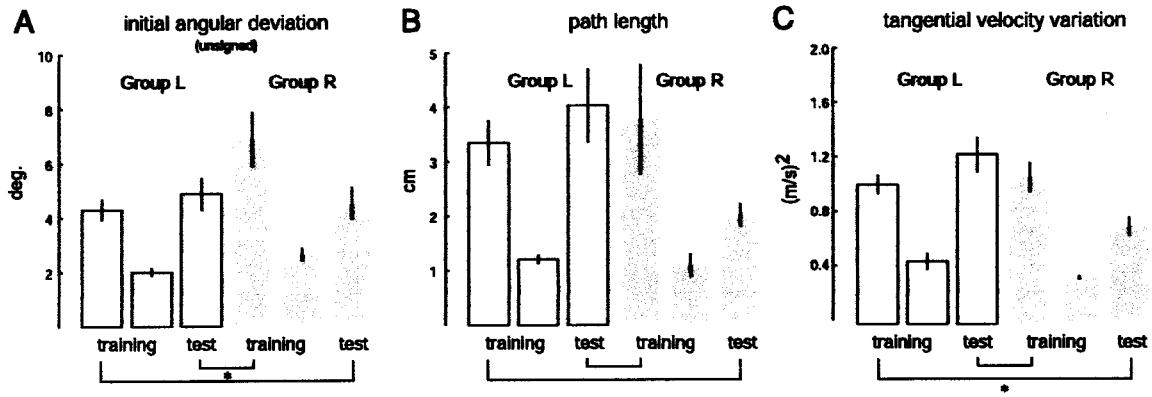

FIG. 7. *Experiment 1* means (±SE) across subjects for the 3 measures of kinematic error: *A*: initial angular deviation (IAD); *B*: path length (PL); and *C*: variation in the tangential velocity profile (TV). The bars are the means for the 1st and last 3 training trials, and the 1st 3 transfer trials. □, subjects who trained at the left and were tested for transfer at the right (*group L*). ▨, subjects who trained at the right and tested at the left (*group R*). Significant differences are indicated by * $\alpha = 0.05$. For path length, the difference between the actual path length and the distance from the center to the target (12 cm) is shown.

transfer cycles. One sees that the curve that corresponds to the transfer test overlaps those for the last training cycles. For statistical tests, we averaged over the first and last three training cycles and over the first three transfer cycles in each direction. For each epoch (early and late training at the left and right and transfer test), we then obtained three global indices of performance, corresponding to the IAD, PL, and TV.

We ran three separate repeated-measures ANOVAs (univariate) that included order of training (1st training at the left vs. 1st training at the right) and initial movement direction as between subjects factors. For all three error indices, a significant main effect of cycles (initial, final, transfer) was observed [$F(4,12) = 16.29$, $P < 0.0001$; $F(4,12) = 15.69$, $P < 0.001$; $F(4,12) = 17.75$, $P < 0.0001$, for IAD, PL, and TV, respectively]. Regardless of the order of training, movements in the transfer trials were less perturbed than those in the initial training trials ($P < 0.01$ for IAD, PL, and TV). Performance in the transfer trials and in the last training trials was comparable ($P > 0.5$ for IAD, PL, and TV, at both locations).

Experiment 3

We compared actual patterns of generalization with those predicted by the intrinsic and extrinsic coding hypotheses. Separate subjects were trained in two different conditions (Fig. 4, *A* and *B*). In both, subjects trained at the left and the right and were then tested for transfer at the center (Fig. 4*C*). Figures 10*A* and 11*A* show initial training trials for subjects of *groups E* and *I*, respectively. Subjects that trained at the left on day 1 (*A*) trained at the right on day 2 (*D*). Subjects that trained at the right on day 1 (*B*) trained at the left on day 2 (*C*).

Figure 12 shows individual trials at the center of the workspace. Hand paths for *group E* are in gray and *group I* is in black. The plot at the *left* shows "force-field catch trials" for all subjects in the familiarization phase of the experiment. Figure 12*A*, *right*, shows the performance of each group in the transfer test. It may be seen that subjects of *group I* produced relatively straight hand paths in all eight movement directions. In contrast, subjects of *group E* had hand paths that deviated substantially in some directions, in particular in directions 2 and 6. As explained in the METHODS, subjects of *group E* would not expect this pattern of torques on the assumption of intrinsic coding.

Figure 13 presents mean values (±SE) over the first three transfer trials using the different measures of kinematic error—IAD, LP, and VT. MANOVAs were run for each movement direction separately with experimental condition (*E* vs. *I*), order of training (left first vs. right first) and initial movement direction as between subjects factors. Because there were no reliable effects of training order or initial movement direction, we report here results from MANOVAs run with experimental condition as the only between subjects variable. We found that the effect of the experimental condition was significant for directions 1, 2, 5, 6, and 7 [$F(3,12) = 18.06$, $P < 0.0001$; $F(3,12) = 31.75$, $P < 0.0001$; $F(3,12) = 9.25$, $P < 0.01$;

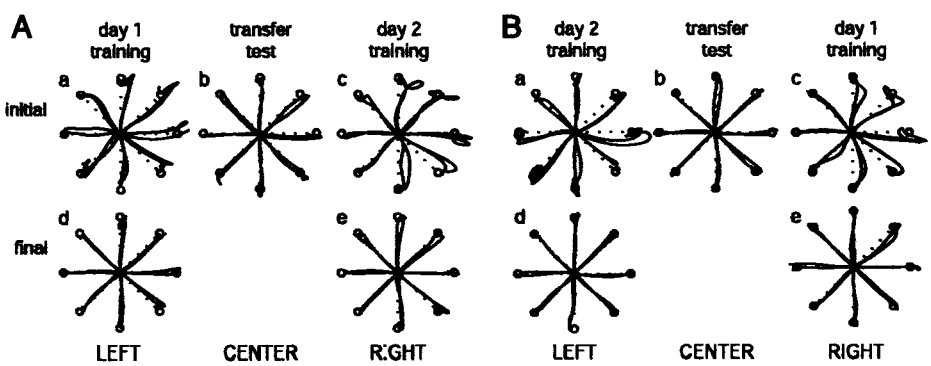

FIG. 8. Hand paths for the 1st and last training trials, and the 1st transfer trials by subjects in *experiment 2*. *A*: hand paths for subjects who trained at the left on day 1 and at the right on day 2. *B*: trials by subjects who trained at the right on day 1 and on the left on day 2.

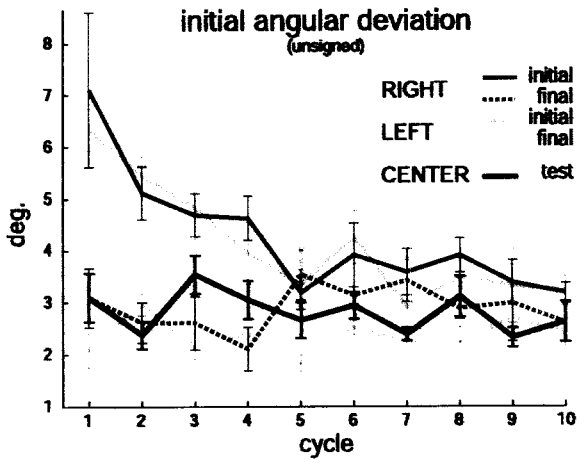

FIG. 9. Means (±SE) across subjects in *experiment 2* for initial and final training cycles at the left and the right, and the transfer test at the center. For each cycle the plot shows the means of the absolute value of the initial angular deviation averaged over movement directions.

$F(3,12) = 9.83$, $P < 0.01$; and $F(3,12) = 5.79$, $P < 0.05$] and not reliable for directions 3, 4, and 8 [$F(3,12) = 1.97$, $P > 0.05$; $F(3,12) = 2.87$, $P > 0.05$; and $F(3,12) = 0.30$, $P > 0.05$].

Complementary information was provided by univariate analyses. Specifically, movements in direction 1 were more deviated for subjects of *group I* than for subjects of *group* E[$F(1,14) = 32.92$, $P < 0.0001$], but the latter had smoother velocity profiles [$F(1,14) = 11.03$, $P < 0.01$]. Path lengths were comparable for the two groups [$F(1,14) = 1.58$, $P > 0.05$]. One should note that the orientation of the deviations was opposite to the field. Thus these deviations might correspond to over-compensations. For direction 2, reliable or near to reliable differences were observed for all three error indices [$F(1,14) = 43.89$, $P < 0.0001$; $F(1,14) = 4.18$, $P < 0.07$; $F(1,14) = 10.82$, $P < 0.01$, for IAD, PL, and TV, respectively]; this was also the case for movements in direction 6 [$F(1,14) = 29.52$, $P < 0.0001$; $F(1,14) = 22.08$, $P < 0.001$; $F(1,14) = 6.91$, $P < 0.5$, for IAD, PL, and TV]. For direction 5, differences between groups were reliable only for velocity profiles [$F(1,14) = 30.57$, $P < 0.0001$]. Transfer trials were comparable in terms of angular deviation [$F(1,14) = 2.83$, $P > 0.05$] and path lengths [$F(1,14) = 0.83$, $P > 0.05$]. For direction 7, subjects of *group I* were less deviated than those of *group E* [$F(1,14) = 11.55$, $P < 0.01$], but the two groups had comparable path lengths [$F(1,14) = 4.13$, $P > 0.05$] and velocity profiles [$F(1,14) = 0.01$, $P > 0.05$]. Note that angular deviations were again opposite to the direction of the force field.

In summary, quantitative tests of differences between the performance of subjects in *groups E* and *I* indicate (with the exception of IAD for direction 1, in which overcompensation was observed) reliably worse performance in transfer tests trials for *group E* subjects in directions 1, 2, 5, and 6. The specific pattern of generalization is in agreement with the predictions for transfer of dynamics learning based on intrinsic coding of information.

Simulation of experiment 3

We used a model of two-joint planar arm movement to test the feasibility of interpolation between patterns of local learning as a means to achieve generalization. Figures 10*B* and 11*B* show the predicted patterns for training trials at the left and the right. Simulation results for subjects that train first at the left are shown in *a* (day 1) and *d* (day 2). The simulated results when training starts at the right are given in *b* (day 1) and *c* (day 2).

In contrast to *a* and *b*, which show the performance of a "naïve model" on initial exposure to the force-field, the patterns of hand path deviations in *c* and *d* correspond to the first trials performed by a "trained model" using as initial motor commands those generated by training at the opposite location. The patterns in the simulations correspond quite closely to those observed empirically.

As in *experiment 3*, we assessed, prior to training, the effect of the force field that would be used for the transfer test at the center. In the simulations, we used as command signals at the center the λ vectors resulting from iterations under "null field" conditions. It may be seen in Fig. 12*B* that when these signals

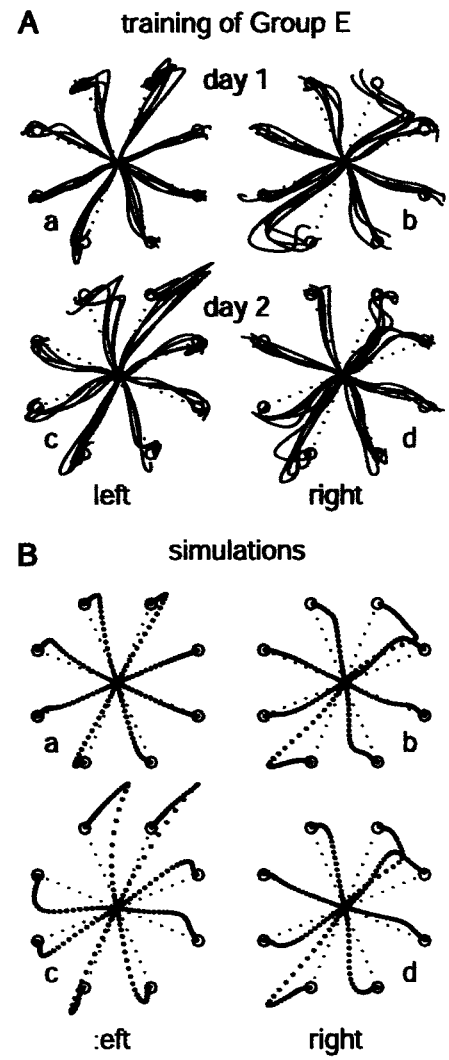

FIG. 10. *A*: hand paths at the start of training by subjects of *group E*. *a* and *d*: trials by subjects who trained at the left on day 1 and at the right on day 2. *b* and *c*: for subjects who trained at the right on day 1 and at the left on day 2. *B*: simulated hand paths obtained in force-field learning conditions analogous to those experienced by subjects of *group E*.

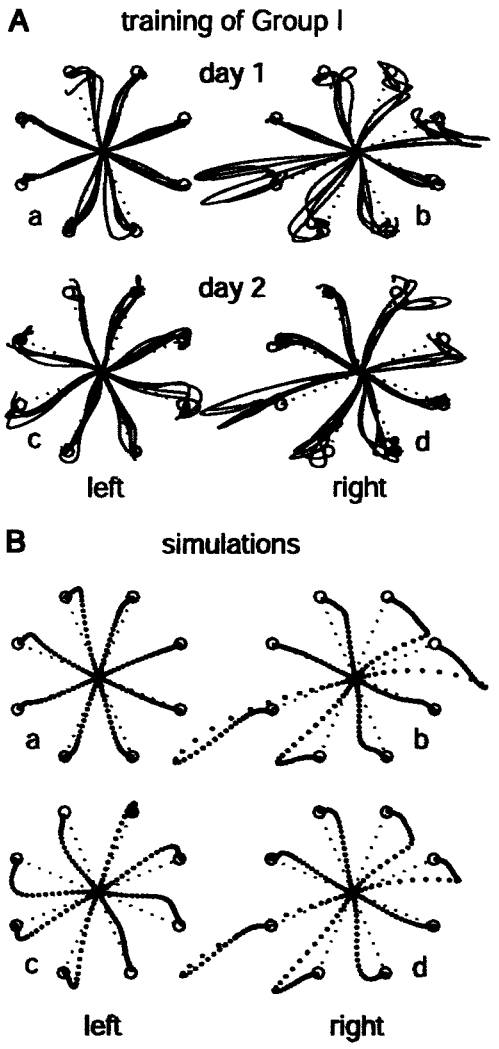

FIG. 11. *A*: initial training trials by subjects of *group I*. *a* and *d*: hand paths by subjects who trained at the left on day 1 and at the right on day 2. *b* and *c*: show subjects who trained at the right on day 1 and at the left on day 2. *B*: corresponding simulated trials.

were used in conjunction with the load applied in the transfer test at the center, the simulated hand paths correspond to those observed experimentally in the prelearning force field catch trials.

For simulation of transfer trials, we averaged the two sets of commands used to produce adapted movement at the left and at the right, respectively. The resulting performance of the model is shown in Fig. 12*B*.

DISCUSSION

Studies of intralimb transfer of learning have provided evidence that information about dynamics is encoded in an intrinsic system of coordinates by showing that generalization depends on similarity in torques in different limb configurations (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994). In the present study, we have examined how generalization occurs when the pattern of torques varies with the configuration of the limb.

In *experiments 1* and *2*, we probed the generality of intrinsic coding by using a viscous force field the direction of which was fixed relative to an external coordinate frame. We tested the possibility that in the absence of invariance in the pattern of torques, the nervous system might generalize on the basis of invariance in the direction of forces and use an extrinsic system of coordinates to capture this property. In fact, we found no evidence that supported this idea.

In *experiment 3*, we designed two different training conditions to distinguish between dynamics learning in intrinsic versus extrinsic coordinates. One training condition (*group E*) was supposed to lead to a good performance in a transfer test at the center of the workspace if forces were encoded in extrinsic coordinates. If dynamics are learned in an intrinsic reference frame, subjects in the other condition (*group I*) were supposed to do well in the transfer test. The patterns of generalization that we predicted, under the intrinsic coding hypothesis, were based on a straightforward idea. Because the movements performed at the left and at the right involved similar joint displacements and differed only in the initial shoulder angle (elbow angles were identical), we assumed that subjects would establish a mapping between the control signals associated with different shoulder angles and different patterns of torque. On this basis, we hypothesized that subjects would expect an intermediate pattern of torques to be associated with an intermediate shoulder angle. The results of *experiment 3* were consistent with these predictions.

We compared the empirical data with simulated patterns of generalization. For the simulations, we used a model of two-joint planar arm movement in which the control signals were based on the λ version of the equilibrium-point hypothesis (Feldman 1986; Gribble and Ostry 2000). The learning process was simulated as a trial-by-trial updating of commands based on the difference between desired and actual positions. Under these conditions, transfer of learning could be predicted on the basis an interpolation between control signals that were adapted to the torques in different training configurations.

The simulations provide a physiological underpinning to the empirical observations. The experimental results show that the information subjects gain about torques at the sides of the workspace (and in turn about the torques they have to apply) can be combined to predict the required torques at the center. However, the torques are outputs and are separated from neural inputs by muscle properties, reflexes, and limb dynamics. The simulations suggest that the proposed approach to interpolation would work at the level of the underlying control. Generalization in motor learning may thus be based simply on an interpolation between locally adapted λ vectors.

The simulation results were strikingly similar to the patterns observed empirically. The postulated process of adaptation was applied first to the untrained limb and was used to generate a straight movement in the absence of load. This initial adaptation is akin to compensating for the dynamics of the limb and results in a pattern of day 1 performance in the force field that closely matches that observed empirically in all movement directions (Figs. 10 and 11, *a* and *b*). The postulated adjustment of control signals also accounts well for the pattern of transfer observed in *c* and *d* of Figs. 10 and 11 on day 2 of the experiment. In this case, the "adapted" control signals at the end of day 1 learning were used as initial commands at the other side of the workspace.

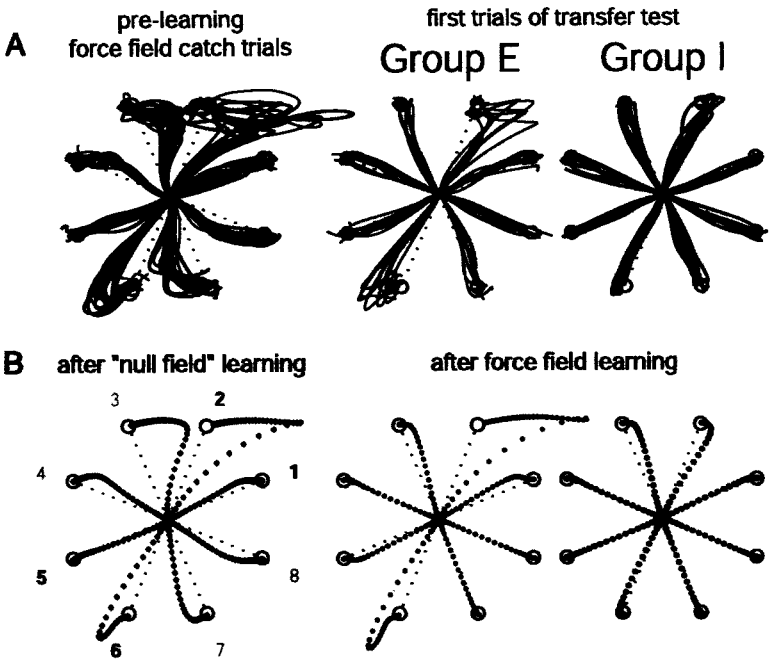

FIG. 12. *A*: hand paths for individual trials in *experiment 3*. *Top left*: force-field catch trials from the familiarization phase. *Group I* is black, *group E* is gray. *Right*: the 1st transfer trial by each subject of *group I* (black traces) and *group E* (gray traces), respectively. *B*: simulated hand paths in *experiment 3*.

The idea that generalization involves the combination of control signals associated with instances of local learning accounts for both the observed transfer of learning and for its specificity (Fig. 12). Note that movement directions that showed positive transfer were separated from those showing considerable interference by as little as 45°. This is consistent with previous results showing learning in the motor system is spatially local (Gandolfo et al. 1996; Sainburg et al. 1999; Witney and Wolpert 2003).

The ability to learn and retain the properties of several different environments has been offered as evidence of a modular structure to motor learning (Doya et al. 2002; Flanagan et al. 1999; Ghahramani and Wolpert 1997; Haruno et al. 2001; Karniel and Mussa-Ivaldi 2002; Kawato 1999; Wolpert and Kawato 1998; Wolpert et al. 1998). As an example, Ghahramani and Wolpert (1997) examined adaptation to opposite visual perturbations that were applied during movements from two different starting locations. They presented evidence consistent with the idea that subjects that learned the two mappings generalized to intermediate starting positions by an interpolation process. According to the authors the motor system uses two distinct visuomotor "expert modules" and interpolates to intermediate starting locations by using a weighted average of the two experts outputs. By this account, the configuration of the limb stands as a contextual cue that indicates which of the expert modules should intervene.

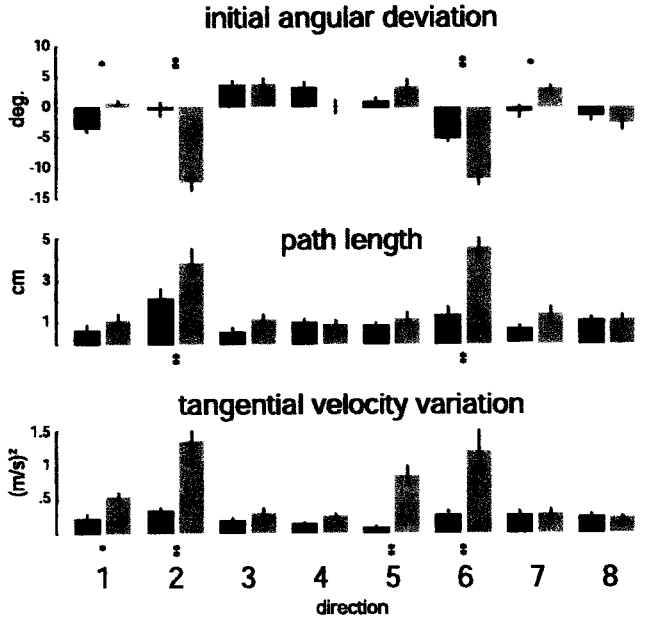

FIG. 13. Means (±SE) across subjects for transfer of learning in *experiment* 3. The means are based on the 1st 3 transfer trials. ■, *group I*; ▨, *group E*.

Gandolfo et al. (1996) have shown that subjects can learn curl fields of opposite orientation if they use different limb configurations. If the limb configuration is fixed, subjects have difficulty learning opposing fields based on visual or somatosensory information alone. These investigators suggest that, in contrast to arbitrary cues, "distinct postures allow the CNS to represent different perturbations as a single field, eliminating prediction ambiguity;" that is, the different arm configurations are an integral part of a unique complex sensorimotor mapping and not "merely" cues associated with different simpler mappings. The present formulation is consistent with this approach.

Hwang et al. (2003) report experimental results that also fit with this view. In particular, they found that learning three distinct force patterns simultaneously was more or less difficult depending on the starting locations with which the patterns were paired. Specifically, large distances between the starting positions facilitated learning, and subjects adapted more easily to a "linear" mapping such as when starting locations ordered from left to right were paired with a counterclockwise, null and clockwise force field. Learning is more difficult with a "non-

linear" mapping that does not respect any ordered location/field matching. This shows that learning can vary in difficulty even though the same number of "experts" is required in each case. Moreover, consistent with Shadmehr and colleagues' position, Gribble and Scott (2002) found that during force-field adaptation neurons in primary motor cortex that were dependent on the movement of one joint also responded continuously to the motion of the other joint; this is in agreement with the idea of a unique controller rather than multiple separate experts.

The design of *experiment 3* was based on previous results that have shown steep gradients of generalization associated with changes in movement direction (Gandolfo et al. 1996; Sainburg et al. 1999; Thoroughman and Shadmehr 2000). Indeed, in predicting, for the two training conditions, patterns of generalization that were selectively similar and dissimilar for different movement directions, we assumed that the nervous system could precisely combine the control signals associated with distinct patterns of torques. Hwang et al. (2003) propose a model in which neural elements simultaneously encode movement direction and limb configuration. The smooth gradient of generalization observed for arm configuration is reconciled with the narrow tuning to movement direction under the hypothesis of "a linear or monotonic encoding of limb position space [. . .] multiplicatively modulated by an encoding of movement direction." Note that our formulation differs from that of Hwang et al. (2003) in terms of the putative mechanism of neural control. In our model, learning proceeds by incremental adjustment of neural commands that are associated with a position based controller. In the Hwang et al. approach, the presumed controller relies on torque specification that is based on position and velocity. The present results show that generalization of dynamics learning is readily accommodated within an equilibrium point formulation.

Our results are consistent with the idea that the nervous system can use information about shoulder angle to interpolate between two learned torque fields. However, they provide no information about the shape of the weighting function that underlies this interpolation process. In our case, the transfer location was equidistant in terms of shoulder angle from two widely separated arm configurations, and subjects performed the same number of trials at each training location. Manipulating the distance between the different locations in parallel with the amount of training could be a first step toward the description of the weighting function. It would also be informative to assess extrapolation of this function beyond the part of the workspace delimited by the training locations, taking as a starting point the data from *experiments 1* and *2* on transfer across the two extreme locations of the workspace.

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