Exp Brain Res (2006) 170: 227–237
DOI 10.1007/s00221-005-0204-x

RESEARCH ARTICLE

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Transfer and durability of acquired patterns of human arm stiffness

Received: 1 February 2005 / Accepted: 22 August 2005 / Published online: 19 November 2005

Abstract Previous studies have shown that the nervous system can produce anticipatory adjustments that alter the mechanical behavior of the arm in order to resist environmental disturbances. In the present paper, we focus on the ability of subjects to transfer acquired stiffness patterns to other parts of the workspace and on the durability of stiffness adaptations. To explore the transfer of stiffness control, subjects were trained at the left of the workspace to resist the effects of a single-axis disturbance that was applied by a robotic device. Following training, they were tested for transfer at the right. One group of subjects experienced similar torques at the left and right of the workspace, whereas the other group of subjects experienced similar forces at the hand. Following the initial training at the left, the observed orientation of the hand-stiffness ellipse rotated in the direction of the disturbance. In tests at the right, transfer was observed only when the direction of disturbance resulted in torques that were similar to those experienced during training. The results thus suggest that under the conditions of this experiment stiffness control is acquired and transfers in a joint- or muscle-based system of coordinates. A second experiment assessed the durability of an acquired stiffness pattern. Subjects were trained on 2 consecutive days to resist a single-axis disturbance. On a third day, the direction of the disturbance was switched by 90°. Substantial interference with the new adaptation was observed. This suggests that stiffness training results in durable changes to the neural signals that underlie stiffness control.

Keywords Arm movement · Motor learning · Coordinate system · Adaptation

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Introduction

Stable mechanical interaction of the human arm with the changing environment is a necessity of daily life. The achievement of stability is aided by modifications to the mechanical behavior of the neuromuscular periphery through changes in neural input and the adjustment of limb geometry, an idea known as impedance control (Hogan 1985; Milner 2002). Consistent with this idea, changes in human arm stiffness—the resistance to imposed displacements—mirror the effects of external loads. The evidence that changes in stiffness reflect the effects of loads has been obtained under static conditions (McIntyre et al. 1996; Gomi and Osu 1998; Perreault et al. 2002; Darainy et al. 2004) as well as during movement (Burdet et al. 2001; Franklin et al. 2003; Osu et al. 2003). During movement, changes in stiffness rather closely match changes in external load, so, for example, the orientation of the maximum stiffness at the hand has been found to realign to correspond to the direction of the perturbation or environmental disturbance (Burdet et al. 2001). Stiffness control under static conditions is less complete in the sense that voluntary changes to the orientation of the hand-stiffness ellipse are typically <30° (Gomi and Osu 1998; Perreault et al. 2002; Darainy et al. 2004). A number of basic characteristics of stiffness control are as yet unexplored. Do acquired patterns of stiffness generalize to new arm configurations, and if so, what is the system of coordinates in which stiffness training is represented? Are changes to neural signals that accompany changes in stiffness sufficiently durable that they persist in behaviors that take place well beyond the time of initial training?

There is considerable evidence that dynamics learning takes place in an intrinsic, joint- or muscle-based system of coordinates (Ghez et al. 2000; Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Moussavi 2000; Malfait et al. 2002). Although one might expect the same of stiffness control, stiffness change is typically required for stability in interactions with objects and thus it would also seem reasonable that stiffness regulation might occur in extrinsic coordinates (Criscimagna-Hemminger et al. 2003; Malfait and Ostry 2004). Here we explored whether subjects could transfer stiffness training to other parts of the workspace and also the specific pattern of generalization as a means to identify the coordinate system in which the adaptation occurs. We report a variant of a procedure used previously in the context of adaptation to new dynamics (Ghez et al. 2000; Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Moussavi 2000; Malfait et al. 2002). We trained subjects at the left of the workspace to maintain limb position in opposition to single-axis mechanical disturbances. Following training, transfer was assessed at the right using disturbances that were similar in terms of the forces involved or similar in terms of torques. We demonstrate that subjects transfer stiffness adaptations to a new workspace location when the torques at the shoulder and elbow are similar to those experienced during training. The pattern of transfer in this study is thus consistent with the idea that the nervous system controls stiffness in intrinsic coordinates.

In a second study, we evaluated the durability of stiffness training. In work on adaptation to new dynamics, it has been shown that learning may persist for days or even months (Shadmehr and Brashers-Krug 1997). Here we trained subjects to maintain the position of the limb in opposition to an environmental disturbance that acted along a single axis. One day later, we changed the axis of the disturbance by 90°. Following this sudden change in the direction, it took almost 200 trials for the orientation of the stiffness ellipse to get back to that observed under null-field conditions. Thus, the original stiffness training substantially affected the acquisition of a new stiffness strategy 1 day later. The present results point to durable changes in the neural underpinnings of stiffness as a consequence of training.

Materials and methods

Experimental setup

Thirty-six right-handed subjects, between the ages of 19 and 30, participated in the study. Twelve subjects participated in Experiment 1 (transfer of stiffness training) and eight subjects participated in Experiment 2 (durability of the acquired stiffness pattern). A further 16 subjects participated in control studies for Experiments 1 and 2. Subjects had no history of sensory or motor dysfunction and had no previous experience in studies involving a robotic device. All procedures were approved by the McGill University Research Ethics Board.

The subjects were seated and held the handle of a two degree-of-freedom planar robotic arm (Interactive Motion, Cambridge, MA). Position signals were obtained with 16-bit encoders (Gurley Precision Instruments). Forces were recorded with a force-torque sensor (ATI Industrial Automation) that was mounted above the handle of the manipulandum. Shoulder movement was restricted by a harness and the wrist was braced (see Fig. 1). The subject's right arm was supported against gravity by an air sled. A computer monitor placed in

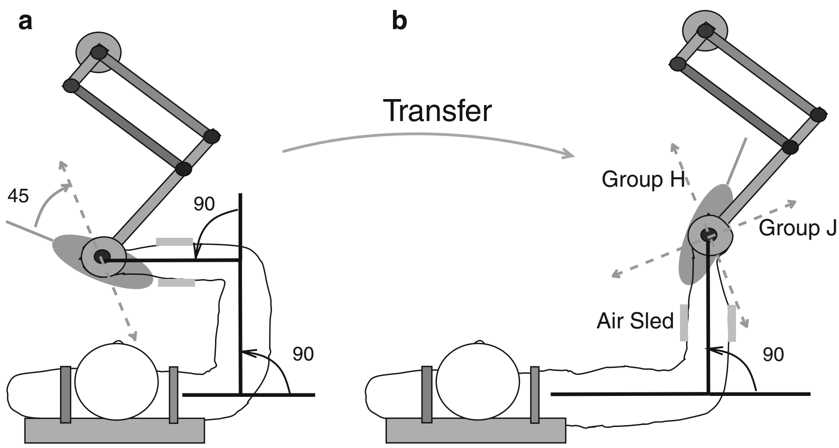

Fig. 1 a Experimental setup and subjects' arm configurations for both Experiments 1 and 2. In Experiment 1, subjects were trained for nine blocks at the left of the workspace and then a transfer test was carried out for three more blocks at the right. All subjects were first trained at the left to resist a force that was applied at −45° relative to the major axis of the null-field stiffness ellipse. For Group J, the direction of force application at the right was rotated by the amount of shoulder rotation and therefore the applied torque to the subject's arm was the same at the left and the right of the workspace. For Group H, the direction of force application at the right was the same as that at the left and was thus unchanged between training and transfer tests in an extrinsic coordinate system. In Experiment 2, subjects were tested at the left of the workspace on each of 3 consecutive days. Direction of force application for the first 2 days was −45° relative to the major axis of the null-field stiffness ellipse. On the third day, the axis of force application was rotated unexpectedly by 90°

front of the subject displayed a 20 mm red circle that represented the target location and a 15 mm yellow circle that specified the position of the hand. Full visual feedback of the subject's arm was provided.

Experiment 1

The experiment had four phases that were completed in a single day. The first phase, which was conducted prior to training, involved the estimation of stiffness under null-field conditions at the left of the workspace. In the second or training phase, the subjects were asked to maintain a hand position at the left in the presence of single-axis force pulses that were interleaved with displacements used for purposes of stiffness estimation. In phase three, transfer of training was assessed at the right of the workspace in response to perturbations that were applied either along the same axis as in the training phase or perpendicular to it. Finally, stiffness was estimated under null-field conditions in the new arm configuration.

Estimation of stiffness under null-field conditions

Subjects were placed in a standard position relative to the robot such that the angles at the elbow and shoulder were 90° (relative to the frontal plane) and the shoulder was abducted to 85° (Fig. 1a). The null-field task consisted of stiffness estimation in the absence of any other manipulation. Subjects were asked to place their hand in the middle of the target zone and not to resist the action of the robot.

To estimate stiffness, we used trapezoidal position servo control similar to that described by Gomi and Osu (1998). The hand was displaced to each of eight equally spaced directions about a circle, and measures of displacement and restoring force were obtained. The displacements were in random order; the stiffness of the manipulandum was 4,000 N/m during position servo control. During servo displacements, the visual feedback of endpoint position was frozen on the monitor. The position servo ramped on and off over 100 ms, the hold time was 200 ms and the commanded amplitude was 6 mm (the mean actual displacement was 5.6 mm). Prior to each displacement, the subject's hand had to be within the target zone and the hand velocity had to be less than 1 mm/s. Once these conditions were satisfied, a measurement was initiated at a randomly selected time between 1.5 and 2.5 s. Position and force data from the 100 ms preceding the measurement displacement and from the final 100 ms of the hold phase were used for purposes of estimating stiffness.

Training session

The training configuration was the same as that used to measure stiffness in null-field conditions at the left of the workspace (Fig. 1a). The task involved the application of single-axis force pulses. The axis of force application was at −45° relative to the direction of maximum null-field stiffness and was chosen on a per subject basis. (We used this angle because it provided us with two directions of load application, for the transfer test that followed, that were equidistant from the major axis of the null-field ellipse). Subjects were instructed to maintain the position of the limb in the middle of the target. The total time that the hand of the subject was outside of the target was displayed as feedback after each block of trials. Subjects were asked to try to reduce this value as much as possible while avoiding excessive cocontraction in order to reduce the likelihood of fatigue.

The timing of the force pulses and their direction on the perturbation axis was unpredictable. The magnitude of each force pulse was 3 N with 300 ms duration. The force pulses were applied at a random interval of between 0.5 and 1.5 s.

In the training session, subjects completed nine blocks of 40 perturbations (force pulses) each. To estimate stiffness during the training session, servo-controlled position displacements, similar to those used in the null-field condition, were interspersed randomly within each block of training trials. On average, one trial in five was a measurement displacement. Stiffness matrices were estimated based on data pooled over each three blocks. For each subject three estimates of stiffness were obtained during the training phase of the experiment.

To guard against the possibility that subjects intervened voluntarily during the hold phase of the displacement that was used for stiffness measurement, we dropped from analysis all trials in which the maximum variability of velocity exceeded 4 mm/s. This resulted in the elimination of $< 2\%$ of measurement trials. In the data that were used for analysis, we assessed during the measurement interval the maximum change in hand position, velocity and restoring force, averaged over subjects, experimental conditions and limb displacement directions. The average maximum was 0.15 mm for position change, 2 mm/s for velocity change and 0.21 N for force change. Moreover, the restoring force was effectively constant as of the end of the ramp up phase of the measurement displacement at 100 ms into the measurement interval. The mean value of restoring force was 3.76 N for the first 100 ms of hold phase and 3.89 N for the last 100 ms. In other words, variation in force ended well in advance of the interval usually associated with voluntary reaction time and remained essentially constant throughout the measurement interval. Taken together, the absence of position or force change suggests that there was little if any voluntary intervention following the displacement of the limb.

Transfer test

After completion of the training session at the left side of the workspace, subjects were tested for transfer at the right (Fig. 1b). In the transfer configuration the shoulder angle was 0° (relative to the frontal plane) and the elbow angle was 90°. To avoid any differences due to the configuration dependence of robot inertia, we held the robot configuration constant and moved the subjects.

Subjects were assigned randomly to two different groups. For one group (Group H), the direction of force application at the right was the same in extrinsic coordinates as in the training session at the left and therefore the applied torque to the subject's arm was different (H designates similarity in training and transfer conditions of the direction of forces at the hand). For the second group, the direction of force application at the right was rotated by the amount of shoulder rotation and therefore the applied torque to the subject's arm was the same at the left and the right of the workspace (Group J, where J designates similarity of joint torques). In the transfer test, three blocks of trials similar to those in the training session were completed, that is, with measurement displacements interleaved among force pulses. Stiffness matrices were calculated based on the data in the first block of trials after the change of arm configuration. Following the transfer trials, null-field stiffness was measured in the new arm configuration.

Based on the results of Darainy et al. (2004), it was expected that the orientation of the stiffness ellipse at the left would rotate in a clockwise direction (relative to the null field), toward the axis of the imposed disturbance. If this training transferred to the right in extrinsic coordinates, then subjects in Group H should show transfer—that is, a clockwise change in the orientation of the ellipse at the left should be matched, at the right, by a counterclockwise change in orientation, that is, by a rotation in the direction of perturbation in Cartesian coordinates (see Fig. 1). On the other hand, if training transferred in intrinsic coordinates, then Group J subjects should show transfer. In this case, the ellipse at the right should be rotated about 90° clockwise relative to that observed at the left since it is in this orientation that applied torques in the training and test configurations are equated.

Experiment 2

The experiment was carried out over 3 consecutive days with the arm positioned at the left of the workspace throughout. Each day began with the estimation of null-field stiffness following the same procedure as in Experiment 1. This was followed by nine blocks of training trials, also identical to those in Experiment 1, in which subjects were trained to resist single-axis disturbances that were interspersed with displacements that were used to estimate stiffness. On Days 1 and 2, the direction of the disturbance was at −45° relative to the major axis of the null-field ellipse as measured on Day 1. On Day 3, stiffness was assessed in response to a new direction of force application, perpendicular to the original one, in the same arm configuration. As in Experiment 1, the timing and orientation of force application were unpredictable. The magnitude of the force pulses was 3 N and the duration was 300 ms. Similarly, position servo-controlled displacements were randomly interspersed for purposes of stiffness estimation, again with an average frequency of one measurement displacement for every five force pulses.

Data analysis

Hand positions and endpoint forces were sampled at 200 Hz and low-pass filtered at 20 Hz (second-order, zero-lag Butterworth filter). Hand positions were numerically differentiated to produce velocity estimates. The relationship between imposed displacements and resulting forces can be written as:

$$\begin{bmatrix} \mathrm{d}f_x \\ \mathrm{d}f_y \end{bmatrix} = \begin{bmatrix} K_{xx} & K_{xy} \\ K_{yx} & K_{yy} \end{bmatrix} \begin{bmatrix} \mathrm{d}x \\ \mathrm{d}y \end{bmatrix} \quad (1)$$

The hand-stiffness matrix K was obtained using the data from three sets of displacements and associated restoring forces in each of eight randomized directions (24 observations in total). In the transfer test in Experiment 1, the estimates of stiffness were based on data from a single block of trials. Differences in the mean value of position between the 100-ms interval prior to the perturbation and the 100-ms interval at the end of the hold phase gave values for $\mathrm{d}x$ and $\mathrm{d}y$. Mean restoring force estimates during the same intervals provided values for $\mathrm{d}fx$ and $\mathrm{d}fy$. Linear regression was used to estimate the hand-stiffness matrix.

Adaptation was also assessed using a joint stiffness measure. The joint-based analysis was carried out to guard against the possibility that the observed patterns of transfer were merely related to the geometry of the limb which influences the hand level measure. The relation between imposed angular displacement and shoulder and elbow torque can be expressed as:

$$\begin{bmatrix} \mathrm{d}\tau_s \\ \mathrm{d}\tau_e \end{bmatrix} = \begin{bmatrix} R_{ss} & R_{se} \\ R_{es} & R_{ee} \end{bmatrix} \begin{bmatrix} \mathrm{d}\theta_s \\ \mathrm{d}\theta_e \end{bmatrix} \quad (2)$$

The R matrix in Eq. 2 is the joint stiffness matrix. R_{ss} and R_{ee} are net shoulder and elbow stiffness relating joint torque to angular displacement while the off-diagonal elements, R_{se} and R_{es}, are measures of stiffness that relate torque at either the shoulder or the elbow to the angular displacement of the other joint. The relation between the joint stiffness matrix R and the hand-stiffness matrix K can be expressed as:

$$R = J^{\mathrm{T}} K J \quad (3)$$

The Jacobian matrix J can be calculated based upon upper-arm and forearm lengths (l_1 and l_2 respectively) and shoulder and elbow angles (θ_s and θ_e).

$$J = \begin{bmatrix} -(l_1 \sin\theta_s + l_2 \sin(\theta_s + \theta_e)) & -l_2 \sin(\theta_s + \theta_e) \\ l_1 \cos\theta_s + l_2 \cos(\theta_s + \theta_e) & l_2 \cos(\theta_s + \theta_e) \end{bmatrix} \quad (4)$$

Following Mussa-Ivaldi et al. (1985), the pattern of stiffness can be visualized as an ellipse in which the restoring force associated with unit displacement is shown for all directions in the horizontal plane. The major axis of the ellipse represents the direction of maximum stiffness while the minor axis is the direction of minimum stiffness. Singular value decomposition of the stiffness matrix provides values for the orientation, shape and size of the ellipse (Gomi and Osu 1998). In the results reported below, we give the mean orientation of the major axis of the stiffness ellipse averaged over subjects. We also report mean differences in orientation between the training and null-field conditions and also between the test conditions and associated null-field condition.

Results

Transfer of stiffness training

The aim of Experiment 1 was to determine whether stiffness adjustments can be transferred to a new arm configuration and if so, to determine the coordinate system for this transformation. The null-field stiffness matrix was estimated for all subjects. The mean orientation of the null-field stiffness ellipse at the hand was $157.0 \pm 9.2°$ relative to the frontal plane at the left of the workspace and $65.6 \pm 7.9°$ at the right. The axis of force pulse application in the training phase of the experiment was $-45°$ relative to the major axis of each subject's null-field stiffness ellipse.

Figure 2a shows typical results for two subjects, one from Group J and the other from Group H, for the training at the left and transfer at the right. Both subjects were trained for nine blocks at the left. It may be seen that in both cases the orientation of the stiffness ellipse at the end of training (in black) rotates toward the axis of force application (null-field ellipse is shown in gray). Following training, both subjects were tested for transfer at the right. For the subject in Group J, the direction of force application rotated with the shoulder such that the applied torque to the arm remained unchanged. For the subject in Group H, the direction of force application remained unchanged in Cartesian coordinates and consequently the direction of torque application was different at the left and the right. Under these conditions, when the Group J subject was tested for transfer at the right, the magnitude and direction of rotation of the stiffness ellipse (in black) was approximately the same as that observed at the left. In contrast, when the Group H subject was tested at the right, little transfer of training was observed.

Figure 2b shows results for the same subjects in joint coordinates. The pattern is similar to that observed at the hand. That is, at the left of the workspace, counterclockwise rotation of the stiffness ellipse is observed relative to the null-field ellipse. In the transfer test at the right, the magnitude and direction of orientation change for the subject in Group J are similar to those observed at the left, whereas for the Group H subject, the ellipse orientation is similar to that observed under null-field conditions.

Figure 3 shows the mean value and one standard error of stiffness orientation change (relative to the null-field orientation) as well as time outside the target zone. In each case, the data are shown for the three successive stiffness estimates at the left and the transfer test at the right. Statistical tests were conducted using repeated-measures ANOVA. Bonferroni-Holm tests were used for post-hoc comparisons. Figure 3a shows the change in the stiffness ellipse orientation relative to null-field measurements at the level of the hand. A reliable

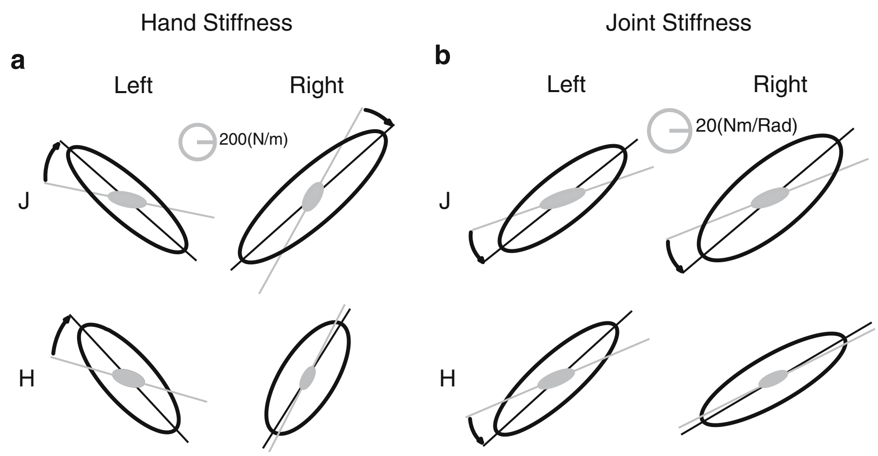

Fig. 2 Stiffness ellipses for two subjects, one labeled J in the *top row* (Group J) and the other labeled H in the *bottom row* (Group H). The ellipses show data for training at the left and transfer trials at the right of the workspace. The data for hand stiffness are shown in (**a**) and for joint stiffness in (**b**). In **b**, the horizontal axis gives values for the shoulder and the vertical axis gives values for the elbow. It may be seen that training at the left transfers to the right for J. For H the training at the left has no effect on the orientation of the stiffness ellipse at the right, relative to the null field

adaptation, that is, a change in orientation relative to null-field conditions, was observed for each of the three stiffness estimates at the left for Group H and Group J ($P < 0.01$). In each case, the stiffness ellipse rotated in the direction of force application. In the transfer test, the change in orientation of the stiffness ellipse for Group J, relative to the null-field ellipse at the right, was reliably different than zero ($P < 0.01$). In contrast, for Group H, the ellipse orientation was similar to that observed in the null field ($P > 0.05$). Pair-wise comparisons for Group J revealed no difference between any of the three estimates of stiffness orientation change at the left and the orientation change in the transfer test at the right (in each case $P > 0.05$). For Group H, there was a significant difference between each of the training estimates at the left and the value obtained in the transfer test ($P < 0.01$ for all three tests). The results thus show that the pattern of stiffness adaptation at the left transfers to a new arm configuration at the right when the torques applied to the subject's arm are unchanged; this is consistent with the idea that stiffness control is acquired in a joint- or muscle-based system of coordinates.

It may be noted that similar orientation estimates in the transfer test were obtained for all three blocks of transfer trials. For Group J, the mean orientation change of stiffness ellipse (relative to null field) for transfer blocks one through three was −16.3, −15.2 and −18.1°. For Group H, the comparable values for the three blocks were −2.0, −0.6 and −2.82°.

Figure 3b shows the same results expressed in joint coordinates. All estimates of stiffness orientation change during training at the left were significantly different than zero ($P < 0.01$ in all cases). In the transfer test at the right, the orientation change relative to the null-field ellipse for Group J was reliably different than zero ($P < 0.01$), whereas the value for Group H was not ($P > 0.05$). Post-hoc pair-wise comparisons show no difference in joint stiffness orientation change between any of the estimates during training at the left and that observed in the transfer test at the right for Group J ($P > 0.05$) and a significant difference for the same comparisons for Group H ($P < 0.02$ or better for each of the three comparisons). The results of the analysis in joint space are thus also consistent with the ability of

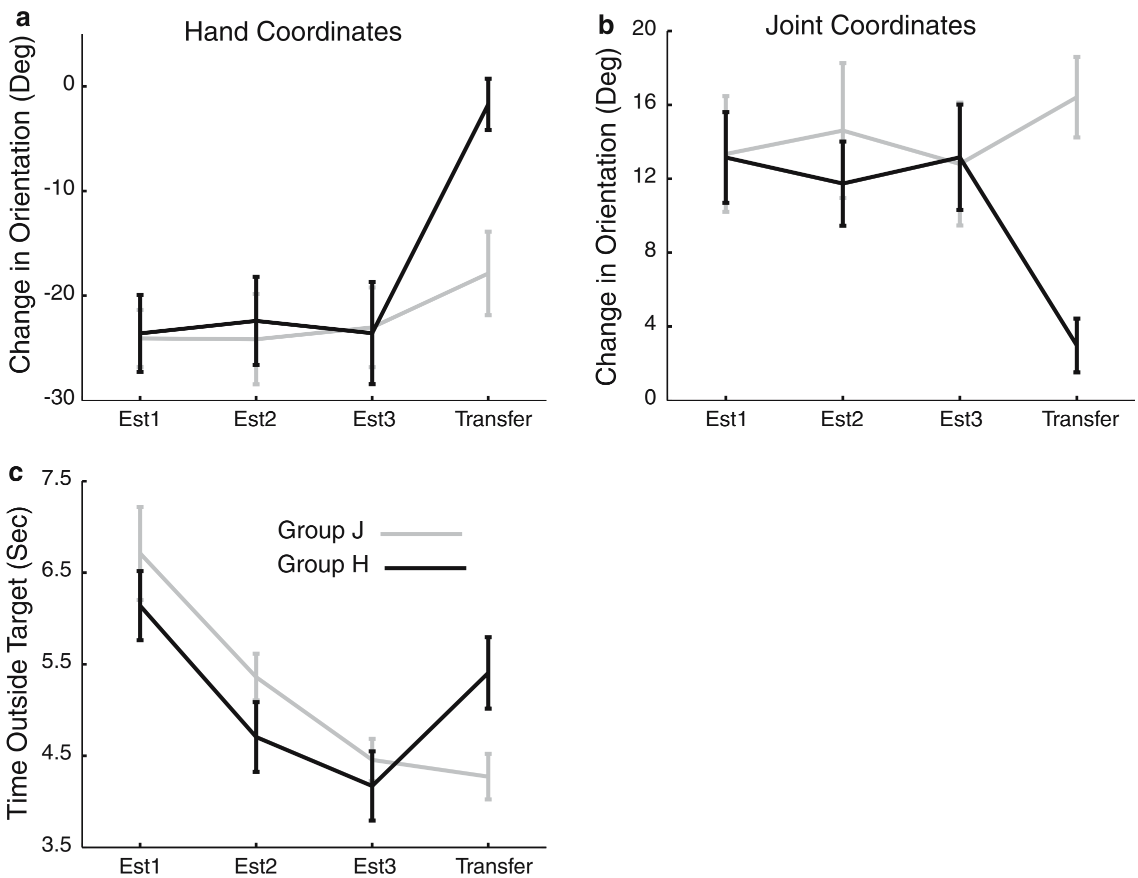

Fig. 3 Transfer of adaptation. **a** Mean and standard error over subjects of the change in orientation in hand coordinates of the major axis of the stiffness ellipse, relative to that observed in the null field. In the transfer test, the change in orientation for Group J is as large as in training session, indicating full transfer of adaptation. In contrast, the orientation observed in the transfer test for Group H is not different than that observed under null-field conditions. **b** Mean and standard error over subjects of change in orientation in joint coordinates. **c** Average change in performance over days as assessed by time outside of target. The performance of subjects in Group H declined during the transfer test at the right

subjects to transfer acquired stiffness patterns across workspace locations in intrinsic coordinates.

Differences in ellipse size and shape were assessed in both hand and joint coordinates in a manner that paralleled tests for differences in orientation. No significant differences were found in either the size or shape of the stiffness ellipse ($P > 0.05$ in all cases).

The total time that the subject's hand was outside of the target zone was calculated to assess performance during training and transfer trials (Fig. 3c). It may be seen that both groups performed better with practice as indicated by the fact that the time outside of the target zone is reliably less for the third stiffness estimate than the first ($P < 0.01$). Post-hoc pair-wise comparisons revealed no difference for Group J between time outside of target for the final estimate at the left and the transfer test at the right ($P > 0.05$), whereas for Group H time outside of target in the transfer test at the right was significantly greater than that observed for the final estimate of the training phase at the left ($P < 0.01$). Thus, while the change in workspace location had no effect on subject's performance in terms of time outside of target in the transfer test for Group J, the subject's performance for Group H declined.

In a control study at the right of the workspace, we verified that the hand-stiffness ellipse could have rotated in an counterclockwise direction had adaptation occurred in extrinsic coordinates. Eight new subjects were trained and tested at the right using a disturbance acting at +45° (counterclockwise) relative to the major axis of the null-field ellipse. The procedure was the same as that used in the training phase at the left. Under these conditions, the null-field ellipse orientation at the hand was 59.5 ± 6.8°. The ellipse orientation after training was 68.5 ± 10.8°, that is, 9° in a counterclockwise direction relative to the null-field orientation ($P < 0.02$). This indicates that subjects can change the orientation of the stiffness ellipse at the right of the workspace in a direction that would have been consistent with hand space adaptation.

In the present experiment, measurement displacements for purposes of stiffness estimation were delivered on average in one trial in five. Although it is desirable to take these measures infrequently, in the present context increases in measurement frequency will tend to act against the development of directional changes in stiffness since these displacements occur equally often in all directions. Since directional changes in stiffness are found with the present measurement procedure, it would seem that it provides a conservative estimate of the magnitude of the directional effect.

A number of methodological points require comment. We report estimates of the directional effect of disturbance inputs relative to the orientation of the hand stiffness under null-field conditions. Our earlier work suggests that the magnitude of the effect would be comparable relative to a uniformly cocontracted limb. Specifically, Darainy et al. (2004) report a comparison of hand-stiffness ellipse orientation under null-field conditions and under conditions in which subjects actively resist the effects of an isotropic load. Under conditions of active resistance, the size of the ellipse increased; however, orientation estimates were not reliably different than those observed under null-field conditions.

The magnitude of the measurement displacement (under 6 mm) was approximately half of the displacement that resulted from the disturbance input. In pilot work, we explored the possibility of using even larger disturbances. We decided against this possibility in part because subjects found the task under those conditions difficult and fatiguing and also because Perreault et al. (2002) have found that as force output level increases, there is a progressively reduced ability for subjects to modify the orientation of the hand-stiffness ellipse. The similarity of the magnitudes of disturbance inputs and measurements appears to have had little effect on the resulting estimates of stiffness orientation: Both Gomi and Osu (1998) and Perreault et al. (2002) report estimates of direction change comparable to those presented here using different techniques.

The perturbations used for stiffness estimation resulted in variation in both the actual displacement magnitudes and associated restoring forces. Table 1 gives mean values and standard deviations of displacement and restoring force during the intervals used for stiffness estimation for all eight directions tested in this

Table 1 Variability of limb displacement and restoring force

Direction	P_x (mm)	P_y (mm)	F_x (N)	F_y (N)
1	5.5 ± 0.41	0.5 ± 0.23	−3.7 ± 1.3	1.3 ± 0.6
2	4.2 ± 0.28	4.2 ± 0.25	−1.8 ± 0.7	−1.7 ± 0.6
3	0.4 ± 0.15	5.3 ± 0.45	1.3 ± 0.3	−4.2 ± 1.2
4	−3.5 ± 0.35	3.4 ± 0.35	3.9 ± 1.0	−3.8 ± 1.1
5	−5.5 ± 0.34	−0.5 ± 0.25	3.9 ± 1.1	−1.2 ± 0.6
6	−4.1 ± 0.23	−4.4 ± 0.27	2.1 ± 0.6	1.4 ± 0.8
7	−0.3 ± 0.14	−5.4 ± 0.43	−0.9 ± 0.4	3.9 ± 1.3
8	3.5 ± 0.37	−3.4 ± 0.42	−3.8 ± 1.1	3.8 ± 1.2

Mean and one standard deviation of limb displacement and restoring force in eight directions about a circle. Direction 1 is 0° (relative to frontal plane), direction 2 is 45°, direction 8 is 315°. The values shown are means based on the last three blocks of training trials, averaged over subjects study. The values shown are averaged over the last three blocks of training trials and over all 12 subjects. Note that while average magnitudes differed for the eight directions, the net displacement was in all cases between 5 and 6 mm.

Durability of stiffness adaptation

On each of 3 successive days, stiffness was first estimated under the null-field conditions. The mean value of the null-field stiffness ellipse orientation at the hand was $156.0 \pm 5.5°$; there were no reliable changes in orientation over days ($P > 0.05$).

A disturbance input (see Materials and methods) was applied on Days 1 and 2 at $-45°$ relative to the null-field orientation; on Day 3 the direction of the disturbance was switched to $+45°$. Figure 4a shows the pattern of hand-stiffness change for a single subject over the course of the 3-day experiment. It may be seen that over the first 2 days the orientation of the major axis of the stiffness ellipse rotated in the direction of force application. On Day 3, even at the end of the session, the stiffness ellipse still shows a residual effect of the original 2 days of stiffness training.

Figure 4b–d shows the mean values of stiffness-ellipse orientation, size change and time outside the target zone. Change in orientation of the stiffness ellipse is shown in

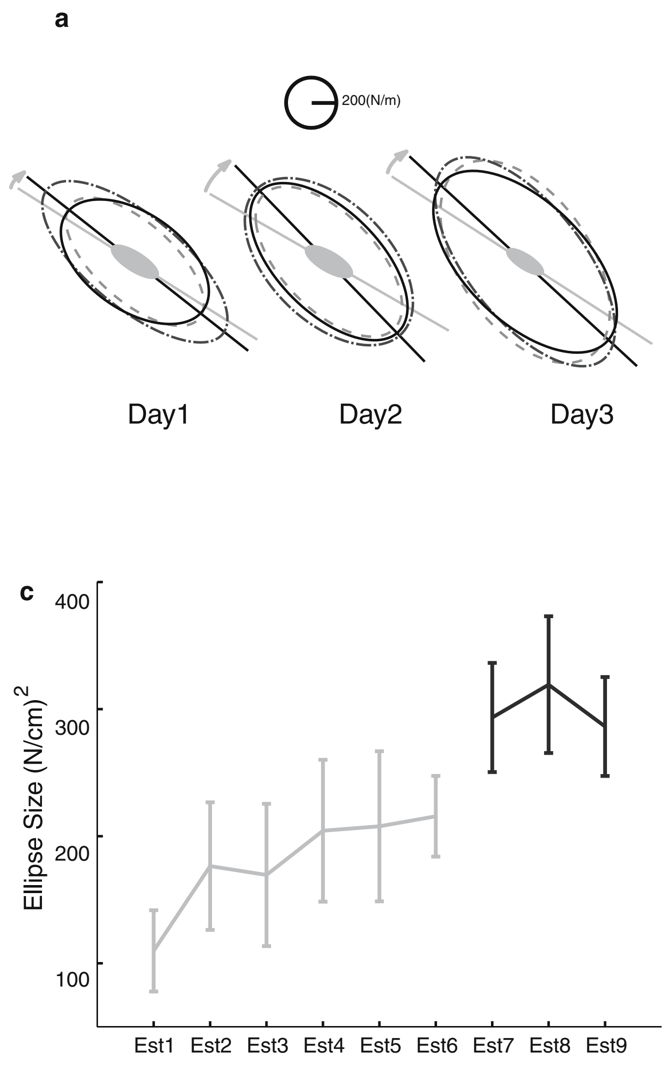

Fig. 4 Durability of adaptation. **a** The typical data of a single subject over the course of 3 days. The *gray* filled area shows the null-field stiffness ellipse at the hand; the *gray line* represents the major axis. The three hand-stiffness ellipses obtained on each day of experiment are shown with *dashes*, alternating *dots* and *dashes*, and as a *solid line*, respectively. For visualization purposes, a *line* is drawn through the major axis of the final ellipse of each day. It may be seen that during the first 2 days of the experiment, the ellipse rotates in the direction of the external disturbance. Twenty-four hours later, on the last day of the experiment, in spite of the change in the direction of force application, the orientation of the stiffness ellipse is similar to that of first 2 days. **b** Mean change in stiffness ellipse orientation (± 1 SE) relative to the null-field ellipse over the course of 2 training days and 1 test day. The first six estimates are obtained during training; the final three were obtained following the change in perturbation direction. **c** Mean area of the stiffness ellipse (± 1 SE). **d** Mean time outside of target (± 1 SE) over the three experimental sessions

Fig. 4b. The six estimates of orientation change obtained over the first 2 days of the experiment are shown in gray. The three estimates obtained after the change in the direction of the disturbance on Day 3 are shown in black. Repeated-measures ANOVA indicated reliable differences in orientation ($P < 0.01$). A post-hoc comparison of first six orientation estimates and the three obtained on the third day revealed a significant difference between two mean values ($P < 0.05$). However, the first two estimates of the stiffness orientation on Day 3 (that is after 192 trials with the new orientation) were not reliably different from the last estimate of stiffness orientation during training ($P > 0.05$ in both cases). The persistence of the effect of the initial adaptation even when the direction of disturbance is switched suggests that training results in quite durable changes in neural commands related to stiffness control.

In a second control study, we verified that disturbances comparable in direction to those used on Day 3, had they been tested alone, would have been sufficient to produce rotation of the stiffness ellipse beyond that observed in the null field toward the direction of the Day 3 perturbation. We tested eight additional subjects with perturbations acting along a lateral axis using a procedure and limb configuration that was the same as that used on Day 3 of the present study. Under these conditions, the null-field ellipse orientation at the hand was $159.7 \pm 6.5°$ and the orientation observed following training with a lateral perturbation was $170.7 \pm 7.1°$, that is 11° beyond that observed under null-field conditions ($P < 0.01$). The results thus indicate that, in the absence of prior training, a change in ellipse orientation toward the direction of the current perturbation would have been expected.

The size of the stiffness ellipse is shown in Fig. 4c. ANOVA indicated that the ellipse size differed over the course of the experiment ($P < 0.05$). The difference in ellipse size between the training sessions and that observed following the change in perturbation direction was marginally reliable by post-hoc comparison ($P = 0.06$). ANOVA also revealed reliable differences in the total time that the subject's hand was outside of the target zone ($P < 0.05$). In Fig. 4d, one can see a gradual improvement in the time outside of target over the course of the first 2 days and then a reliable increase in the time outside of the target when the direction of the disturbance is switched. The time outside the target in the first estimate on Day 3 was reliably greater according to post-hoc comparison than that obtained at the end of the second day of training ($P < 0.05$).

Discussion

We have focused on the pattern of generalization of stiffness control and the durability of stiffness adaptation. In a first experiment, in order to identify the coordinate system for stiffness control, we examined transfer across different limb configurations (Ghez et al. 2000; Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Moussavi 2000; Malfait et al. 2002). We trained subjects at the left of the workspace to resist displacement of the hand in opposition to single-axis disturbances. As a result of the training, the hand-stiffness ellipse was observed to rotate in the direction of the disturbance (Perreault et al. 2002; Gomi and Osu 1998; Darainy et al. 2004). Subjects were then tested for transfer of training at the right. We applied perturbations that were similar to those used during training trials either in direction in extrinsic Cartesian coordinates or in terms of the torques applied at the shoulder and elbow. We found transfer of the acquired stiffness patterns when torques in training and transfer trials were similar. The findings thus support the idea that under the conditions of this experiment stiffness control is acquired in an intrinsic, muscle- or joint-based system of coordinates.

The idea that we acquire patterns of arm stiffness in an intrinsic system of coordinates is consistent with the findings of studies of dynamics learning in which transfer is observed when the pattern of joint torques is similar in training and transfer configurations (Ghez et al. 2000; Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Moussavi 2000; Malfait et al. 2002). The findings fit with the general idea that impedance regulation and movement have a common basis in neural control. In simulation studies of generalization of dynamics learning, we have observed transfer in intrinsic coordinates (Malfait et al. 2005), using a model in which the control signals were based on the λ version of the equilibrium-point hypothesis (Gribble and Ostry 2000). Transfer of learning could be predicted on the basis of an interpolation between control signals that were adapted to the torques in different training configurations.

The fact that there is transfer between workspace positions merits comment. By design, the torques applied to the elbow and shoulder were similar in the two workspace locations. On the other hand, the lengths of elbow and shoulder muscles that resist the torques are configuration dependent. Nevertheless, it is reasonable to assume that the balance of torques was more or less unchanged in spite of these differences in limb configuration. Specifically, there have been numerous experimental demonstrations that the dependence of torque on joint angle is voluntarily reset in conjunction with changes in joint configuration (Asatryan and Feldman 1965). Thus, for example, a change in joint angle of some specified amount results in almost the same change in torque for different initial joint configurations. This would effectively leave the balance of torques unchanged with changes in the configuration of the limb. Indeed, this is consistent with the good transfer observed between the left and right of the workspace when the torques applied during training and test are equated.

The observed patterns of stiffness reflect the combined contribution of limb geometrical factors, passive tissue properties, active motor units and reflexes. Since the displacements that were used to measure stiffness were the same for all conditions, that is, in the null condition and for both directions of disturbance input, any observed change in stiffness is not likely to be due to either intrinsic muscle properties or to unmodified reflex responses. Rather, stiffness change is presumably central in nature, due either to the commands preceding movement that underlie muscle cocontraction, to altered reflex excitability or both. Our modeling studies suggest that stiffness patterns arise from both central and reflex effects (Gribble et al. 1998). Central commands that produce changes in cocontraction likewise alter the tonic stretch response. Both reflexes and central commands are reflected in measures of resistance to displacement. Changes in limb configuration also affect patterns of stiffness (Mussa-Ivaldi et al. 1985). However, the differences in the orientation observed here for Group J and Group H are not geometry dependent; both groups were tested at the right of the workspace with the same limb configuration.

In a second study on properties of stiffness control, we assessed the durability of adaptation. As in Study 1, subjects were trained to resist hand displacement in opposition to a single-axis disturbance that was oriented at −45° relative to the major axis of the null-field stiffness ellipse. After 2 days of training at the same orientation, the direction of the disturbance was unexpectedly switched on the third day by 90° and subsequent changes in stiffness were assessed over the course of several hundred trials as subjects attempted to again resist the applied disturbance.

The initial 2 days of training resulted in a rotation of the hand-stiffness ellipse of about 20° in the direction of the perturbation. On Day 3, in response to the switch in direction, the ellipse rotated away from the newly acquired direction and back toward null-field orientation, over the course of about 200 trials. However, even after 300 trials following the switch in the orientation, the stiffness ellipse had yet to show any evidence of moving beyond the orientation observed in the null field toward the direction of the current disturbance. The initial training thus resulted in changes to the control of stiffness that were quite durable. The original stiffness training affected the course of the new adaptation over several hundred trials even when a day intervened between the initial training and the switch in the direction of perturbation.

The experimental design decision to reverse the direction of the field rather than eliminate it altogether (as is sometimes done in the context of adaptation to velocity-dependent force fields) should be explained. The reversal of the field was motivated by the findings of Darainy et al. (2004). In that study, in which we assessed stiffness learning, we measured null-field stiffness at the start and end of each of 3 days of training. We observed that when the disturbance input was removed at the end of the day, the orientation and size of the null-field ellipse returned almost immediately to what we had measured in the absence of training—following one cycle of eight measurement displacements without any other intervening inputs, the hand-stiffness ellipse was no different than that measured at the beginning of that day of training, nor than at the beginning of training at the start of the experiment. The effect is striking; the pattern of stiffness changed suddenly from one in which the magnitude and orientation of the stiffness ellipse mirrored the characteristics of the perturbation to one which was not measurably different from that recorded under null-field conditions. In contrast, when the disturbance was reintroduced, as it was for example, on the next day of training, a persistence of adaptation was apparent. Thus, there was retention of adaptation that was not seen when the disturbance was removed. We thus decided to reinstate and alter the direction of the perturbation rather than remove it altogether in order to assess durability.

Previous studies of dynamics learning have provided evidence of a medium term persistence of changes to neural coding related to the acquisition of new dynamics. Shadmehr and Brashers-Krug (1997) report that when subjects learn velocity-dependent force fields, the learning may be retained for many months indicating persistence in the altered neural code that underlies the movement. Persistence in motor learning is also demonstrated in tasks in which subjects learn two opposing kinematic or dynamic transformations at various delays. Under these circumstances the initial learning is observed to interfere with the subsequent learning for periods that range from several minutes to 1 day or more (Caithness et al. 2004). The present study shows a comparable persistence in the acquired stiffness pattern—changes in the orientation of the hand-stiffness ellipse that arise from resisting single-axis disturbances interfere for at least a day with the acquisition of a new stiffness strategies in which stiffness change orthogonal to the first is required.

The interference that we see in the present study is presumably related to the dissimilarity of the initial and subsequent training task. Indeed, when the same field is applied several days in succession with the training carried out at 24-h intervals, there is positive transfer of stiffness learning from 1 day to the next (Darainy et al. 2004). Thus, the initial adaptation may be adaptively modified by new input or in cases such as that seen here when the initial adaptation and subsequent training involve contradictory sensorimotor mappings the new adaptation is impeded as a result of previously acquired changes to control.

The persistence of adaptation documented in Experiment 2 and in Darainy et al. (2004) may be contrasted with the findings of Experiment 1. An examination of Fig. 3a and b shows that quite a rapid deterioration of initial adaptation can occur when the direction of torque application is switched immediately following training. Thus, the initial adaptation was labile and interfered with by an incompatible transfer task at short delays, but following overnight retention, the adaptation became capable of substantially delaying new motor acquisitions. The results obtained at a 1-day interval are thus quite different than those observed immediately and underscore the medium term retention of stiffness adaptation.

Differences in the durability of adaptation between Experiments 1 and 2 might also be explained by the fact that limb configuration changes in the first experiment and remains fixed in the second. Gandolfo et al. (1996) showed that when arm configurations differed subjects could switch between opposing force fields. Similarly, Osu et al. (2004) demonstrated that subjects can learn different force patterns by providing visual and auditory cues. Wainscott et al. (2005) have shown the subject can learn opposite fields simply on the basis of order of exposure. Hence, changes in limb configuration in Experiment 1 may serve as a cue that contributes to differences in durability.

We have assessed properties of stiffness control under static conditions in order to avoid the contamination of characteristics of stiffness estimates by forces that are associated with phasic muscle activation during movement. Stiffness measures taken during movement of necessity include a component of resistance to displacement that arises as a result of the forces generated to move the limb. Although these forces may provide a very real contribution to estimates of stiffness, they have little if anything to do with the neural control and associated patterns of muscle activity that stabilize the limb. The tests reported here are carried out under static conditions with the specific goal of avoiding this potential confound.

Acknowledgements We thank P.L. Gribble and G. Houle for advice and assistance. This work was supported by the Ministry of Science, Research and Technology of Islamic Republic of Iran, the National Institute of Child Health and Human Development Grant HD048924, the Natural Sciences and Engineering Research Council of Canada, and Fonds québécois de la recherche sur la nature et les technologies.

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