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Rapid Adaptation to Scaled Changes of the Mechanical Environment

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Hinder MR, Milner TE. Rapid adaptation to scaled changes of the mechanical environment. *J Neurophysiol* 98: 3072–3080, 2007. First published September 26, 2007; doi:10.1152/jn.00269.2007. We investigated adaptation to simple force field scaling to determine whether the same strategy is used as during adaptation to more complex changes in the mechanical environment. Subjects initially trained in a force field, consisting of a rightward lateral force with a parabolic spatial profile (PF). The field strength was then unexpectedly increased or decreased (ΔPF) for repeated sets of five consecutive trials, with intervening PF trials. Stiff elastic walls, which prevented lateral movement of the arm, randomly replaced 25% of ΔPF trials. Lateral deviation on ΔPF trials and lateral force against the elastic walls were used to assess the extent to which feedforward adaptations could be attributed to changes in lateral force or increased stiffness of the arm. When force field strength was increased or decreased hand paths were perturbed to the right or left, respectively. Performance error was significantly reduced between the first and second ΔPF trial positions of the set, whereas the lateral force impulse exerted against the elastic walls did not change until the third trial position. The lateral force was scaled upward or downward in response to the change in force field strength, suggesting a gradual change in the internal model. The results support a dual strategy of cocontraction (increased stiffness) and internal model modification. The development of an accurate internal model is a slower process than cocontraction and error reduction. This may explain the need to represent motor learning as two parallel processes with varying timescales, as recently proposed by Smith and colleagues.

INTRODUCTION

Humans have the ability to adapt relatively quickly to changes in the magnitude or nature of external forces. Compensation for external forces is learned as predictive feedforward motor commands that replace reactive feedback motor commands (Conditt et al. 1997; Kawato 1990; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999). The time course of adaptation in terms of error reduction and modification of joint torques, as well as the changes in muscle activation responsible for the adaptation, have been investigated in several recent studies (Franklin et al. 2003; Hinder and Milner 2005; Milner 2004; Milner and Franklin 2005). In the early phase of adaptation, when subjects are naïve to the exact nature of the perturbing forces, and motor commands do not fully compensate for these forces, pairs of antagonistic muscles are activated simultaneously (cocontraction) to increase the impedance of the limb. This leads to a relatively rapid reduction of the performance error caused by the perturbing forces. As subjects become more familiar with the nature of the perturbing forces through practice, they are able to reduce

cocontraction without sacrificing performance. This is achieved by learning appropriate patterns of reciprocal activation within antagonistic pairs of muscles (inhibition of the antagonist muscle together with an increase in excitation of the agonist muscle) to more specifically compensate for the perturbing forces. However, these modifications in muscle activation continue long after performance has stabilized.

Initially, errors are corrected by a combination of reflex muscle activation and voluntary muscle activation after errors are perceived. Presumably, both reflex and voluntary corrective actions are progressively replaced by predictive feedforward actions as adaptation proceeds (Franklin et al. 2003). However, this is an assumption that has not been rigorously tested because of the difficulty in separating feedforward and feedback actions. Recently, Scheidt et al. (2001) introduced a paradigm in which lateral error is eliminated by guiding the movement between stiff elastic walls (virtual channel). This creates the possibility of probing the evolution of changes in feedforward actions by eliminating the stimulus for feedback actions.

Previous studies of adaptation to dissimilar environments (e.g., a null field followed by a curl field, or a velocity-dependent field followed by a position-dependent field) have found that a common feature of the initial response to the disturbance created by the change in the mechanical environment is an increase in limb stiffness by muscle cocontraction. However, it is possible that this occurs only because the change is too complex for the CNS to model with sufficient certainty in the space of a few trials. A much stronger test of the generality of cocontraction as an initial response would be to demonstrate that it occurs even for a very simple change in the mechanical environment, e.g., scaling of the force field strength—thus we investigated the initial response to scaled versions of the same spatial force field.

In this study, we unexpectedly either increased or decreased the strength of a position-dependent baseline force field to which subjects had already adapted (Hinder and Milner 2005) for repeated sets of five consecutive trials. Consolidation of learning was prevented by interposing unpredictable numbers of baseline force field trials between the sets and by random selection of upward or downward scaling of the force field strength for a given set. Consequently, it was possible to average the data for each trial position across sets to obtain reliable measures of early learning. Errors in hand path were used to quantify performance. On a randomly selected trial in each set we replaced the scaled force field with stiff elastic walls (i.e., a "channel" trial) similar to that used by Scheidt et

al. (2001) to investigate the evolution of feedforward actions by measuring lateral forces against the channel. Catch trials (e.g., Shadmehr and Mussa-Ivaldi 1994) can provide an indirect estimate of changes in the feedforward command, but it will generally be very inaccurate because of the confounding effects of complex muscle mechanics and limb dynamics and simultaneously changing feedback responses. In contrast, a channel trial eliminates these confounds and provides a direct measure of the feedforward command in the form of the lateral compensatory force. Furthermore, because channel trials do not produce hand path deviations, they are less likely than catch trials to interfere with the evolution of the adaptation to the novel forces. By combining information about hand path error and lateral channel force we were able to explore the relative contribution of feedforward actions to changes in endpoint force and endpoint impedance to compensate for the intermittent changes in the mechanical environment. Our results suggest that the same processes as have been observed for adaptation to complex changes in the mechanical environment are also used when adapting to simple changes. Significant feedforward changes in endpoint stiffness and compensatory lateral force were found almost immediately after the mechanical environment changed. Endpoint stiffness increased on the second trial, whereas lateral endpoint force was appropriately modified to compensate for the change in the mechanical environment, beginning on the third trial.

METHODS

Subjects

Nine subjects (five male, four female; age range 20–31 yr) volunteered to participate in this study. All subjects were (self-reported) right-handed and gave informed consent to the procedures, which were approved by the institutional ethics review committee and conformed to the Declaration of Helsinki.

Apparatus

Two-dimensional horizontal movement of the elbow and shoulder was studied using the parallel-link direct-drive air and magnet floating manipulandum (PFM). Details of its design and operation have been described previously (Gomi and Kawato 1996, 1997). Subjects were seated and a harness was used to constrain the trunk such that the elbow and shoulder joints could move only in the horizontal plane. The forearm and wrist were held in a thermoplastic splint rigidly attached to the manipulandum, constraining movement to two degrees of freedom. Forces were applied to the hand by means of two torque motors driving the parallel linkage (Fig. 1).

The chair's height was adjusted such that the arm was in an approximately 80° abduction. A circular cursor 0.5 cm in diameter, representing the current hand position, was initially positioned in a 2.5-cm start circle, the center of which was located 31 cm directly in front of the shoulder. Both the cursor and the start and target circles were projected onto an opaque horizontal screen suspended above the arm. Thus subjects could not see their arm throughout the experiment.

The PFM generated a position-dependent force field with a parabolic spatial profile (PF), described by the following equation

$$F_x = -G(y_{start} - y)(y - y_{end}) \quad (y_{start} - y)(y - y_{end}) \geq 0$$
$$F_x = 0 \quad\quad\quad\quad (y_{start} - y)(y - y_{end}) < 0 \quad (1)$$

where F_x is the force in the x direction (positive to the right), y_{start} and y_{end} define the boundaries of the force field (0 and 10 cm), and y is the current location of the hand. G was set at 0.32, to produce a maximum
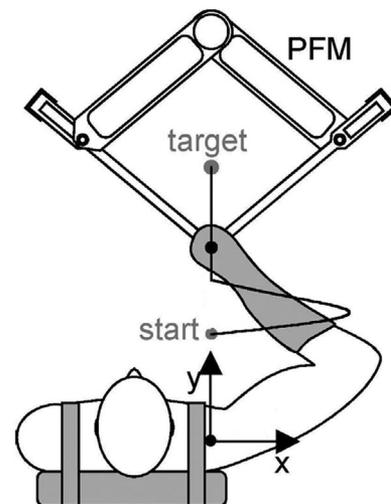

FIG. 1. Schematic view of the parallel-link direct-drive air and magnet floating manipulandum (PFM). Subjects made reaching movements of 25 cm, from the start position, located 31 cm from the shoulder. Parabolic force profile is shown schematically. Force acted over the first 10 cm of the movement, with a peak x force occurring 5 cm from the start position.

lateral force of 8 N in the PF, which was sufficient to produce a significant lateral perturbation of the hand path. G was reset to produce lateral force magnitudes of either 4.5 or 12 N in perturbed trials (see *Procedure*). Force and position signals, sampled at 500 Hz, were acquired from 400 ms before movement onset for a total of 1,400 ms.

Procedure

Subjects made 25-cm horizontal point-to-point movements, away from the body along the y-axis (sagittal plane) to a 2.5-cm-diameter target circle, synchronized with brief tones separated by 600 ms. No forces were present until after movement had been initiated, nor was any force applied by the PFM as subjects moved back to the start position between trials. Subjects initiated each trial on hearing the third tone of a preparatory series of tones. Two tones after completion of the movement indicated the time that the subject should remain in the target circle before returning toward the start position. The final hand position (OK or OUT) and movement duration (OK, LONG, or SHORT) were presented to subjects on a screen. The final position was deemed OK if the cursor ended in the target circle. The duration was deemed OK if it was within ±100 ms of the desired movement time. Subjects were instructed that their goal was to produce movements that always met the OK criteria. The knowledge of results was presented primarily as an incentive for subjects to improve performance. All trials, irrespective of whether the duration and hand position were deemed OK, were used in subsequent data analysis. The nature of the force fields (specifically that they were active only in the first 10 cm of the reach), together with the relatively short movement duration, was intended to encourage feedforward adaptation rather than adaptation of feedback or reflex mechanisms, which would tend to compensate mainly for errors occurring beyond the boundary of the force field.

Training in the PF consisted of 150 trials in which subjects aimed to accurately locate the target within the correct time window. Results pertaining to the kinematic performance and adaptation mechanism used during this PF learning phase have recently been reported (Hinder and Milner 2005). After PF learning, subjects had a short break, to prevent any possible effects of fatigue, before being refamiliarized with the PF for 27 trials. The strength of the force field was then altered on 24 occasions (ΔPF) during a set of five consecutive trials. Trials where the force field strength was altered are designated

as $\Delta PF1, \Delta PF2, \ldots, \Delta PF5$, representing trial position 1, trial position 2, and so forth in the five-trial sequence. Although the spatial profile of the force field did not change, the force field was scaled so that peak force decreased to 4.5 N (ΔPF_{low}) or increased to 12 N (ΔPF_{high}). Whether the force field strength increased or decreased for a given ΔPF set was selected pseudorandomly, such that there was a total of 12 sets for each force field strength. Interposed between each ΔPF set were six to eight PF trials (number selected randomly). In this manner we aimed to study the early stages of adaptation to the two new environments, without allowing full adaptation to occur. Subjects were permitted to rest between trials at any point in the experiment, if they desired.

Each five-trial set consisted of four trials in which the force field strength was altered and one trial where the hand path was mechanically constrained by stiff elastic walls in the lateral (x) direction. This channel trial (Hinder and Milner 2005; also see Scheidt et al. 2001) occurred in place of $\Delta PF2$, $\Delta PF3$, $\Delta PF4$, or $\Delta PF5$. The position of the channel trial (CT) was randomly selected for each ΔPF set with equal probability. Thus CTs occurred three times in each of the four trial positions ($\Delta PF2–\Delta PF5$) for both ΔPF_{low} and ΔPF_{high} sets. Force against the channel provided a measure of subjects' active force production, in isolation from forces imposed by the force field, and without confounding voluntary and involuntary (reflex) forces related to error correction.

In total 315 trials were performed in the ΔPF experiment reported here, in addition to the initial 150-trial PF learning. The entire experiment was completed within 90 min.

Analysis

Maximum lateral deviation from a straight path joining the start and target position was used as the measure of hand path error. Absolute maximum lateral deviation was used to assess errors in each ΔPF trial position relative to PF trials, whereas signed maximum lateral deviation was used to highlight differences in the direction of these errors. Consistent with the PF learning (Hinder and Milner 2005), the largest hand path deviations on initial exposure to the ΔPF and subsequent straightening on later trials occurred beyond the boundary of the force field, i.e., past the first 10 cm of the reach. To assess error before any secondary, corrective movements near the target (located at 25 cm), our measure was calculated in the region from 10 to 23 cm from the start position.

We first determined whether maximum lateral deviation on the 10 PF trials immediately before the first ΔPF set differed from that on the final 10 PF trials, following all ΔPF sets. This enabled us to determine whether PF (baseline) performance remained similar before and after exposure to the ΔPF sets. We also tested whether maximum lateral deviation on the PF trial before each PF set differed from that of PF trials before the first ΔPF set to determine whether six to eight PF trials between ΔPF sets were adequate for subjects to return to baseline performance. To ensure that there was no consolidation of learning between repeated ΔPF sets, we compared hand path error over the 12 repetitions and five trial positions for both types of ΔPF sets. To assess overall trends in performance we compared signed maximum deviation on the ΔPF trials to that on the PF trials before any ΔPF trials (baseline performance), using ANOVA.

Our previous work (Hinder and Milner 2005) showed that a CT had a negative effect on performance of the subsequent PF trial. Thus ΔPF trials immediately after a CT were not included in any analyses of performance. Of course, CTs were also excluded because the lateral error was artificially reduced on these trials.

Trends in the force measured on CTs provided an indication of how subjects modified their lateral force to compensate for the change in force field strength. The lateral force impulse that subjects exerted on CTs within ΔPF sets was compared with the average force impulse on the last three CTs of the PF training session, using one-way ANOVA.

If an internal dynamics model was being progressively refined, we hypothesized that the lateral force impulse on the CTs that replaced ΔPF_{low} trials in positions 2 to 5 would progressively decrease relative to the lateral force impulse recorded in CTs at the end of the PF learning period. In CTs that replaced the ΔPF_{high} trials in positions 2 to 5, we hypothesized that internal model refinement would be characterized by progressive increases in the lateral force impulse to compensate for the higher-strength force field. By combining information about average changes in lateral CT force and reduction in hand path error on each of the five ΔPF trials it was possible to determine whether reductions in hand path error were due solely to increased arm stiffness.

All statistical tests were conducted at the $\alpha = 0.05$ significance level, with the appropriate corrections for low sphericity being made to downward-adjust the degrees of freedom, when required (Howell 1997).

RESULTS

Baseline PF performance

Two-way repeated-measures ANOVA revealed that the maximum lateral deviation was not significantly different between the first 10 and last 10 PF trials of the experiment (first–last main effect: $F = 0.005$, $P = 0.95$); i.e., baseline performance in the previously learned PF did not change as a result of performing the 24 sets of ΔPF trials. The trial number main effect was not significant either ($F = 0.570$, $P = 0.73$), suggesting that there was no systematic change in the adaptive response; i.e., subjects had attained steady-state performance. A one-way ANOVA comparing the 12 PF trials before the first ΔPF set to the PF trial before each of the 12 ΔPF_{high} and 12 ΔPF_{low} sets did not reveal any significant differences ($F = 0.565$, $P = 0.56$), indicating that performance in the PF returned to the baseline level between ΔPF sets. These results provide evidence that the baseline PF performance was the same before the commencement of each ΔPF set and verify our comparisons of ΔPF performance to equal numbers of PF trials, performed before the first ΔPF set.

ΔPF learning

On the first ΔPF trial ($\Delta PF1$, i.e., trial position 1) of each set, subjects were perturbed to the left, in the ΔPF_{low}, and to the right in the ΔPF_{high}, relative to the PF path (Fig. 2). The initial signed maximum deviations, averaged over the 12 sets and nine subjects, were 2.5 cm (rightward) and -1.5 cm (leftward) for the ΔPF_{high} and ΔPF_{low}, relative to the straight line joining the start and target. This represented maximum lateral deviations of 1.9 and -2.0 cm, relative to the PF hand path, indicating that the perturbing effects of the increment and decrement in force field strength were well matched. Figure 3 shows signed maximum lateral deviations, averaged over the ΔPF trials in each position and PF trials that followed ΔPF sets. Rapid initial error reduction occurred in both ΔPF fields between $\Delta PF1$ and $\Delta PF2$, with little further improvement over the next three trials. On returning to the PF there was an aftereffect (error in the opposite direction).

Two-way repeated-measures ANOVA was used to compare the signed maximum deviation of the five consecutive ΔPF trials in both of the perturbed fields. After exclusion of CTs and
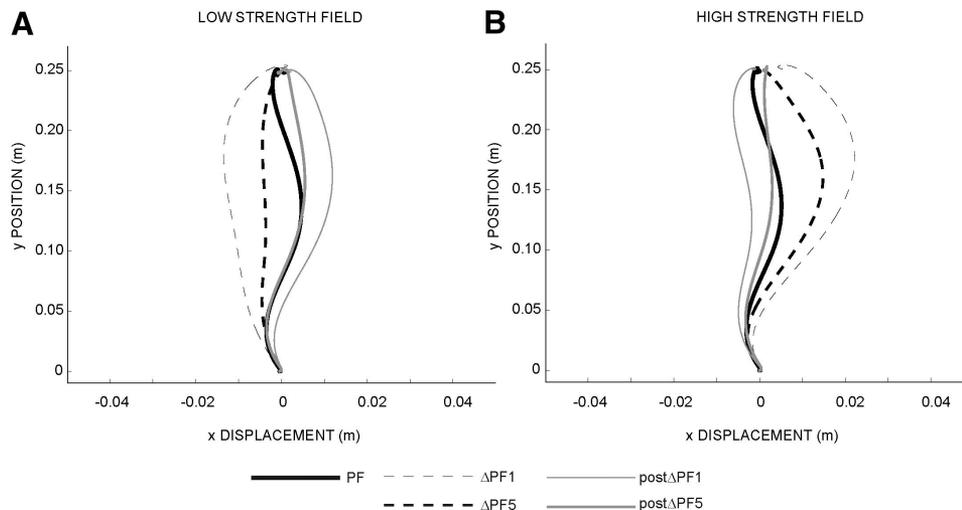
A LOW STRENGTH FIELD

B HIGH STRENGTH FIELD

FIG. 2. Hand paths after changing force field strength and on reexposure to the baseline force field (PF). *A*: ΔPF_{low}. *B*: ΔPF_{high}. Learned hand paths in the PF are shown as a thick black line in both panels. Initial trials in the ΔPF (thin dashed line) were displaced in the direction of the change in force, but were straightened by the $\Delta PF5$ trial (thick dashed line), although trajectories were still displaced with respect to the learned-PF path and straight line. Clear aftereffects occurred on reexposure to the PF (thin gray line), visible as substantial displacements in the opposite direction to that of the $\Delta PF1$ trial. Readaptation to the PF resulted in paths (thick gray line) that were not dissimilar to the learned-PF path. Each plot shows a single subject and represents the average hand paths over all exposures to the perturbed strength field.

PF — $\Delta PF1$ - - - post$\Delta PF1$ ——

$\Delta PF5$ - - - post$\Delta PF5$ ——

ΔPF trials that immediately followed a CT (see *Analysis*), 6 $\Delta PF3$, 6 $\Delta PF4$, and 6 $\Delta PF5$ remained. We randomly selected 6 of the 12 $\Delta PF1$ and 6 of the 9 $\Delta PF2$ for the ANOVA (such that there were equal numbers of trials in each position).

In both perturbed fields there was a significant trial position main effect, i.e., the signed maximum deviation varied across ΔPF trials in positions 1–5 of the ΔPF sets ($F = 18.4$, $P < 0.001$; $F = 16.1$, $P < 0.001$ for ΔPF_{high} and ΔPF_{low}, respectively), indicating a reduction of the magnitude of maximum lateral deviation as subjects adapted to each ΔPF field. The ΔPF set main effect was not significant for either the low or the high strength fields ($F = 0.998$, $P = 0.41$; $F = 2.29$, $P = 0.12$ for ΔPF_{high} and ΔPF_{low}, respectively), suggesting that the intervening PF trials interfered to prevent consolidation of learning between each exposure to the scaled environments. This justified averaging over the ΔPF trials in each position to obtain reliable measures of performance in each scaled environment. The interaction between the position and exposure ($F = 0.545$, $P = 0.72$; $F = 1.04$, $P = 0.41$ for ΔPF_{high} and ΔPF_{low}, respectively) was also not significant.

Post hoc repeated pairwise contrasts were conducted to compare performance between the consecutive trial positions

within the ΔPF sets. For ΔPF_{high}, the magnitude of the signed maximum deviation in $\Delta PF2$ was significantly less than that in $\Delta PF1$ ($F = 18.8$, $P = 0.003$). There was a tendency, although not statistically reliable, for reduction of signed maximum deviation between $\Delta PF2$ and $\Delta PF3$ ($F = 4.49$, $P = 0.067$). Differences between the remaining trial positions were nonsignificant ($P > 0.50$). For ΔPF_{low}, there was a significant decrease in the magnitude of the signed maximum deviation between $\Delta PF1$ and $\Delta PF2$ ($F = 13.9$, $P = 0.006$), but not between any of the subsequent pairs of trial positions ($P > 0.20$).

In the fifth trial position of the ΔPF_{low} set, absolute maximum deviation did not differ significantly from that of PF trials ($P = 0.23$), although signed maximum deviation was different ($P < 0.05$) because ΔPF_{low} trials deviated to the left, whereas PF trials deviated to the right of a straight line joining the targets. In contrast, in the fifth trial position of the ΔPF_{high} set, absolute (and signed) deviation was still greater than that of PF trials ($P < 0.05$). One feature of the ΔPF_{low} hand paths, which is different from both PF and ΔPF_{high} hand paths, is that they curve in only one direction, i.e., to the left, and that this curvature is almost completely eliminated by $\Delta PF5$.
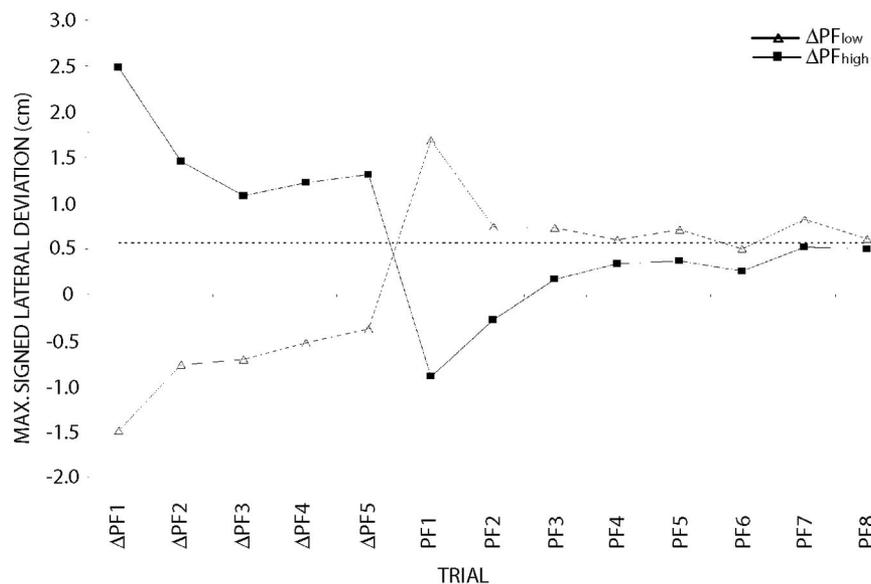

ΔPF_{low}

ΔPF_{high}

FIG. 3. Signed maximum deviation in the 5 ΔPF trials and 8 subsequent PF trials. ΔPF_{high} and subsequent PF trials are indicated by solid squares (and thin line), whereas ΔPF_{low} trials are indicated by open triangles (and thin line). Horizontal dotted line represents baseline performance, i.e., mean signed maximum deviation of PF trials after PF learning and before the first ΔPF set. Data are averaged across all subjects and repeated ΔPF sets.

Reexposure/relearning in the PF following ΔPF sets

On reexposure to the PF, following ΔPF sets, subjects were perturbed in the opposite direction to the kinematic error observed in ΔPF1 (Fig. 3, *right*). This characteristic aftereffect indicates that subjects did not adapt to the perturbed strength fields by merely increasing the stiffness of their arm to reduce lateral deviation. Rather, the aftereffects indicate that subjects modified their lateral force to more accurately compensate for the change in magnitude of the force field.

We hypothesized that subjects would quickly readapt to the PF between ΔPF sets. Two-way repeated-measures ANOVA was used to determine whether the signed maximum deviation in each trial position following the ΔPF sets was significantly different from the signed maximum deviation of PF trials before the first ΔPF set (baseline performance). Sets where postperturbation PF trials followed trials in which a CT had replaced ΔPF5 were not included in the analysis, due to possible attenuation of aftereffects by the CT (Milner et al. 2007). This left 9 sets for the analysis in the first PF reexposure position; thus we randomly selected from 9 of the 12 PF reexposure trials in positions 2–6, and compared these to the 9 PF trials before the first ΔPF set. Postperturbation PF trials in positions 7 and 8 were not included in the analysis because there were fewer trials in these positions since the number of PF trials between ΔPF sets varied randomly from 6 to 8.

There was a significant main effect of PF trial number ($F = 12.2$, $P < 0.001$; $F = 9.95$, $P < 0.001$ following ΔPF_{high} and ΔPF_{low}, respectively), highlighting that the magnitude of the lateral deviation was reduced as subjects performed more PF trials. The exposure (post-ΔPF set) number main effect ($F = 1.20$, $P = 0.33$; $F = 0.748$, $P = 0.56$, following ΔPF_{high} and ΔPF_{low}, respectively) and the interaction term ($F = 1.29$, $P = 0.28$; $F = 1.02$, $P = 0.47$, for the ΔPF_{high} and ΔPF_{low}, respectively) were both nonsignificant, indicating that the relearning of the PF did not change with the number of ΔPF_{high} and ΔPF_{low} sets.

Post hoc pairwise comparisons of PF trials in each of the six positions following ΔPF trials to PF trials before the first ΔPF set (pre-ΔPF) revealed that the magnitude of the signed maximum deviation of the first two trial positions following the ΔPF_{high} ($F = 36.3$, $P < 0.001$; $F = 13.8$, $P = 0.006$ for the first and second trial positions, respectively) was significantly higher than that of the pre-ΔPF trials, whereas the signed maximum deviation of the PF trials in the remaining positions was not significantly different ($P > 0.45$ in all cases). Similarly, the signed maximum deviation of the first two PF trial positions following ΔPF_{low} sets was greater in magnitude ($F = 14.8$, $P = 0.005$; $F = 23.6$, $P = 0.001$ for the first and second trial positions, respectively) than that of the pre-ΔPF trials. The signed maximum deviation of the remaining trial positions was not significantly different from that of the pre-ΔPF trials ($P > 0.17$ in all cases). These results indicate that subjects successfully readapted to the PF after each ΔPF set.

ANOVA of the percentage reduction in signed maximum deviation between the first and second trials, after a change in force field strength, showed no significant difference for the original PF learning, ΔPF learning, and relearning of the PF following ΔPF sets ($F = 0.789$, $P = 0.50$).

Force recorded in channel trials

Despite the lack of significant improvement in performance after the second ΔPF trial, learning may not have ceased. Previous studies have shown that the early responses to a change in mechanical environment involve generalized muscle cocontraction to increase limb stiffness (Franklin et al. 2003; Thoroughman and Shadmehr 1999). Consequently, although hand paths may not have changed significantly after ΔPF2, subjects could have reduced limb stiffness and modified the applied force to more accurately compensate for the change in force field strength. Channel trials provided a means to assess subjects' applied lateral force in the absence of confounding effects of the force field or feedback error correction.

Most subjects scaled-down their lateral force for ΔPF_{low} sets (Fig. 4), whereas they scaled-up their lateral force for ΔPF_{high} sets (Fig. 5), relative to the force recorded after PF learning. Spatial profiles of lateral force exerted on channel trials were generally not parabolic in shape; i.e., they did not mimic the shape of the force field. Nor did they match the spatial *extent* of the force field; i.e., the lateral force did not drop to zero until the movement had passed about 5 cm beyond the force field boundary. However, this was also the typical adaptation to the baseline PF (Hinder and Milner 2005). Consequently, we concluded that it was more appropriate to compare ΔPF hand paths to the baseline PF hand path than to the straight line joining the start and end targets. Using the ΔPF force (*Eq. 1*) and the mean baseline PF trajectory, the lateral force required to reproduce the PF path was computed from inverse dynamics. These are compared with the actual ΔPF force profiles in Figs. 4 and 5 to illustrate the extent to which force error was reduced. In both figures it is clear that almost all subjects reduced the force error to some extent and that several subjects had almost completely eliminated force error after five ΔPF trials.

Figure 6 shows mean force impulses on the CTs, normalized to the average force impulse of the last three CTs of the PF training session. Note that there were no differences in electromyographic (EMG) profiles (not shown) between ΔPF trials that preceded CTs and the CTs until 175 ms after movement onset. Therefore any voluntary or reflexive responses to the imposition of a CT are not reflected in force responses before this time. Furthermore, reflex responses later in the trial are unlikely because channel trials produced little hand path error with respect to the learned trajectory. Consequently, these force impulses can be considered to represent feedforward commands to muscles. One-way ANOVA revealed that for both ΔPF_{low} and ΔPF_{high} there was a significant trial position main effect ($F = 5.25$, $P = 0.015$ and $F = 4.94$ $P = 0.011$, respectively). Subjects progressively adapted to altered force field strength by respectively decreasing or increasing the lateral force impulse, relative to the force impulse of CTs at the completion of the PF training.

Pairwise comparisons were conducted to compare the force impulses on CTs in positions 2 to 5 with CTs at the end of PF training (CT0). For ΔPF_{low} sets, force impulse on CT2 was not significantly different from the CT0 force impulse ($P > 0.2$), whereas the force impulses on CT3, CT4, and CT5 were all significantly lower than the CT0 force impulse ($P < 0.05$). For ΔPF_{high} sets, force impulse on CT2 exhibited a tendency to be
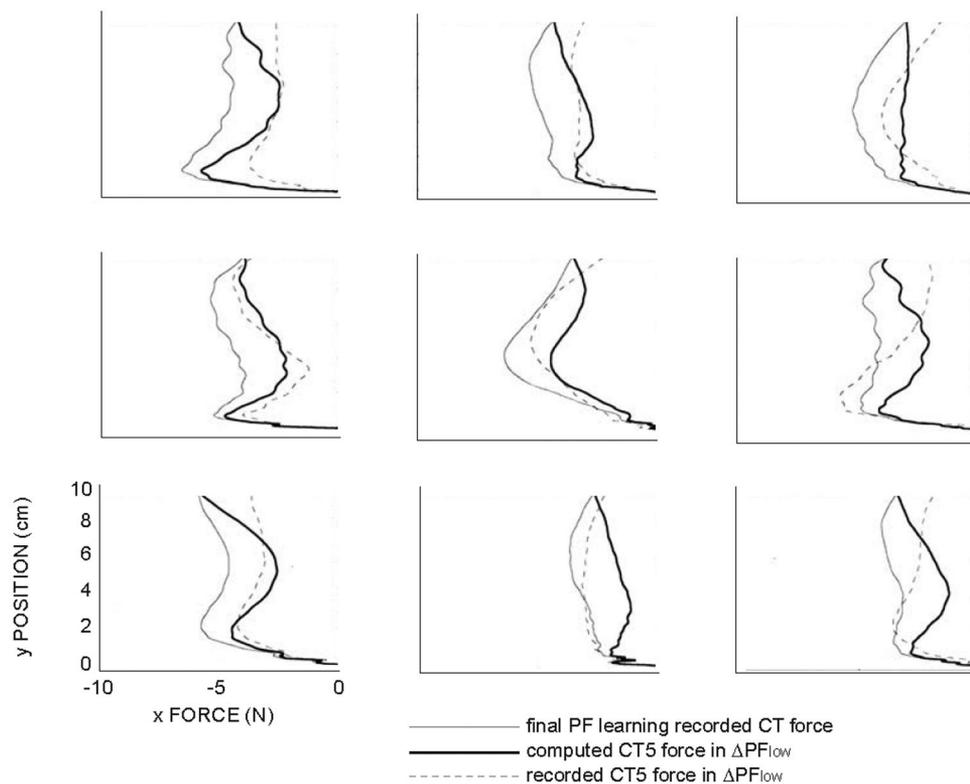
FIG. 4. Force profiles in the ΔPF_{low}. Thin solid line represents the average force recorded in the final 5 channel trials (CTs) of PF learning. Thick solid line represents the computed force required to move along a path similar to the learned-PF path in the ΔPF_{low}. Dashed line represents the average force recorded in the 3 CTs that replaced ΔPF_{low} trials in position 5. Nine individual subjects are shown in the 9 panels.

——— final PF learning recorded CT force
——— computed CT5 force in ΔPF_{low}
- - - - - recorded CT5 force in ΔPF_{low}

higher than the CT0 force impulse, although this did not reach statistical significance ($P = 0.06$). Force impulses on CT3, CT4, and CT5 were all significantly higher than the CT0 force impulse ($P < 0.05$).

DISCUSSION

This study was designed to investigate the adaptive responses to one of the simplest changes in the mechanical environment: scaling of the perturbing force. This was done by
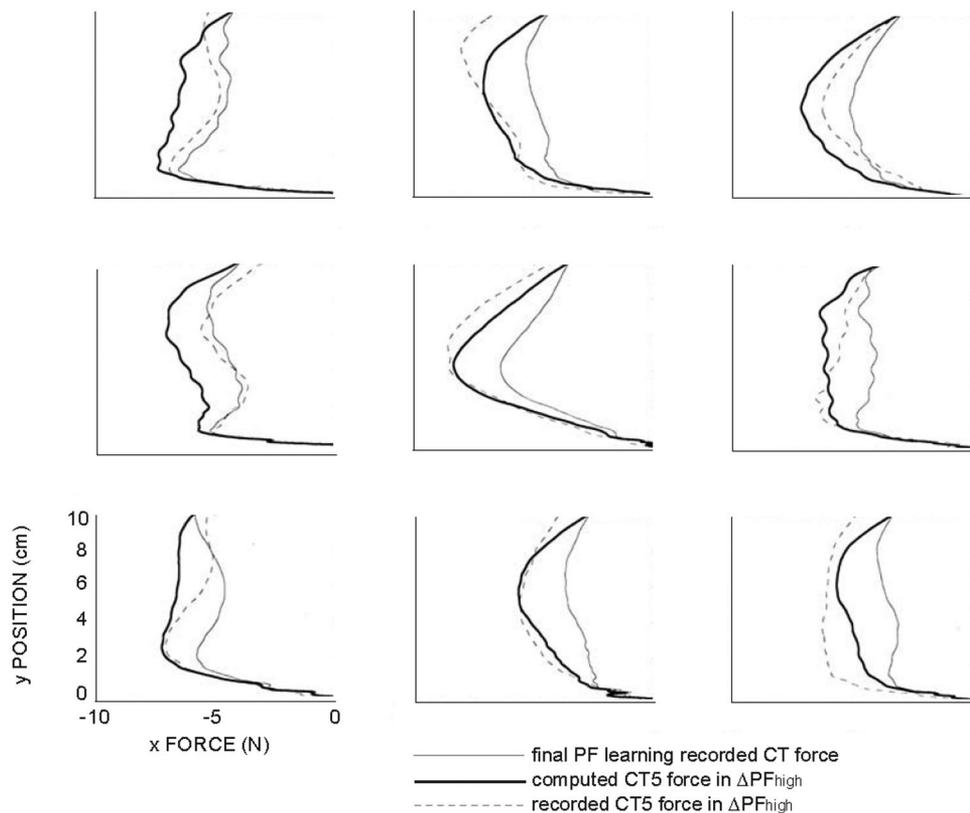

FIG. 5. Force profiles in the ΔPF_{high}. Thin solid line represents the average force recorded in the final 5 CTs of PF learning. Thick solid line represents the computed force required to move along a path similar to the learned-PF path in the ΔPF_{high}. Dashed line represents the average force recorded in the 3 CTs that replaced ΔPF_{high} trials in position 5. Nine individual subjects are shown in the 9 panels.

——— final PF learning recorded CT force
——— computed CT5 force in ΔPF_{high}
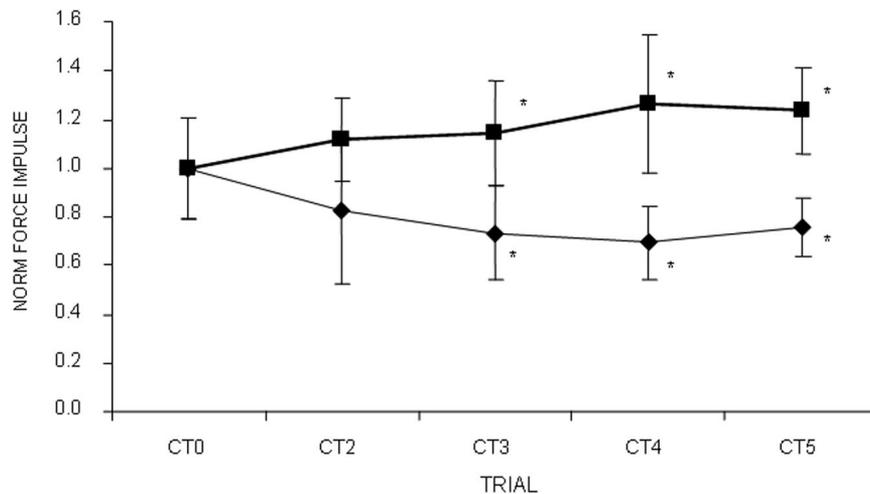- - - - - recorded CT5 force in ΔPF_{high}

FIG. 6. Force impulse in CTs that replaced ΔPF trials in positions 2–5. Normalized force impulses calculated from movement onset to 175 ms. Force impulses in this interval can be considered to represent subjects' feedforward force production. Data are averaged over the 3 CTs in each position and represent the average across all subjects. * indicates force impulses in that were significantly lower (ΔPF$_{low}$) or higher (ΔPF$_{high}$) than the force impulse of PF trials, i.e., CT0 ($P < 0.05$).

intermittently changing the magnitude of the perturbing force (ΔPF) on repeated occasions for sets of five trials, with variable numbers of baseline force field (PF) trials between consecutive ΔPF sets. As well as investigating basic mechanisms of motor learning, it addresses an important issue in motor control that we encounter in our everyday lives: the ability to quickly adapt to a change in the magnitude of an expected perturbing force. Results indicated that the hand path error was similar each time the ΔPF occurred. Thus the intervening PF trials prevented consolidation of learning of the ΔPF. Hand path error on ΔPF trials indicated that the majority of the error reduction occurred by the second trial position after a change in force field strength, whereas lateral force recorded on channel trials (CTs) suggested that compensatory force did not begin to change until the third trial position. Taken together these findings imply that hand path error was initially reduced by increasing the stiffness of the arm and that lateral force was then progressively modified as a more accurate internal model of the altered force field was acquired.

Subjects changed their feedforward responses after the first ΔPF trial in each set, modifying their motor commands to produce significantly straighter hand paths on ΔPF2 trials. However, no further significant improvements in hand path occurred between ΔPF2 and ΔPF5. This is not completely unexpected because we previously found a statistically significant incremental improvement in performance on the second but not the third trial after a change in the mechanical environment (Milner and Franklin 2005). In addition, incremental improvement in performance in ΔPF4 and ΔPF5 may have been partly masked by an interference effect of prior CTs. In previous studies, we found that imposing a CT during the early stage of learning reduced the adaptive response on the following trial (Hinder and Milner 2005; Milner et al. 2007). Although trials that were immediately preceded by a CT were excluded, the average error in ΔPF4 was likely inflated by the effect of CT2 and in ΔPF5 by the effect of CT2 and CT3. Thus it is conceivable that a significant reduction in error in ΔPF5 compared with ΔPF2 would have been found had there been no CT in the ΔPF set.

In a previous study (Lai et al. 2003), we found that altering the force field magnitude, without modifying the structure of the field, did not affect the percentage error reduction after five trials. In the present study, all ΔPF5 trials were preceded at

some point by CTs, as were most ΔPF4 trials. Consequently, we could not make a valid comparison of the learning rate during ΔPF sets compared with the baseline PF. Instead, we focused on the first and second trials after a change in force field strength. Our results indicated that the percentage reduction in maximum lateral deviation from the first to the second trial was no greater on ΔPF or post-ΔPF trials than that for the original PF learning (i.e., from null field to PF). Consequently, there did not appear to be any savings in learning, although it is possible that differences might have been uncovered had we been able to compare learning rates. For example, Davidson and Wolpert (2004) reported that adaptation to upward scaling of the force field strength occurred more rapidly than adaptation to downward scaling.

By design, we did not expect to find consolidation of learning from one ΔPF set to another. Our objective was to repeat the initial phase of learning multiple times to improve the reliability of the data. In this respect, our study differed from that of Davidson and Wolpert (2004), where force field strength was scaled upward or downward only once after a relatively long adaptation period (160 trials) and remained scaled thereafter. Although they were able to compare learning rates, their experimental design did not allow them to specifically address the nature of the adaptation that occurred in the scaled force fields. The success of our experimental design in preventing consolidation is attributable to interference from intervening PF trials between ΔPF sets and from interference attributable to random selection of an increment or decrement in the force field strength from one ΔPF set to the next. Such interference would arise if there were only a single internal dynamics model that had to be incrementally modified each time the force field strength changed. This would imply that there could not be multiple internal models of the same force field structure for different force field strengths that could be independently selected. A parsimonious strategy for allocating resources for neural computation could be that separate internal models exist only for relatively large differences in the structure of the environmental dynamics and when the differences are small the current internal model must be incrementally corrected. Such a strategy could also place limitations on the amount of savings when force field strength changed.

After five consecutive trials in the ΔPF$_{low}$, subjects were able to move along a path that was as straight, relative to a

straight line, as the path after the completion of training in the PF, although the maximum lateral deviation was now to the left rather than to the right; i.e., subjects *overcompensated*. The greater lateral deviation at the end of ΔPF_{high} sets compared with baseline PF hand paths may result from neuromuscular limitations in the ability to produce the required patterns of torque (Hinder and Milner 2005) or it may be a trade-off strategy between higher muscle activation and lower error. One reason to suggest that the latter may be the case is that the maximum lateral deviation is actually lower in the second PF trial position after the end of a ΔPF_{high} set than baseline. This demonstrates that subjects are capable of producing straighter paths than baseline. However, this is almost certainly attributable to higher muscle activation where increased stiffness of the arm compensates for inaccuracies in torque profiles. It is unlikely that any of our observations are related to the physical strength of subjects. This varied greatly, yet we found little difference in the magnitude of hand path errors among the subjects.

It is likely that the reduction in performance error that occurred between $\Delta PF1$ and $\Delta PF2$ was principally due to an increase in the stiffness of the arm because the lateral force impulse in CT2 was not significantly different from that after PF learning, suggesting that there was no change in the internal model. Although there was no statistically significant progressive reduction in performance error after $\Delta PF2$ for either the low or high strength field, evidence from the channel trials indicated that force adaptations were still occurring. Subjects modified their lateral force over the course of the five ΔPF trials. In particular, force measured in CT2 and CT3 indicated that subjects significantly altered lateral force between $\Delta PF2$ and $\Delta PF3$ in accordance with the change in force field strength. The feedforward nature of the force adjustments is clear because subjects learned to overpower the force field at the onset of movement, deviating into rather than away from the force field. The amount of deviation clearly changed between $\Delta PF1$ and $\Delta PF5$. The time at which the change was initiated was too early in the movement to be attributed to feedback error correction, whether reflex or voluntary. An additional argument for its not being a delayed response to error produced by the force field (feedback) is that the initial lateral movement was always opposite to the action of the force field. The progressive change in the lateral force impulse is thus convincing evidence that the internal model was being progressively updated despite the lack of additional straightening of the hand path. The data in Fig. 6 suggest that this trend continued for $\Delta PF4$, although not for $\Delta PF5$. However, the lack of an incremental change in the force impulse from $\Delta PF4$ to $\Delta PF5$ may simply reflect normal trial-to-trial variability. For example, during the first 75 trials of the original PF training session decrements of up to 20% in the mean force impulse were occasionally observed despite a significant overall positive slope (Hinder and Milner 2005). Therefore the results support an incremental modification of the force impulse consistent with the change in force field strength.

As pointed out earlier, the paradigm used in this study addresses the issue of the ability to rapidly adapt to a change in the strength of an expected perturbing force. One of the most common situations where this occurs is during reaching movements. Coriolis and centrifugal forces during reaching will tend to perturb the hand laterally with respect to the target direction.

These forces vary with the mass and moment of inertia of an object carried in the hand and with the relative and absolute angular velocity of the shoulder and elbow joints. Although the CNS expects these forces and adapts motor commands appropriately to compensate for them, inaccurate estimation of the mass or moment of inertia of a handheld object or an attempt to execute a movement faster than previous rehearsals would produce an error orthogonal to the principal direction of motion. The rapid adjustments in cocontraction and compensatory feedforward commands observed in this study allow us to adapt quickly and avoid the sort of bumbling behavior that would arise from using only feedback error correction.

A model of learning that involves two processes was recently proposed by Smith et al. (2006) and has been used to account for faster adaptation to downward scaling of a force field than readaptation to the baseline condition, as reported by Davidson and Wolpert (2004). In the Smith et al. model, one process responds weakly to error but retains information well (long timescale), whereas the other responds strongly but has poor retention (short timescale). The long time constant reported by Smith et al. (2006) is similar to the time constants that we have found for reduction in muscle activation (Franklin et al. 2003; Hinder and Milner 2005), whereas the short time constant is similar to our time constants for error reduction (Franklin et al. 2003; Hinder and Milner 2005; Milner and Hinder 2006; Osu et al. 2003). EMG recordings in previous studies (Franklin et al. 2003; Hinder and Milner 2005; Milner and Franklin 2005) suggest that the short time constant (fast process) is related to the combined effect of stiffening the arm through muscle cocontraction and relatively inaccurate force compensation for the perturbation—i.e., a gross increase in muscle activation. The slower process (long time constant) represents gradual shaping of the pattern of muscle activation for accurate force compensation for the perturbation with concomitant reduction of muscle cocontraction. Only the faster process would have been present during the ΔPF sets and the relatively rapid return to baseline performance in the PF can be explained by there being very little interference with the accurate force compensation already learned for the PF, during the ΔPF sets.

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