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Position Information But Not Force Information Is Used in Adapting to Changes in Environmental Dynamics

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Milner, Theodore E. and Mark R. Hinder. Position information but not force information is used in adapting to changes in environmental dynamics. *J Neurophysiol* 96: 526–534, 2006. First published April 12, 2006; doi:10.1152/fn.00022.2006. This study investigated how movement error is evaluated and used to change feedforward commands following a change in the environmental dynamics. In particular, we addressed the question of whether only position-error information is used or whether information about the force-field direction can also be used for rapid adaptation to changes in the environmental dynamics. Subjects learned to move in a position-dependent force field (PF) with a parabolic profile and the dynamics of a negative spring, which produced lateral force to the left of the target hand path. They adapted very rapidly, dramatically reducing lateral error after a single trial. Several times during training, the strength of the PF was unexpectedly doubled (PF2) for two trials. This again created a large leftward deviation, which was greatly reduced on the second PF2 trial, and an aftereffect when the force field subsequently returned to its original strength. The aftereffect was abolished if the second PF2 trial was replaced by an oppositely directed velocity-dependent force field (VF). During subsequent training in the VF, immediately after having adapted to the PF, subjects applied a force that assisted the force field for ~15 trials, indicating that they did not use information about the force-field direction. We concluded that the CNS uses only the position error for updating the internal model of the environmental dynamics and modifying feedforward commands. Although this strategy is not necessarily optimal, it may be the most reliable strategy for iterative improvement in performance.

INTRODUCTION

Humans have the ability to adapt relatively quickly to changes in the mechanical environment. However, acquiring proficiency and skill may require considerable practice. Studies investigating how adaptation to novel dynamics is achieved, when using the upper limbs, suggest that compensatory forces are learned as predictive feedforward motor commands, which replace feedback motor commands that are needed initially to compensate for errors (Brashers-Krug et al. 1996; Krakauer et al. 1999; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999). In an elegant study, Conditt et al. (1997) provided convincing evidence that the CNS learns a functional representation between limb states and perturbing forces, which has been referred to as an internal model. Nevertheless, the domain of generalization of the internal model is limited only to regions of the state space in the vicinity of those that have been explored during training (Gandolfo et al. 1996; Sainburg et al. 1999; Shadmehr and Moussavi 2000). Thoroughman and Shadmehr (2000) and

Donchin et al. (2003) have suggested that the functional representation comprises basis functions that encode different regions of the movement space. However, the sensory feedback mechanisms contributing to formation of the internal model have yet to be elucidated. When environmental dynamics change, it has been hypothesized that the CNS updates the internal model by reducing the error in the model's representation of required force and in this way modifies feedforward commands to muscles so as to reduce position error on subsequent movements (Thoroughman and Shadmehr 2000).

Once an internal model has been formed, it is resistant to immediate change. Shadmehr and Brashers-Krug (1997) investigated the ability of subjects to adapt to two oppositely directed force fields with an intervening interval of 5 min to 24 h. The force fields created velocity-dependent lateral forces of the same magnitudes but opposite in direction. When subjects attempted to adapt to the second force field, 5 min after the completion of training in the first force field, there was a clear aftereffect for the first 30–40 trials in the new force field during which subjects exerted a gradually diminishing lateral force in the direction that opposed the first force field but assisted the second force field. They found that the rate of formation of the internal model for the second force field was not affected by prior learning of the first force field. However, despite the same rate of internal model formation it took longer to reach the same level of performance (internal model accuracy) in the second force field because the initial position error was greater. This suggests that the CNS could not use information about the change in force field direction to accelerate formation of an internal model for the second force field.

Sensory information about limb position and force are both available to the CNS and theoretically could both be used to correct for movement error. Because actual position can be compared with desired position, it is obvious how sensory information about limb position can be used to compute movement error. Indeed, there is convincing evidence that position error is critical for rapid adaptation to changes in environmental dynamics (Scheidt et al. 2000). Although position information would appear to provide sufficient feedback about error for formation of an internal model, there are situations where force information could accelerate the process. For example, similar position errors could arise when a large environmental force decreases and when a small environmental force reverses direction. The optimal response to a decrease in the environmental force would be a corresponding decrease in the applied force, whereas the optimal response to a reversal in the direc-

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tion of the environmental force would be to similarly reverse the direction of force applied by the arm. The present study was undertaken to specifically test the hypothesis, suggested by the observations of Shadmehr and Brashers-Krug (1997), that force information is *not* used to update the internal model when the direction of a force field changes.

In a recent study, we showed that information about the process by which the internal model is updated can be obtained by analyzing movement errors when the environmental dynamics are intermittently altered for several trials in succession (Milner and Franklin 2005). We employed this technique in the present study. Subjects adapted to a position-dependent force field (PF), which was intermittently doubled in strength (PF2) or changed to an oppositely directed velocity-dependent force field (VF) to create large movement errors in opposite directions. The error created by the PF2 served as a "conditioning stimulus," whereas the error created by the VF served as a "test stimulus." Doubling the force-field strength created a position error in the same direction as the PF. Having a VF trial follow a PF2 trial created a position error in the opposite direction. We predicted that after two PF2 trials in succession, there would be a large aftereffect on returning to the PF, in the opposite direction to the error in the PF2, as a consequence of rapidly updating the previous (PF) internal model. In contrast, we predicted that if a VF trial followed a PF2 trial, there would not be an aftereffect in the opposite direction to the error in the VF. This was based on the hypothesis that information about position error but not force direction is used to update the internal model. We anticipated that any change to the internal model evoked by the transition from PF to PF2 would be reduced or annulled by the subsequent transition from PF2 to VF but that the force commanded by the internal model would not reverse direction. To test the hypothesis further, we had subjects adapt to the VF after the final PF2 trial. In this case, we predicted that even after several trials the force commanded by the internal model would still be in the direction that assisted rather than opposed the VF based on the rate at which information about position error could be used to update the internal model.

The reason why we used the PF as our baseline, rather than the conventional null field, was to demonstrate that the iterative process of correcting for errors when the dynamics unexpectedly change is the same whether the reference internal model already exists or whether it is still under formation. The PF was designed so that the force profile along the desired hand path was similar to the force profile of velocity-dependent force fields, which have been more commonly used. The advantage of using this particular PF was that subjects adapted very rapidly. We chose to switch from the PF2 to the VF to create an error in the opposite direction rather than simply reversing the direction of the PF so that adaptation to the novel environmental dynamics could not simply be achieved by reversing the sign of an already formed (or partially formed) internal model.

METHODS

Nine male subjects participated in this study. All subjects gave informed consent prior to participating in the study. The protocol was approved by the institutional ethics review committee and conformed to the ethical standards set down in the Declaration of Helsinki.

Experimental setup

The subjects made goal-directed movements in the horizontal plane with their right arm while holding the handle of a 2 df serial-link robot manipulandum. The subject's arm was supported against gravity by means of a sling suspended from the ceiling that cradled the arm near the elbow. The handle rotated freely about its central axis to prevent torque from being applied. A 6 df load cell at the handle measured the force applied by the subject. High-resolution optical encoders on the shafts of the motors driving each link, measured shaft angle, permitting x and y handle position to be accurately determined. Tachometers on the motor shafts measured shaft velocity. The apparatus is described in greater detail by Conditt et al. (1997) and Scheidt et al. (2000). Analog signals were acquired with a 16-bit A/D converter. All signals were acquired at 1,000 Hz, which was also the update rate for control of the robot manipulandum.

Protocol

Subjects moved the manipulandum handle from a start position ~30 cm in front of the shoulder to a target located 25 cm forward of the initial position. They performed 20 trials during which the manipulandum applied no force to the hand (null field) followed by 175 trials during which the manipulandum applied forces, which were generally predictable. Between trials the subject's hand was returned to the initial position under servo-control. Subjects were instructed always to move at the same peak velocity (75.0 ± 5.6 cm/s; target window) and to stabilize the handle in the end target window. The start and end targets for each movement were displayed as 2-cm squares (in workspace coordinates) on a computer monitor situated above the manipulandum. The instantaneous position of the handle was displayed as a 0.6-cm square cursor (in workspace coordinates) on the monitor. Prior to initiation of the movement, two parallel lines appeared, joining the edges of the start and end target boxes. These lines were used as an aid to guide the subject in performing straight movements. If the cursor touched either line during the movement, that portion of the line was erased from the display. In this way, the subject was made aware of any deviation from a straight path. Subjects were told that to successfully complete the task, they had to keep the cursor from touching the lines. A display of peak velocity was provided immediately after completion of the movement. It consisted of a horizontal bar the length of which was proportional to peak velocity, shown just above the target velocity window. If the peak velocity was too low, the bar was shown in red, if it was too high, the bar was shown in blue, and if it was within the target window, the bar was shown in green and a tone sounded. Trials were self-initiated, allowing subjects to pause between trials if they desired. All trials were included in subsequent analysis, regardless of the peak velocity.

For the majority of the first 125 trials, subjects adapted to the following PF

$$F_x = K[x + 3.2(y - y_s)(y - y_e)] \qquad (1)$$

where x was measured with respect to the shoulder (with left being negative and right being positive), y was the current position of the hand, y_s the start location and y_e the center of the final target zone. Note that the y term in the equation defines a locus of unstable equilibrium points, located along a parabolic path that meets the straight line joining the targets at the center of the target zones (Fig. 1A). The magnitude of the force field gradient, K, was 150 N/m. The force-field gradient acted like negative stiffness, pushing the hand away from the parabolic path, i.e., to the left or to the right, depending on which side of the parabolic path the hand was located. Because subjects tried to follow the straight line between targets, they were always on the left of the parabolic path except near the final target when they sometimes crossed to the right (Fig. 2). The force field was not activated until the subject had moved 3 mm from the center of the start target. Prior to this, the subject stabilized the hand in the target
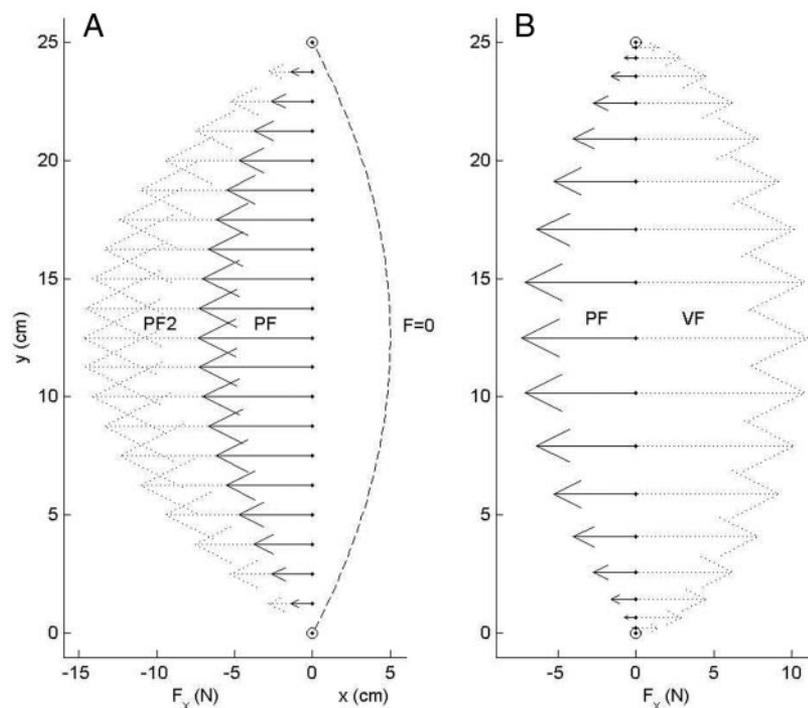
FIG. 1. *A*: dotted parabola with positive *x* displacements indicates locus of 0 force points for position-dependent force field (PF; unstable equilibrium positions). Arrows indicate lateral force of PF (150 N/m, solid arrows) and PF2 (300 N/m, dotted arrows) as a function of *y* position for a straight trajectory between targets (circled points). *B*: comparison of lateral force produced by PF (solid arrows) and velocity-dependent force field (VF; 15 N/ms^{-1}, dotted arrows) for a straight trajectory with a minimum-jerk velocity profile. In both *A* and *B*, the size of the arrow represents the lateral force.

zone while opposing a 0.5 N force directed to the left. This bias force was used so that subjects could not detect any change in the force field until after movement had been initiated. The bias force was approximately equal to the PF force at the point where the force field was activated. On randomly selected trials, the force-field strength was increased or the nature of the force field changed as described later on.

After the first 125 trials, the force field unexpectedly changed to a VF given by the following equation

$$F_x = B\dot{y} \qquad (2)$$

where $\dot{y}$ is the velocity in the *y* direction and *B* was 15 N/ms^{-1}. This force field was designed to have a similar spatial and temporal force profile to the PF along the straight line target path, assuming a bell-shaped velocity profile. This ensured that adaptation to the PF and VF would require similar temporal modulation of joint torque so that differences in adaptation rate would not be due to differences in the temporal complexity of joint torque profiles. The direction of force produced by the VF was opposite to that of the PF when moving along the target path ($x = 0$), i.e., the VF force was directed to the right (Fig. 1*B*), whereas that of the PF was directed toward the left (Fig. 1*A*). After the unexpected change in dynamics, subjects performed 50 consecutive trials in the VF.

On 11 trials, randomly selected and uniformly distributed among the first 125 trials, the strength of the force field was unexpectedly doubled, i.e., $K = 300$ N/m (PF2, Fig. 1*A*). Five of these trials were followed by another PF2 trial, whereas the other six were followed by

the VF. The original force field (PF) was restored on the following trial. On trials 3, 61, and 120, the force field was unexpectedly replaced by a stiff elastic wall with its boundary along $x = 0$, which limited lateral deviation to the right. Such trials allowed measurement of the lateral force exerted by the hand without having to consider the dynamics of lateral arm motion. A damped elastic force was applied to the hand whenever it deviated to the right of the line. The stiffness and viscosity of the wall were 1,000 N/m and 50 N/m-s^{-1}, respectively.

Analysis

The overall kinematic error was represented by the signed error, i.e., the integral of the hand path relative to a straight line joining the targets, such that deviation to the left ($-x$) was negative error and deviation to the right ($+x$) was positive error. The sign of the integral represented the direction of the subject's net deviation from a straight line movement. The integration was performed from the start position to a point 1 cm from the target along the line joining the targets. This eliminated the effect of zigzag corrective movements very close to the target on the signed error. These movements were not related to correction for the initial deviation (Fig. 2), which occurred earlier and was included in the error analysis. Rather they were related to the destabilizing effect of the force-field gradient at the target position, which pushed the hand past the target position. They were excluded from the analysis because stabilization at the target position was not
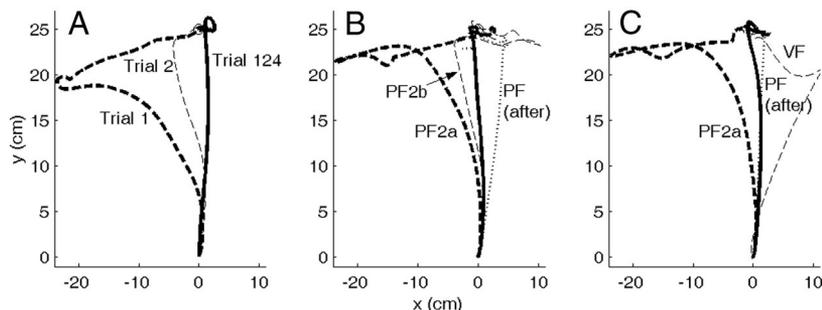

FIG. 2. *A*: hand paths for the 1st and 2nd trials (- - -) compared with the final trial (*trial 124,* —) of the PF learning session. *B*: hand paths for 1st (PF2a) and 2nd (PF2b) trial after doubling the PF strength (- - -) compared with the trial before doubling of the PF strength (—) and the aftereffect of returning to the initial PF strength (· · ·). *C*: hand paths for a PF2a trial followed by a VF trial (- - -) compared with the trial before doubling of the PF strength (solid line) and the aftereffect of returning to the initial PF strength (· · ·). Data in each panel are for a single subject and single trials.

a focus of this study unlike some of our previous studies (e.g., Milner 2002). This measure of kinematic performance enabled us to track learning as a result of a combination of feedforward and feedback processes. Maximum lateral deviation to the right and left is also reported but was not used in the statistical analysis because it varied in the same way as the signed error. To relate changes in kinematic error more directly to changes in feedforward commands to muscles, signed error and maximum lateral deviation were also evaluated between movement onset and peak velocity, which was well before any reductions of kinematic error occurred within each trial.

Peak lateral force measured on the three wall trials was also used as an indicator of adaptation. For VF trials, the lateral force (measured by the load cell) was used to compute a force impulse from the time of movement onset to peak velocity. The difference between this force impulse and the nominal force impulse computed from *Eq. 2,* over the same time interval, was used to determine the direction of the subject's force on the handle of the manipulandum. The effect of the chronological position of the intermittent change in environmental dynamics on kinematic error was tested for statistical significance by ANOVA with subjects as a random factor Differences in kinematic error or force between specific conditions were tested for statistical significance by means of paired *t*-tests. Differences were considered to be statistically significant at the $\alpha = 0.05$ level. When multiple statistical comparisons of kinematic error were made, i.e., between the first two PF training trials, between the two PF2 trials, between the PF trials before and after PF2/PF2 and PF2/VF sets, and between the first two VF training trials, the Bonferroni correction was applied for multiple comparisons by setting $P < 0.01$ as the level of statistical significance.

RESULTS

Adaptation to the PF

The hand path was markedly perturbed on the first trial in the PF, although subjects were able to recover and stabilize the hand at the target (Fig. 2*A*). Perturbed movements were characterized by lateral hand path deviation that increased in an exponential fashion with distance moved in the *y* direction. Subjects eventually arrested the lateral deviation after they had traveled ~20 cm toward the target and had deviated by approximately the same amount to the left of the target path [-19 ± 9.2 (SD) cm]. On the first trial, they then made one or more corrective movements toward the target. The average signed error was -100 ± 53 cm^2.

On the second trial, the leftward deviation was decreased markedly (Fig. 2*A*). The mean lateral deviation was reduced to -6.3 ± 4.5 cm and mean signed error was reduced to -16 ± 34 cm^2, i.e., by >80% ($P = 0.0068$). This reduction in kinematic error was not simply due to stiffening of the arm. This was demonstrated by introducing a stiff elastic wall on the third trial, which guided the hand along a straight line toward the target. The average maximum lateral force exerted against the wall was 5.8 ± 1.3 N. The lateral force profile for a representative subject (Fig. 3, —) is compared with the computed profile to move along the same hand path, assuming that the lateral force perfectly compensated for the PF (Fig. 3,- - -). Although the spatial force profiles were quite different, indicating that subjects were not yet accurately compensating for the PF, the peak lateral force against the wall was large compared with what would be expected in the null field (Scheidt et al. 2001). Consequently, we can conclude that by the third trial subjects were actively producing a significant compensatory force in response to the initial perturbation and not simply stiffening the arm.

With training, the kinematic error was reduced further (Fig. 4) so that by trial 60 the average signed error was only 7.3 ± 26 cm^2, and it remained relatively unchanged for the remainder of the training session. The average maximum lateral force exerted against the wall on trial 61 had increased to 8.6 ± 2.7 N. The similarity of the computed and actual lateral force profiles for trial 61 (Fig. 3, *middle*) suggests that subjects no longer relied heavily on the impedance of the arm to compensate for the PF but instead more accurately compensated for the PF force.

The maximum lateral force exerted against the wall on trial 120 was similar to that on trial 61 (8.1 ± 1.8 N). A comparison of the computed and actual lateral force profiles on trials 61 and 120 (Fig. 3, *middle* and *right*) suggests that subjects matched the spatial profile of the PF force better at the end of the training session than halfway through. Although the mean absolute force error with respect to the PF force profile was reduced by 0.37 N, the reduction was not statistically significant ($P = 0.076$), which is consistent with the lack of change in kinematic error.
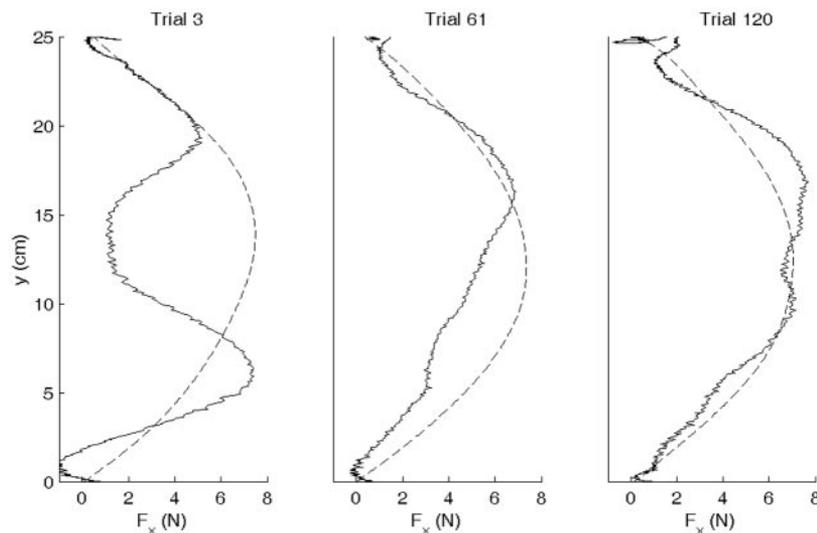

FIG. 3. Lateral force profiles for virtual wall trials. —, force applied to the wall. - - -, force that would be needed to compensate for the PF along the same hand path. Data are that of a single subject.
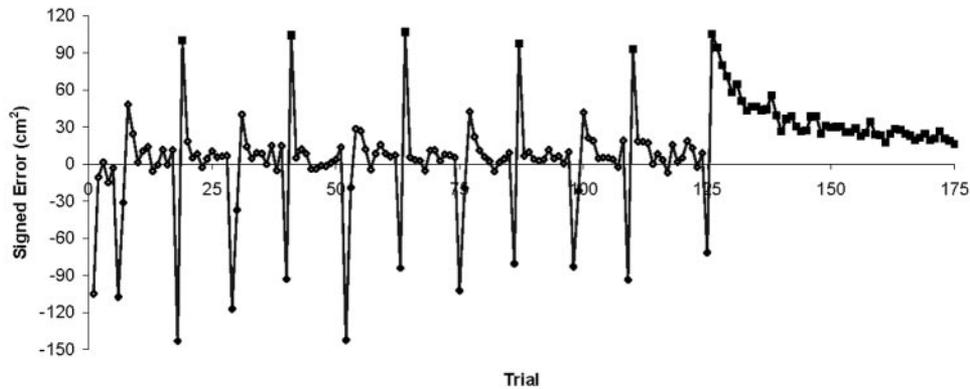
FIG. 4. Signed error averaged across all 9 subjects for all trials of the training session. ◇ PF and wall trials; ◆, PF2 trials and ■ VF trials.

Unexpected intermittent changes in environmental dynamics

As described in METHODS, the force field was unexpectedly doubled in strength (PF2a, Fig. 2*B*) to 300 N/m on 11 occasions during the training session, the first time being on trial 6 and the last on trial 124. Doubling the strength of the force field produced an average maximum lateral deviation of -17 ± 2.0 cm and signed error of -97 ± 48 cm². There was no significant main effect of the chronological position of a PF2a trial, i.e., trial number, on signed error ($P = 0.25$), indicating that there was no effect of repeated exposures (compare the ◆, Fig. 4). In addition to confirming that subjects could not predict when PF2a trials would occur, this also indicates that the stiffness of the arm did not change over the training session, otherwise the lateral displacement should have changed. When the force field strength remained at 300 N/m for two trials in succession (PF2/PF2), subjects were able to reduce the maximum lateral deviation to -7.6 ± 4.1 cm and the signed error to -22 ± 29 cm² on the second trial ($P = 0.0001$). We denote the two consecutive PF2 trials as PF2a and PF2b. There was no main effect of the chronological position of a PF2b trial on the signed error ($P = 0.93$). On the following trial, the force field returned to its initial strength (PF2-post, Fig. 2*B*). The average

signed error on this trial was 43 ± 12 cm², significantly larger than the value of 6.1 ± 17 cm² obtained for the PF baseline trials that preceded the PF2/PF2 sets ($P < 0.0001$) and significantly greater than zero ($P < 0.0001$). There was no main effect of the chronological position of a PF2b trial on the signed error of the aftereffect ($P = 0.15$). The mean difference in hand path between the PF baseline trial and the postPF2 trial is shown for all subjects in Fig. 5 (*left*). This aftereffect to the right would *not* have occurred if subjects had simply increased the stiffness of the arm without increasing their lateral force to the right (opposite to the direction in which they were pushed by the PF). Performance did not immediately return to the baseline value. The aftereffect persisted on the second PF trial after the PF2/PF2 sets, with an average signed error that was still 17 cm² greater than that of the PF baseline trial ($P = 0.0011$). However, by the third postPF2b trial, the error was no longer significantly different from the PF baseline value ($P = 0.45$).

When the force-field dynamics were changed to velocity-dependent dynamics (VF, Fig. 2*C*), where the external force pushed subjects to the right rather than the left after the PF2a trial, there was, as expected, a large kinematic error to the right
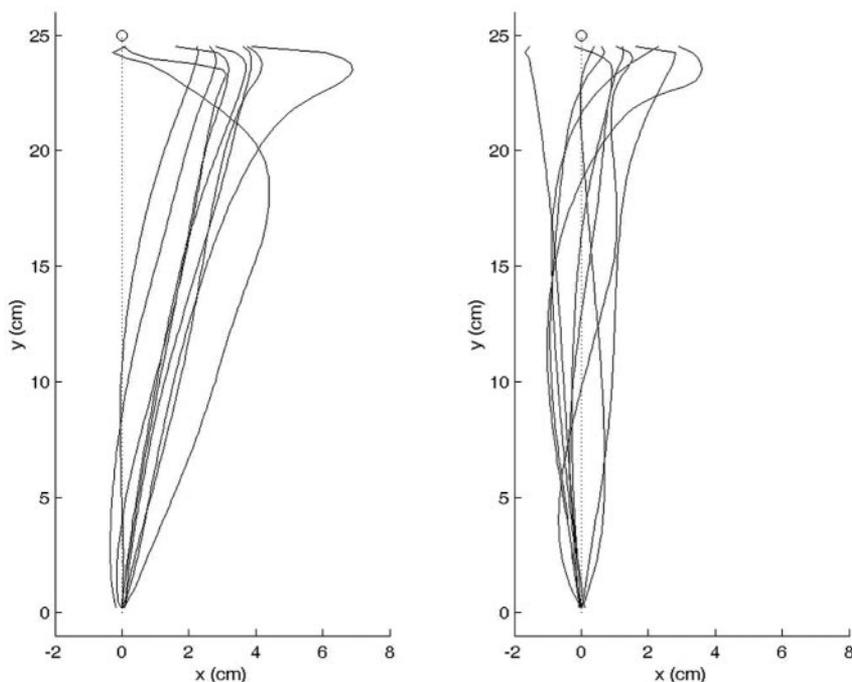

FIG. 5. Average difference in hand paths between PF trials that preceded (baseline) and followed (aftereffect) PF2/PF2 sets (*left*) and PF2/VF sets (*right*) are shown for all 9 subjects. ····, straight line path from the start to target for reference purposes.

(Fig. 4, ■). The average maximum lateral deviation was 10 ± 2.3 cm and the signed error was 100 ± 26 cm². There was no significant main effect of chronological position on signed error ($P = 0.52$). When the dynamics of the initial force field were restored on the next trial, there was no aftereffect compared with the PF baseline trial ($P = 0.95$). The signed error on returning to the initial PF dynamics was 12 ± 18 cm² compared with 12 ± 18 cm² on the PF baseline trial. The mean difference in hand path between the PF baseline trial and the post-VF trial is shown for all subjects in Fig. 5 (*right*). Some subjects did show a small aftereffect to the left, i.e., in the direction opposite to the VF, whereas other subjects showed no aftereffect or an aftereffect to the right. In all cases, they applied a force to the right and the observed effect depended on the magnitude of this force, i.e., whether it was greater or less than the magnitude of the PF force which they were opposing. No subject applied a leftward force, which would have been in the direction to oppose the VF.

To focus on how the internal model of the force field changed in response to the error produced by unexpectedly changing the force field strength or dynamics, we computed the lateral deviation at peak y velocity and the signed error between movement onset and peak y velocity relative to the final PF hand path (mean of PF trials 112–119). Expressing the movement error relative to the final PF hand path rather than the straight line between targets simplifies the interpretation of changes in movement error. Because there were no obvious corrective movements until after peak velocity, we believe that any changes in the movement error prior to peak velocity were due to changes in feedforward commands to muscles brought about by changes to the internal model. Note that this includes feedforward changes in the limb impedance that results from changes in patterns of muscle activation and/or changes in reflex gains. The results of this analysis reinforced the principal findings reported in the preceding text, but provided additional insight. Mean lateral deviation at peak velocity on post-PF trials (aftereffect) was 1.3 cm with a mean signed error of 6.9 cm², which was significantly greater than 0 ($P < 0.0001$). In contrast, the mean lateral deviation at peak velocity on post-VF trials (aftereffect) was only 0.010 cm with a mean signed error of −0.27 cm², which was not significantly different from 0 ($P = 0.77$).

Adaptation to the VF

After trial 125, the VF dynamics was maintained until the end of the training session (trials 126–175). It is evident from Fig. 4 that the signed error was reduced much more slowly during VF training than during PF training. To further explore why the error was not reduced more quickly, we examined changes in the force applied by subjects to the manipulandum. Because the first VF trial in the series was preceded by PF2 and PF trials, we expected that subject would produce a feedforward lateral force that initially assisted the VF, i.e., during the acceleration phase of the movement they would apply a rightward force. As in the preceding text, we used peak y velocity, i.e., the end of the acceleration phase, as a convenient cutoff point for feedforward commands. In Fig. 6*A,* we compare the force measured by the load cell attached to the manipulandum handle with the theoretical VF force calculated from *Eq. 2*. When the load cell force was less than the VF force, it
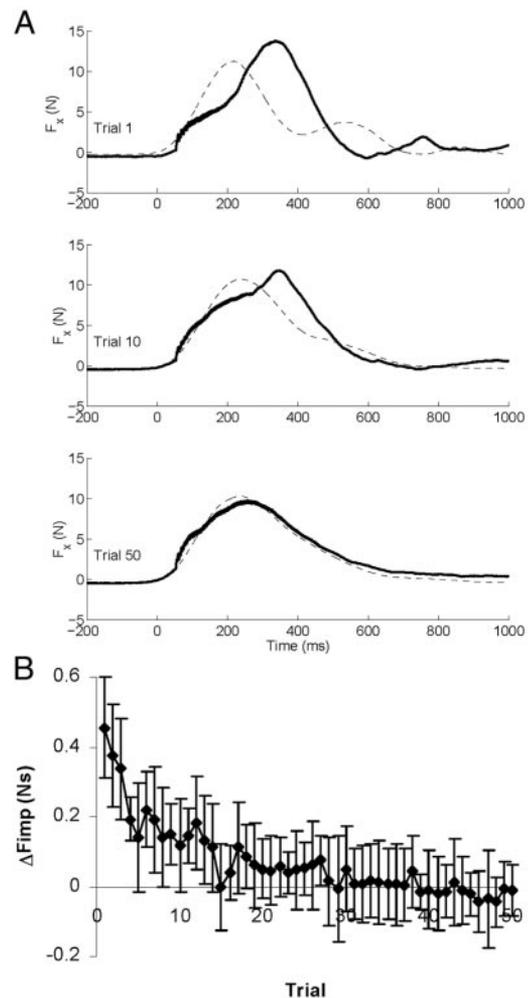

FIG. 6.   *A*: load cell force in the *x* direction (—) for VF training session trials (*trial block 126–175*) averaged across all 9 subjects compared with VF force (- - -). *Trials 1* (*top*), *10* (*middle*), and *50* (*bottom*) of the 50 VF training trials. *B*: mean ± SD of the difference in force impulse (area) between the force profiles in computed from movement onset (0 ms) to peak *y* velocity for the 50 VF trials. Note that *trials 1–50* in this figure correspond to *trials 126–175* in Fig. 4.

indicated that subjects applied a force in the same direction as the VF, i.e., a rightward force, thereby unloading the load cell. From Fig. 6*A* (*top 2 panels*), it is evident that, on average, even after 10 consecutive VF trials, subjects were still applying a net force to the right, i.e., they assisted the VF. We quantified the difference between the VF force and the force measured by the load cell as the mean difference in force impulse from movement onset until peak *y* velocity (Fig. 6*B*). A positive difference indicated that subjects applied a net rightward force between movement onset and peak *y* velocity. The data in Fig. 6*B* show that, on average, subjects applied a net force impulse to right for about half of the training trials, although the size of the SDs suggest that the net force impulse was not significantly different from zero after about 15 trials. We tested the net force impulse of the first 15 VF trials (126–140) using Dunnett's test for multiple comparisons with the control value set to 0. With all nine subjects included, the net force impulse was significantly greater than zero for 7 of the first 15 VF trials, i.e., trials 125–128, 130, 131, and 136 ($P < 0.05$). However, the net force impulse for one subject was frequently negative in contrast to

a net positive force impulse of the other eight subjects. When this subject's data were excluded from the analysis, the net force impulse was significantly greater than zero for 14 of the first 15 VF trials ($P < 0.05$), the only exception being trial 134. This implies that the reason why signed error was reduced so slowly was because subjects did not begin to resist the initial rightward perturbing effect of the VF until they had performed ≥ 15 trials. We fit an equation of the form $a + be^{-t/c}$ to the net force impulse. The parameters of the best-fit equation were $a = 0$, $b = 0.39$ Ns, and $c = 9.2$ trials.

The rate of learning in the PF and VF were estimated by fitting an equation of the form $a + be^{-t/c}$ to the mean signed error (data shown in Fig. 4). Wall trials were removed because they transiently reduced error, whereas PF2a, PF2b and VF trials were removed because they transiently increased error. As described in the preceding text, two PF trials were necessary to reduce error to the baseline PF value after PF2/PF2 sets so these were removed, as well. It was not necessary to remove these latter trials for PF2/VF sets. The parameters of the best-fit equation for the PF learning were $a = 4.5$ cm^2, $b = -72$ cm^2, and $c = 0.82$ trials, whereas the parameters of the best-fit equation for the VF learning were $a = 25$ cm^2, $b = 75$ cm^2, and $c = 7.2$ trials. Note that the time constant for VF learning was about nine times higher than for PF learning. However, the time constant for reduction of signed error during VF learning was similar to the time constant for reduction of net force impulse.

DISCUSSION

The principal finding of this study was that when the direction of the force field changed unexpectedly, the CNS appeared to be unable to use information about the direction of the perturbing force to adapt more quickly to the new environmental dynamics. The lack of an aftereffect following a single VF trial after doubling the PF strength suggested that subjects did not use information about force direction to adjust the feedforward commands for the subsequent trial. Furthermore, all but one subject continued to exert lateral force in a direction appropriate for resisting the PF, but inappropriate for resisting the oppositely directed VF, for at least the first 15 VF training trials. This is consistent with the use of position error to update the internal model but not with the use of information about force direction. It is also noteworthy that the size of the aftereffect after doubling of the force-field strength did not depend on whether it occurred early or late in the PF training, which we attribute to independence of working memory and longer-term memory.

Adaptation to the PF

Adaptation to the PF was extremely rapid. The lateral deviation on the first PF trial was close to 20 cm, resulting in a lateral force of >30 N. Nevertheless, all subjects were able to recover from this perturbation and correct for the error well before the trial ended. On the second trial, they reduced the lateral deviation by >50% and within a few trials it was ~1 cm. The signed error was reduced just as dramatically. Such a large error reduction on the second trial is similar to our previous observations of adaptation to a velocity-dependent force field (Milner and Franklin 2005). Because of the large

negative force-field gradient, subjects not only had to produce a mirror-image force profile to follow the target hand path, but they also had to maintain a lateral limb stiffness of >150 N/m to guarantee that the trajectory would remain stable. The stiffness generated by the muscle activity required for the task was likely sufficient to meet this requirement over most of the hand path (based on relations between stiffness and force derived from Perreault et al. 2001).

Interference in motor learning

The failure to see an aftereffect opposite to the direction of the VF after PF2/VF sets supports the hypothesis that information about force direction was not used to update the internal model as does the persistent net assisting force impulse during the first 15 VF training trials. The similarity of the rate of reduction of the net positive (assisting) force impulse and the rate of reduction of position error during adaptation to the VF supports the hypothesis that only position-error information is used in updating the internal model. It should be noted that the assisting force that the subjects exerted was considerably larger than represented by the net force impulse computed from the measurement of hand force (shown in Fig. 6). Subjects exerted an assisting force impulse to move the inertia of the arm, which was over and above what could be measured because it was completely internal to the subject. It is clear that this additional force impulse must have been relatively large given that the arm accelerated faster than the manipulandum for ≥ 200 ms (the period during which the net force impulse was positive).

Shadmehr and Brashers-Krug (1997) conducted an experiment in which they had subjects adapt to one velocity-dependent force field then reversed the lateral direction of the force and had them adapt to the new force field. Although they found a larger initial error in the second force field than in the first force field, because of the aftereffect of training in the first force field, they did not find any difference in the rate of error reduction. They interpreted this as preservation of the rate of internal model formation. In our study, we found a lower rate of error reduction in the second force field (VF). However, this may simply reflect greater difficulty in adapting to velocity-dependent force fields. In two previous studies where subjects adapted to velocity-dependent force fields, while performing movements similar to those of our study, the mean time constant for reduction of signed error was 3.3 trials (Franklin et al. 2003) and 6.6 trials (Osu et al. 2003). These time constants are considerably greater than what we found for the PF.

Shadmehr and Brashers-Krug (1997) speculated that during the initial stage of motor learning, prior to consolidation, information is temporarily stored in a type of working memory. If we assume that this information is represented as neuronal firing patterns as they suggest, the neuronal firing patterns in working memory would be dependent on the current state of the environmental dynamics. Improvement in performance when environmental dynamics change would require that the existing firing patterns be modified to reflect the altered dynamics. Our results would suggest that the time constant for modification of these firing patterns is independent of how long they have been in working memory. We found no effect on the size of error reduction in PF2/PF2 sets or on the aftereffect size for PF2/PF2 and PF2/VF sets, related to where the sets occurred during the PF training session. It also suggests that

working memory and active memory (Caithness et al. 2004) do not share common neural circuits. Otherwise, we would have expected that the same position error would lead to different incremental changes in the neuronal firing patterns in working memory early in training (when active memory held a internal model of the null field) compared with late in training (when active memory held an internal model of the PF) and hence, differences in the size of the error reduction and the size of aftereffects when environmental dynamics were intermittently altered.

Mechanism of movement error reduction

To address the question of whether only position information or whether both position and force information are used in updating the internal model, we first describe how position information could be used to reduce error during training based on a model (Burdet et al. 2004) originating from our experimental observations (Franklin et al. 2003; Milner and Franklin 2005). It uses a mechanism of iteratively increasing the activation of muscles that are stretched by the position error and simultaneously increasing the activation of their antagonists to a lesser extent until the position error drops below a desired threshold, after which the activity of all muscles is incrementally reduced as long as the position error remains below the threshold. We have suggested that stretch reflex amplitude may serve as a template for the size of incremental changes in muscle activation on the subsequent trial (Milner et al. 2006). Under the conditions of the current study, activation would initially build up in muscles that oppose the leftward perturbing effect of the PF. When the force-field strength is doubled, the feedforward activation of these muscles will increase dramatically on PF2b trials, reflecting a large stretch reflex on PF2a trials. When a VF trial follows a PF2 trial, the less active antagonist muscles would be stretched but smaller stretch reflex responses would be expected than on PF2a trials. The net change in joint torque on the following trial should be relatively small because the increase in the activation of these muscles would continue to be opposed by increasing activation of their antagonists until the position error is reduced below the desired threshold. Consequently, net joint torque would change much more gradually during initial adaptation to the VF than during initial adaptation to the PF, resulting in a slower rate of error reduction and a force that would not begin to oppose the VF until a relatively large number of trials had been performed due to the long time constant for the change in net joint torque.

If force information can also be used in updating the internal model, we would expect that it would it would have its greatest effect on changes in muscle activity when it could enhance the information provided by position error alone. Some ambiguity in the information conveyed by position error can arise when the force-field direction changes. In particular, when the force field changed from PF2 to VF, the position error could be interpreted as a large reduction in PF strength. A change in force-field direction or a reduction in the force-field strength would both have produced a rightward movement error. In this case, information about the direction of the force field would resolve the ambiguity, i.e., force information would enhance the information provided by position error. Reducing the voluntary compensatory force would reduce position error when the direction of the force field changed. However, a more optimal response would be to exert lateral force in the opposite direction on the subsequent trial. Therefore if force sensors can provide information about force-field direction, we would predict that subjects would begin exerting a detectable force to the left to oppose the VF on the second VF training trial. However, our subjects did not do this.

The reason why the CNS did not use force information in this way may be because peripheral force sensors cannot provide the necessary information. To determine the force-field direction, it would be necessary to detect the direction of the external force applied at the hand. Force sensors in muscle, Golgi tendon organs, would not be able to unambiguously signal the direction of the external force. A reduction in force-field strength or a change in force-field direction would both unload the Golgi tendons organs of contracting muscles, resulting in a similar change in their output. Signals from other potential force sensors, cutaneous sensory receptors in the hand, could also be ambiguous. For example, if the subject exerted a force in the same direction as the force field, but larger than that of the force field, pressure on the hand would indicate a force opposite to the direction of the force field. It would not be possible to unambiguously determine whether the force arose from a force field pushing to the left (PF) or from an inertial force pulling to the left (due to rightward acceleration of the manipulandum) with greater force than a force field pushing to the right (VF). To avoid making potentially larger errors by misinterpreting such ambiguous information, the CNS may rely only information about position error to update the internal model. Although this may not be optimal in terms of reducing internal model error, it guarantees that performance will improve iteratively (Burdet et al. 2004).

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