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Persistence of Motor Adaptation During Constrained, Multi-Joint, Arm Movements

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Abstract

We studied the stability of changes in motor performance associated with adaptation to a novel dynamic environment during goal-directed movements of the dominant arm. Eleven normal, human subjects made targeted reaching movements in the horizontal plane while holding the handle of a two-joint robotic manipulator. This robot was programmed to generate a novel viscous force field that perturbed the limb perpendicular to the desired direction of movement. Following adaptation to this force field, we sought to determine the relative role of kinematic errors and dynamic criteria in promoting recovery from the adapted state. In particular, we compared kinematic and dynamic measures of performance when kinematic errors were allowed to occur after removal of the viscous fields, or prevented by imposing a simulated, mechanical “channel” on movements. Hand forces recorded at the handle revealed that when kinematic errors were prevented from occurring by the application of the channel, recovery from adaptation to the novel field was much slower compared with when kinematic aftereffects were allowed to take place. In particular, when kinematic errors were prevented, subjects persisted in generating large forces that were unnecessary to generate an accurate reach. The magnitude of these forces decreased slowly over time, at a much slower rate than when subjects were allowed to make kinematic errors. This finding provides strong experimental evidence that both kinematic and dynamic criteria influence motor adaptation, and that kinematic-dependent factors play a dominant role in the rapid loss of adaptation after restoring the original dynamics.

INTRODUCTION

There is considerable theoretical and experimental support for the notion that reaching movements are generated by the CNS executing a set of commands programmed in advance of the movements (Bock 1993; Ghez et al. 1990; Happee 1993; Hoff and Arbib 1992; McIntyre et al. 1995; Scheidt and Rymer 2000). Preprogramming of movements is also called “feed-forward” control, in contrast to feedback control, where motor commands are generated by the CNS in response to sensory information as movements proceed. Feed-forward control is necessary due to the long delays associated with visual and proprioceptive feedback pathways. The presence of these delays in any feedback controller would lead to well-known and severe forms of instability (cf. Houk and Rymer 1981). However, for a feed-forward controller of the arm to be useful, it must be able to predict (and compensate for) the limb's response to disturbances as might occur during the usual manipulation of objects. That is, a feed-forward controller must contain an *internal model* of how the controlled system behaves (e.g., a model of limb dynamics) (Jordan 1993; Kawato 1991; Wolpert et al. 1995). An essential feature of any such model is the capacity to adapt. For example, a model that captures the dynamics of a child's arm would not be much use in controlling an adult's arm. Similarly, changes in load and orientation with respect to gravity will also impact the limb's response to any given motor command sequence (Miall and Wolpert 1996). Several experimental studies have shown that human arm movements do indeed exhibit adaptive behavior when subjects are presented with predictable, perturbing, mechanical environments (Conditt et al. 1997; Dizio and Lackner 1995; Lackner and Dizio 1994; Shadmehr and Brashers-Krug 1997; Shadmehr and Mussa-Ivaldi 1994). Furthermore, this adaptation also exhibits characteristic patterns of generalization beyond the training region of the workspace (Shadmehr and Mussa-Ivaldi 1994) as well as beyond the set of training movements within the same region of the workspace (Conditt et al. 1997; Sainburg et al. 1999).

Recently, there have been significant advances in our understanding of how the CNS adapts arm movements to changes in arm and environment dynamics. However, we still do not know which factors trigger and drive the adaptation process. There are two competing views on this issue. According to one view, movement adaptation is guided by the requirement to maintain an “invariant plan” of movements. This movement plan dictates the

desired shape and temporal profile of the movement (i.e., the movement kinematics) (Hogan 1984; Wolpert et al. 1995). According to the opposite view, movement adaptation is guided by the physical demands of the movement. That is to say, adaptation is aimed to optimize dynamical characteristics of movement such as effort, power, joint torque or muscle force (Gordon et al. 1994; Stein et al. 1985; Uno et al. 1989). The observed kinematics would then be a consequence of this dynamical optimization.

It is experimentally difficult to discriminate between dynamic and kinematic optimization because change in dynamics (for example, in the pattern of muscle-generated torques) typically leads to a change in kinematics (i.e., in the limb's trajectory). In these experiments we have developed a new paradigm that allows separation of the effects of dynamic and kinematic optimization. This paradigm is based on the observation that if the hand path is constrained by a rigid, rectilinear guide, then torques that tend to move the hand away from this path result in increased contact force between the hand and the guide, without altering the movement trajectory. Under these circumstances, two patterns of control torque that differ greatly in the force produced orthogonal to the guide would result in very similar trajectories of the arm. If the motor system performed only kinematic optimization, then it would presumably not alter either control pattern. Otherwise, one would expect to see gradual changes of the contact forces reflecting a progression toward the more optimal dynamic pattern.

We asked 11 subjects to execute reaching movements of the hand between 2 targets in the horizontal plane. Subjects first practiced the movements while holding the endpoint of a low-impedance manipulator that generated no active resistance to movement (the *null field* condition). Then we let subjects execute the same movement against a disturbing force generated by the manipulator and acting orthogonal to the line joining the two targets. After adaptation, subjects had learned to generate the reaching movement while producing an orthogonal force equal and opposite to the perturbation. At this point a second mechanical environment was presented to seven of the subjects: the manipulator was programmed to generate a stiff mechanical guide (the *channel field* condition), enforcing a straight-line path between the two targets. The remaining four subjects were exposed to an alternating sequence of channel field and null field trials following adaptation. Measurements of hand position and force following adaptation suggest that while both kinematic and dynamic factors may motivate the loss of adaptation, kinematic errors (specifically, *path* errors) led to quicker loss of adaptation (disadaptation) than dynamic criteria such as the presence of contact force against the guide. In particular, in the absence of kinematic errors, subjects persisted for more than 15 times longer in an adapted state even though they generated considerable force at the hand that did negligible work and was not required to achieve accurate reaching. Portions of this work have appeared in abstract form (Scheidt et al. 1997).

METHODS

Eleven subjects with no known neuromotor disorders, ranging in age from 23 to 38 yr, consented to participate in this study. The subjects made goal-directed movements in the horizontal plane while holding the handle of a two-joint, robotic manipulator (Fig.1A). The robotic apparatus employed was similar to that described in detail by Mussa-Ivaldi and colleagues (Conditt et al. 1997; Shadmehr and Mussa-Ivaldi 1994). The manipulandum is equipped with position encoders that were used to record the angular position of the two robotic joints with a resolution exceeding 20 arcsec of rotation (Teledyne Gurley, model 25/045-NB17-TA-PPA-QAR1S). The position, velocity, and acceleration of the handle were derived from these two signals. The robot is equipped with two torque motors that were used to generate both the viscous field of Fig. 1B and the mechanical channel field of Fig. 1C (PMI Motor Technologies, model JR24M4CH). Endpoint forces and torques were monitored with a six degree-of-freedom load cell fixed to the handle of the robot (Assurance Technologies, model F/T Gamma 30/100). The subjects' arms were supported against gravity either via a sling attached to the 8-ft ceiling (*test subjects T1, T3, T4, and T6; control subjects C1, C2, C3, and C4*) or via a low-mass arm support (North Coast Medical, model NC38017; *test subjects T2 and T5; truncated test subject TT1*; Fig.1A). The supports were

adjusted so that the upper arm was abducted by 90°. The shoulders were restrained using a Velcro torso support.

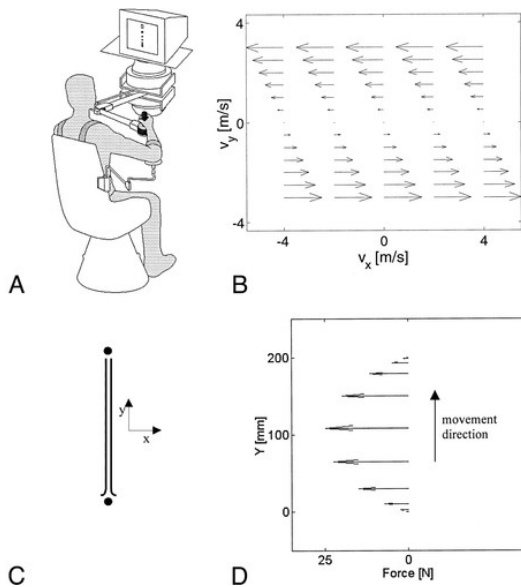


Fig. 1. A: reaching movements in the horizontal plane were made as the subject grasped and moved the handle of a 2 degree-of-freedom robot manipulandum. The robot was comprised of a 5-bar linkage with torque motors controlled by a dedicated PC. Targets were presented to the subjects via a computer monitor situated directly above the robot arm. A typical subject could see his or her hand and the visual cursor representing it at all times. B: graphical representation of the perpendicular field presented to the subjects. The perturbation was perpendicular to the direction of intended motion, and its magnitude was proportional to the hand velocity along the intended movement direction. C: graphical representation of the shape of the mechanical channel. The channel was approximately 1 mm wide, and the stiffness of the walls was 6,000 N/m. The initial target (at the mouth of the channel) and final targets were separated by a distance of 20 cm. D: sketch of the forces a subject might experience at the hand in the perpendicular field if he or she made a reaching movement with a bell-shaped (Gaussian) velocity profile.

“Beginning” and “end” targets were presented on a computer monitor situated above the manipulandum. These visual targets were separated by a distance corresponding to 20 cm in the plane of the arm and were situated along the line passing through the approximate center of rotation of the subject's shoulder. The position of the hand was displayed as a small cursor on the overhead monitor. Typical subjects were able to see their hand and the visual cursor representing it at all times.

Throughout the entire experimental session, subjects were instructed to “make a reaching movement from the ‘beginning target’ to the ‘ending target’ in one half second.” The computer provided qualitative feedback of movement duration after each trial (either too fast, too slow, or just right; 0.45–0.55 s). The subject was also instructed to relax after each movement while the manipulandum moved the hand slowly back to the beginning target. This protocol was designed to allow subjects to experience the limb's mechanical environment along a limited set of state trajectories. Subjects were allowed a brief rest (~2–3 min) after every 200 movements. During the rest period, they were instructed to remain still and to simply relax.

Three different mechanical environments were presented to the subjects: a *Null Field* (\emptyset), a *Perpendicular Field* (∇) and a *Channel Field* (\parallel). To generate the null field, the torque motors were commanded to output zero torque. In this case subjects moved the small inertia of the manipulandum. During the adaptation phase of the

experiment, the subjects experienced the perpendicular field as a force at the hand ($[F_x F_y]^T$), which was proportional to the velocity of the hand ($[u_x u_y]^T$; Eq. 1)

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} 0 & -15 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} u_x \\ u_y \end{bmatrix}$$

Equation 1

Here, the endpoint force, $[F_x, F_y]^T$, is given in Newtons (N), the viscosity is in Newtons per meter per second, and the velocity, $[u_x, u_y]^T$, is in meters per second. The viscous field is designed to deflect the hand perpendicularly from its intended path with a force proportional to hand velocity along its path. A subject performing the movement in the allotted time could expect to experience a peak deflecting force of about 25 N (Fig. 1D).

During the channel phases of the experiment the subjects moved in a very stiff mechanical guide bounding the straight-line path between initial and final targets (Fig. 1C). It is important to note that the channel constrained the hand path, but not movement timing since the subjects could move at any speed and with almost any force they chose. The overall effect of the channel was to minimize the kinematic consequence of any off-direction (perpendicular) force exerted by the subject. The channel was implemented as in Eq.2

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -6000 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} g(x) \\ y \end{bmatrix} + \begin{bmatrix} -60 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} u_x \\ u_y \end{bmatrix} \quad [N]$$

$$g(x) = \begin{cases} x - h(y) & x \geq h(y) & [m] \\ 0 & -h(y) < x < h(y) & [m] \\ x + h(y) & x \leq -h(y) & [m] \end{cases}$$

$$h(y) = \begin{cases} \frac{0.05}{y - y_0} & y > y_0 & [m] \\ 0.05 & y \leq y_0 & [m] \end{cases}$$

Equation 2

Here again, the endpoint force is given in Newtons (N), the stiffness in Newtons per meter and the position in meters. A velocity-dependent term is added to maintain stability in the direction perpendicular to the intended movement (the off-axis direction) and consequently does not impede nor assist movement toward the target. In addition to the off-axis viscosity term, it was found necessary to implement a smoothly diminishing dead-zone $[h(y)$; region of zero-commanded motor torque] within the channel $g(x)$ to minimize chatter (high-frequency oscillations due to discontinuous control laws such as Eq. 2), which could provide a significant cue to the subjects that the operating environment of Eq. 1 had been replaced by that of Eq. 2. y_0 is the y -axis location of the starting target.

Experimental conditions and procedures

The task consisted of a single reaching movement of approximately 0.5 s duration directed along the line passing through the subject's shoulder center of rotation and the robot "shoulder" center of rotation (Fig. 1A). Subjects were separated into two groups: a "Test Group" ($n = 7$) and a "Control Group" ($n = 4$). The experiment was conducted in six phases. The first phase consisted of 100 null field (\emptyset) movements performed with the manipulandum motors generating no torque. The second phase consisted of 100 channel (\blacksquare) movements performed in the presence of a very narrow and very stiff mechanical guide bounding the straight-line path connecting the two visual targets. The third phase consisted of another set of 100 null field movements to

reassert initial conditions following the channel movements. These first three phases were intended to reveal the subject's unadapted motor behavior in both the null and channel environments. The fourth phase consisted of 150 movements in the perpendicular field (⊥; Fig. 1B) designed to perturb subjects away from their unadapted pattern of limb control during this simple reaching task. Phase five was different for the two groups. Six of the seven subjects in the “Test Group” were required to make 150 channel movements (Fig. 1C) while subjects in the “Control Group” performed 150 alternating channel and null field movements interleaved in a 1:1 ratio (mixed fields: ||∅||∅). (The 7th test subject performed a truncated version of the Test Group experiment as described below to explore the effects of limited exposure to the mechanical channel environment). Finally, all subjects made 50 null field movements to bring the typical session total to 650 movements.

The mechanical channel we employed was designed to be compatible with both the adapted and unadapted patterns of motor control. By this we mean that subjects would move along a straight-line hand path and thereby achieve the desired reaching movement whether they reverted to the unadapted motor controller or maintained the adapted pattern of control following adaptation.

Data analysis

We used simple measures of kinematic and dynamic behavior to assess subject performance on this goal-directed reaching task. Hand path error was defined as deviation of the hand from a straight-line trajectory passing between the initial and final targets. Kinematic error was quantified by averaging the unsigned, hand path error over the entire movement. For the purpose of discussion we will regard this integrated deviation as a measure of kinematic performance, assuming that subjects intended to make straight-line movements of their hands. Dynamic performance was quantified by calculating, over each movement, the peak hand force perpendicular to the direction of movement. This measure of dynamic performance was found to provide compelling evidence of motor adaptation without exposing subjects to periodic “catch trials.” A catch trial is a null field trial interjected in a block of trials where the endpoint field is significant; catch trials have been used to assess adaptation by characterizing its aftereffect. However, recent evidence suggests that catch trials may themselves influence and degrade adaptation (Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 1997). Our protocol allowed us to probe for aftereffects of adaptation without disturbing the adaptation process itself.

We estimated the time course of disadaptation by fitting a falling exponential function to the dynamic performance data from phase 5 for each subject. This model has three free parameters: gain, A , time-constant, λ , and offset, B (Eq. 3). Offset is a baseline value taken to be the mean of the peak force within phase 2 of the experiment

$$y = Ae^{-(i/\lambda)} + B$$

Equation 3

The parameter i is a trial index taking its origin at the boundary between experimental phases 4 and 5.

RESULTS

Kinematic performance

Figure 2 shows the effects of the perpendicular force field and channel perturbations on the hand trajectories of a control and a test subject (Fig. 2, A and B, respectively). Selected trials from each of the six blocks of movements are presented side-by-side to facilitate direct comparison of trajectories under all environmental conditions. It is clear from the first three blocks of movements that there was minimal kinematic consequence of imposing the channel constraint (||) following movements made in the null field (∅); movements in both cases

were quite straight. These observations were consistent across subjects; the peak penetration into the channel wall during the first block of channel movements was small: 1.38 ± 0.52 mm (mean \pm SE; $n = 11$) with a average kinematic error of 0.30 ± 0.26 mm ($n = 11$). The hand paths observed in the first movements made in the perpendicular field (\updownarrow) were markedly perturbed (average kinematic error of 12.59 ± 1.33 mm; $n = 11$). However, subjects learned to compensate for this perturbation quickly; hand trajectories returned to normal long before the end of this adaptation phase (usually within 5–10 trials).

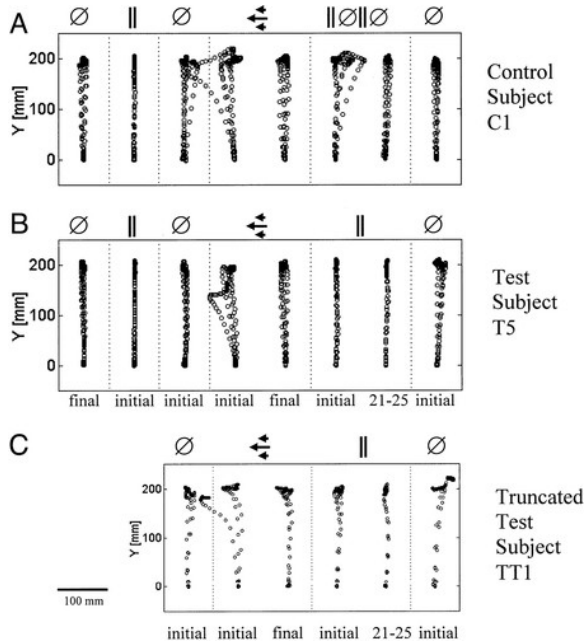


Fig. 2. Endpoint kinematics for selected trials from control and test subjects. The trials presented are indicated below the figures for the experimental phase indicated above the figures. Null field: \emptyset ; Channel Field: $||$; Perpendicular field: \updownarrow ; Mixed fields: $||\emptyset||\emptyset$. Transitions between phases of the experiment are indicated by vertical dashed lines. *A: control subject C1.* Within the mixed block of trials ($||\emptyset||\emptyset$), the initial and some intermediate null field movements are presented for this subject. *B: test subject T5.* Within the 2nd block of channel trials ($||$) the 1st 5 movements are presented since they were all channel field movements. *C: truncated test subject TT1.* This subject performed a shortened version of the “Test” experiment protocol as described in the text. Transient kinematic after-effects are observed in the final block of Null field movements (\emptyset) even though this subject had just performed 50 trials in the channel environment ($||$). The scale bar indicates an excursion of 100 mm.

Removing the channel constraint on alternating trials following adaptation to the perpendicular field ($||\emptyset||\emptyset$) caused control subjects to generate arm movements with considerable kinematic error (Fig.2A), but this kinematic error decreased rapidly. The first five trials without the channel constraint are shown, as are trials in the middle of the mixed block of movements from this control subject. The first two or three movements following adaptation reveal “aftereffects” of adaptation. Aftereffects were observed consistently across control subjects yielding average kinematic errors in the first five movements without the constraint of 13.14 ± 3.28 mm, $n = 4$. Kinematic aftereffects have been observed elsewhere (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994), and their occurrence has been found to influence the motor adaptation process (Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 1997). Our experimental protocol was unique in that the test group subjects were not allowed to make kinematic aftereffects (i.e., obvious path errors) since their hands were constrained by the channel field to follow a straight-line path. Specifically, peak channel penetration in the first five movements of the second block of channel movements was still quite small (4.54 ± 1.01 mm; $n = 7$), with a mean kinematic error of 0.82 ± 0.27 mm (test subjects; $n = 7$).

If adaptation were motivated solely by the presence of kinematic errors, then subjects who made movement in the channel should have persisted in the adapted state as long as they were not allowed to make kinematic errors (even though the environmental dynamics changed considerably). If this were true, test subjects should exhibit kinematic aftereffects in the final block of null field movements similar to those displayed by control subjects in the mixed block of trials. But test subjects did not display such behavior in the final block of null field movements. As we shall show below for the majority of subjects, the adapted behavior decayed slowly as the block of 150 channel trials progressed. The level of adaptation at the end of this block was insufficient to elicit significant kinematic errors. To explore behavior following an abbreviated exposure to the channel environment, we had an additional subject perform a truncated form of the test group experiment. For this subject (*TT1*), an initial practice session in the null field was followed by a block of 150 perpendicular field movements. The block of channel movements following adaptation was shortened to 50 movements. Figure 2C presents selected endpoint kinematic profiles collected during this experiment. As with the other subjects, initial exposure to the perpendicular field caused the hand to deviate from its intended target. These kinematic errors were quickly compensated for. The subject was then required to make 50 movements in the channel field environment. After 50 movements in the channel, the subject generated kinematic aftereffects consistent with the persistence of adaptation to the perpendicular field environment (final block of \emptyset movements).

Dynamic performance

We quantified dynamic performance using the perpendicular endpoint forces measured during each movement. Figure 3 presents averaged hand force profiles for two subjects and reflects the development and collapse of contact forces generated by the subjects against the manipulandum as the movements progressed. This figure shows how a control and a test subject modified the hand forces generated in different mechanical environments (Fig. 3, A and B, respectively). As was the case with endpoint kinematics presented in the previous figure, there was minimal consequence of imposing the channel constraint following movements made in the null field. To perform the reaching task in the presence of the perpendicular field, subjects had to generate substantial forces at the hand opposed to those imposed by the manipulandum (Fig. 1B). Large perpendicular forces persisted for many trials within the mechanical channel for the test subject (Fig. 3B, phase 5; **||**). In contrast, collapse of the perpendicular force profile within the mixed block of trials (Fig. 3A, phase 5; **|| \emptyset || \emptyset**) was rapid for the control subject.

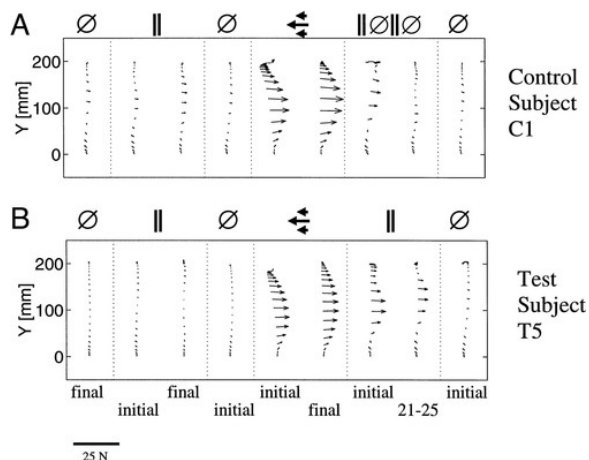


Fig. 3. Average hand forces for selected trials from a control and a test subject. The selected trials averaged are indicated below the figures for the experimental phase indicated above the figures. The scale bar below the figures indicates an average hand force of 25 N. Transitions between phases of the experiment are marked by vertical dashed lines. *A: control subject C1.* Within the mixed block of trials, only the initial 5 channel field movements are averaged and presented for this subject. *B: test subject T5.* Within the 2nd block of channel trials, the initial 5 movements are averaged and presented since they were all channel field movements.

Figure 4 shows in greater detail the evolution of the measured, perpendicular hand forces in the trials immediately preceding and immediately following the transition from perpendicular field movements to mixed field movements (control subject) or channel field movements (test subject). Each plotted trace of A and C represent the perpendicular hand force profile as measured during a single trial within the adaptation (trials 401–450) and postadaptation (trials 451–500) blocks of movements. B and D present the force data of A and C as grayscale intensity maps to highlight the regularity of hand force profiles in time and across trials. By comparing these panels, one can see that after adaptation was allowed to take place (trials 401–450), the control and test subjects utilized motor strategies exhibiting similar perpendicular hand force profiles. These hand force profiles were generally monophasic, were not perfectly symmetric about their peak, and had peak amplitudes ranging from 15 to 25 N. When the control subject was exposed to the null field and channel environments on alternating trials (Fig. 4, A and B; trials 451–500), he rapidly ceased generation of large perpendicular forces at the hand, whereas the test subject, being exposed only to the channel environment (Fig. 4, C and D; trials 451–500) continued to make movements with perpendicular hand force profiles that were generally monophasic and not symmetric about their peak with large peak amplitudes. We attribute the behavioral differences between the control and test subjects (as observed in Figs. 3 and 4) to the regular interjection of null field trials following adaptation for the control subjects (cf. Thoroughman and Shadmehr 1997). During these trials, the channel field was unexpectedly removed and the hand was free to move in any direction. Thus postadaptation null field trials penalize the persistence of large perpendicular endpoint forces by allowing considerable kinematic errors to emerge during movement. These postadaptation null field trials are identical (in all respects except frequency of occurrence) to “catch trials” used elsewhere with great success to characterize the evolution of adaptation to novel mechanical environments (Shadmehr and Brashers-Krug 1997; Shadmehr and Mussa-Ivaldi 1994).

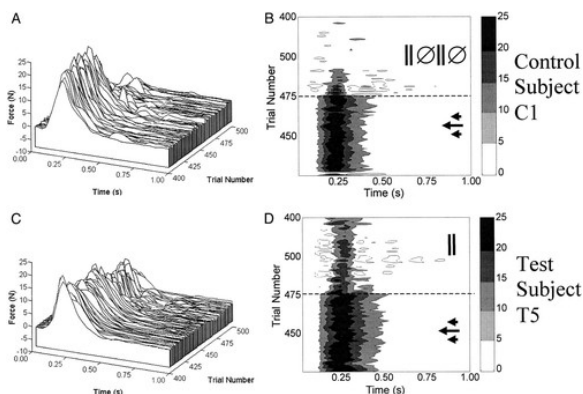


Fig. 4. Hand force profiles *perpendicular* to the direction of movement on the trials immediately preceding and immediately following the transition from perpendicular field (⊕) movements to mixed field movements (⊗; control subject) or channel field movements (||; test subject). Each plotted trace of A and C represent the perpendicular hand force profile as measured during a single trial within the adaptation (trials 401–450) and postadaptation (trials 451–500) blocks of trials. B and D present the data of A and C via grayscale intensity maps to highlight the regularity of hand force profiles in time and across trials. A and B: perpendicular hand force profiles for *control subject C1*. Note the collapse of perpendicular hand force profiles after the transition from perpendicular field environment to mixed field environment. C and D: perpendicular hand force profiles for *test subject T5*. Note the persistence of perpendicular hand forces following the transition from perpendicular field to channel field environments.

Figure 5 presents trial series plots of the dynamic measure used to characterize subject performance. Dynamic performance was quantified as the peak hand force perpendicular to the direction of movement during each trial. Figure 5, A and B, presents data from the same subjects as was displayed in Figs. 3 and 4. As was also seen

in Fig. 3, we observe here that the presence of the channel constraint following the first block of null field movements did not alter markedly these subjects' performance of the task. The off-direction endpoint forces generated in the adaptation phase (↔) were substantial (between 15 and 25 N). Figure 5A presents a plot of dynamic performance for a control subject. This control subject rapidly lost adaptation to the perpendicular field as indicated by the sharp drop in perpendicular hand force at the onset of the mixed field phase (||∅||∅). However, exposure to only the channel field following adaptation (test subject; Fig.5B) reveals a persistence of adaptation that lasts for 150 trials (shaded region). Loss of adaptation during this block of trials was gradual and much slower than that for the control subjects. The off-direction forces were still substantial at the end of this block of movements (around 5 N).

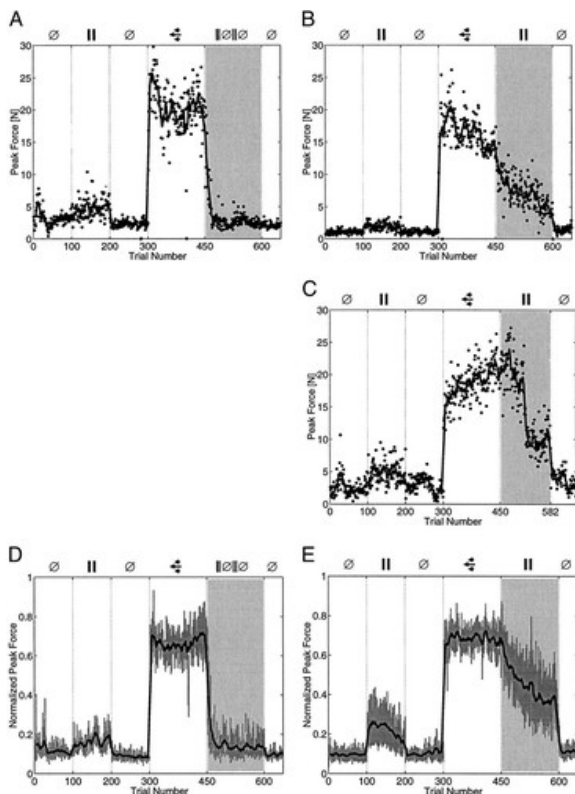


Fig. 5. Trial-series plots of peak endpoint force *perpendicular* to the direction of movement during each phase of the experiment. Transitions between phases of the experiment are marked by vertical dashed lines. The thick line in each figure represents the sliding average of an 11-point window centered on the trial number indicated on the ordinate. *A*: control subject *C1*. *B*: test subject *T5*. *C*: test subject *T1*. Note how this subject disadapted to the perpendicular field in 2 discrete steps. *D*: trial average of all 4 control subjects. Dark shading represents the SE bounds. *E*: trial average of all 6 complete test subjects.

The results displayed in Fig. 5, *A* and *B*, were consistent across subjects with the exception of one test subject whose dynamic performance is presented in Fig. 5C. This test subject (*T1*) did not exhibit a gradual change in performance on imposition of the channel following adaptation. Rather, this subject disadapted to the perpendicular field in two discrete steps. Clearly, persistence of adaptation to the perpendicular field was quite strong for this subject.

Fig. 5, *D* and *E*, presents the normalized behavior of the control and test groups averaged on a trial-by-trial basis. Each subject's dynamic performance data were normalized with respect to the maximum value of perpendicular force taken over the entire series of movements and therefore ranged from 0 to 1. As a group, test subjects

clearly persisted in adaptation to the perpendicular field for many more movements than did the control subjects (Fig. 5, *E* and *D*, respectively).

Time course of disadaptation

We quantified the persistence of adaptation for the test and control subjects by estimating the time constant associated with the loss of adaptation. We did this using a least-squares fit of a falling exponential to each subject's dynamic performance data from phase 5 (Eq. 3). Figure 6 presents these time constants for each of the control and test subjects. The means for the two groups were significantly different ($P < 0.05$; Student's *t*-test) with the controls having an average time constant of 8.5 trials and the test subjects having a time constant of 138.2 trials.

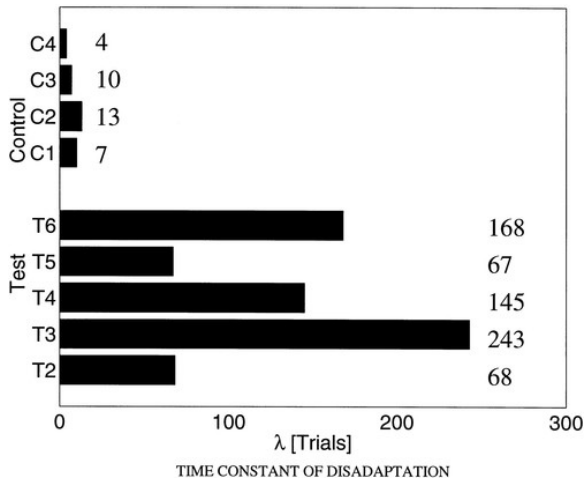


Fig. 6. Persistence of adaptation as quantified by the time constant of disadaptation for those subjects exhibiting exponential decay of adaptation to the perpendicular field environment. The time constant, λ , relating the loss of adaptation to trial number, i , is presented for each of the 4 control subjects (C1–C4) and for 5 of the test subjects (T2–T6). The time constant has the units [Trials] since the sampling interval for our measures of performance was 1 Trial.

The choice of a simple exponential model of the loss of adaptation was driven primarily by data such as that presented in Fig. 5B. But not all subjects lost adaptation to the perpendicular field gradually as the block of channel trials progressed (e.g., Fig.5C). Clearly, a simple exponential model is inappropriate in this case. A model capable of recreating discontinuities in behavior would be a better choice. Furthermore, while the simple exponential model captures the gross behavior of most subjects following adaptation, it does not capture the trial-by-trial variations in behavior of any of the subjects. It is likely that there is information regarding the nature of the motor adaptation process contained within these variations that may be revealed if studied under appropriate experimental conditions.

Could the slow decay of adaptation be a consequence of finite channel wall stiffness?

While our channel constraint enforced linear motion of the hand fairly well (Fig. 2), the constraint was not perfect. When subjects were initially exposed to the channel environment, their hands penetrated the channel wall to a very modest extent (1.38 ± 0.52 mm). However, after adapting to the perpendicular field, test subjects' hands penetrated the wall to a somewhat greater extent (4.54 ± 1.01 mm). This was to be expected if the subjects were employing the same motor strategy in the perpendicular field that they used in the channel environment because the stiffness of our channel was finite. An independent *t*-test reveals that the difference in peak penetration of the channel before and after adaptation was statistically significant ($P < 0.05$), but it is unclear whether this slight alteration in performance could trigger the gradual loss of adaptation observed in our test subjects.

If small kinematic errors motivated the disadaptation observed in Fig.5, *B* and *F*, then those subjects experiencing greater channel penetration should lose adaptation at a greater rate than subjects moving with less channel penetration. Figure7 presents a plot of disadaptation trial-constant as a function of peak channel penetration. The linear least-mean-square (LMS) regression ($r = 0.825$) is plotted with a positive slope ($P < 0.01$), implying that subjects who penetrated the channel wall to a greater extent (i.e., pushed harder against the wall) were more likely to persist in the adapted state than those who did not penetrate the channel substantially. The data are *not* consistent with the hypothesis that larger deviations from straight movements within the channel environment are more efficient in driving the loss of adaptation observed in test subjects.

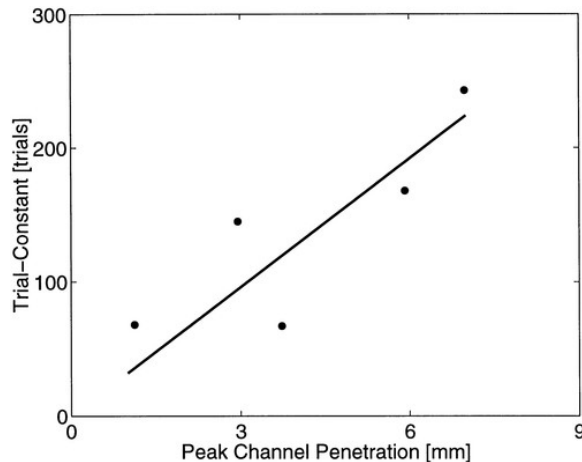


Fig. 7. Plot of disadaptation trial-constant (λ) as a function of peak channel penetration for the 5 test subjects exhibiting exponential decay of adaptation while in the mechanical channel following adaptation. Peak channel penetration is a measure of kinematic error experienced while in the mechanical channel. Channel penetration is a direct consequence of the finite wall stiffness due to limitations of our manipulandum. The least-mean-square (LMS) regression line ($r = 0.825$) is plotted with a positive slope of 32.0, implying that subjects who penetrated the channel wall to a greater extent (i.e., pushed harder against the wall) were more likely to persist in the adapted state than those who did not penetrate the channel substantially.

Is visual feedback required for rapid disadaptation?

To explore whether vision of the limb during movement is required for rapid disadaptation, we repeated the control experiment on a single control subject who was deprived of visual feedback of limb movement (Fig. 8A). The methods used were identical to those described for control subjects earlier except that 1) the subject's view of his limb was blocked using an opaque cloth screen and 2) the cursor representing the hand was eliminated during movement in the mixed field block of trials. The time constant of disadaptation for this "no-vision control" subject was three trials (within the 95% confidence interval of the mean time constant for the control group subjects). A visual representation of either the limb, the hand-path, or hand-path errors was not required for this subject to rapidly disadapt to the perpendicular field when presented with frequent null-field environments. Proprioceptive input alone appears adequate to drive the rapid loss of adaptation within the mixed field block of movements.

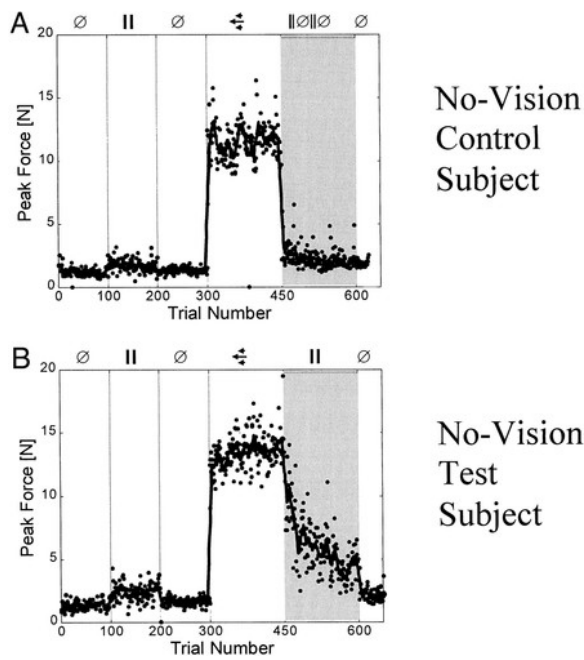


Fig. 8. Trial-series plots of peak endpoint force *perpendicular* to the direction of movement during each phase of the *no-vision* experiments. Transitions between phases of the experiment are marked by vertical dashed lines. The thick line in each figure represents the sliding average of an 11-point window centered on the trial number indicated on the ordinate. *A*: no-vision control subject. *B*: no-vision test subject.

Does visual feedback of straight handpaths suppress disadaptation?

We also repeated the test experiment on a single “no-vision test” subject to determine whether visual feedback of straight handpaths acts to suppress the loss of adaptation (Fig. 8*B*). Again, the methods used were identical to those described for test subjects earlier except that 1) the subject's view of his limb was blocked using an opaque cloth screen and 2) the cursor representing the hand was eliminated during the channel field trials that followed adaptation. The time constant of disadaptation for this subject was 48 trials (within the 95% confidence interval of the mean time constant for the test group subjects). Removing the visual representation of the moving limb or the hand path did not cause this subject to rapidly lose adaptation within the channel field environment; visual feedback of limb motion does not appear necessary for adaptation to persist within the second block of channel constraint trials.

DISCUSSION

The main purpose of these experiments was to investigate the stability of the behavioral changes associated with the adaptation to an external force field. We devised a new experimental protocol that allowed us to remove the external force field while, at the same time, minimizing the occurrence of kinematic aftereffects (i.e., path errors). We found that when the kinematic errors were eliminated, the process of disadaptation was much slower compared with when aftereffects were allowed to take place. This finding suggests that while both kinematic and dynamic criteria influence disadaptation, kinematic optimization occurs much more rapidly.

Kinematic errors are minimized during reaching movements

Generally speaking, the CNS may adopt a variety of possible motor command sequences to perform the same task within a given environment. This is a useful consequence of redundancies in the neuromuscular system that is known as “motor equivalence” (Bernstein 1967). For example, a task can be specified in terms of a movement endpoint; when a frog wipes an irritating stimulus from its back, the leg can follow multiple pathways to the

stimulus location (Berkinblit et al. 1984; Giszter et al. 1989; Sergio and Ostry 1993). In this case, multiple commands and multiple trajectories produce the same result. One may also think of motor equivalence in the absence of movement, that is, in isometric tasks: if we wish to push with the hand against a wall, we may achieve the desired contact force through a variety of muscle activations. Multiple motor command options are offered because of the presence of multiple muscles acting about the joints, and because of the many motor units comprising each muscle. A dominant question in the study of the motor system has been “What factors influence the choice of one motor command sequence over the many possible alternatives?” (Bernstein 1967).

Our experimental methods enforced kinematic equivalence on two very different motor control patterns with markedly different dynamic performance characteristics. As seen in Figs. 3 and 4, the first control pattern was characterized by low perpendicular forces generated by the hand (1st block of channel trials; phase 2). This control pattern was very similar to that observed in the null field trials. The second control pattern was characterized by large perpendicular forces (2nd block of channel trials; test subjects; phase 5). This second pattern was similar to that observed in the perpendicular field trials. Following adaptation to the perpendicular field, subjects who were allowed to make movements with obvious kinematic errors rapidly regained their preadaptation performance, whereas subjects who had been prevented by the channel from deviating from the straight-line trajectory showed a persistence of adaptation that lasted, on average, for over 100 movements. These results provide evidence that subjects persist in adaptation to a novel perturbing environment when kinematic errors are artificially minimized even though the subjects are capable of making the same movement with substantially less force generated at the hand. If economy of effort were the primary (or only) factor motivating adaptation, we would have expected test subjects to lose adaptation at a rate similar to that observed in the control subjects (Fig. 5, *E* and *D*, respectively). This is because the mechanical channel only enforced a *kinematic* equivalence of the two possible control patterns.

The data presented in Fig. 5 both support and extend the findings of Wolpert et al. (1995). In that study, Wolpert and colleagues manipulated visual feedback such that subjects perceived their hand movements to be either more or less curved than they actually were. Subjects consistently modified their performance so that they made movements they perceived to be straight at the expense of objective measures of straightness. Wolpert and collaborators presented data indicating that motor adaptation during reaching movements occurs primarily as an attempt to minimize kinematic errors with respect to some reference trajectory and that this trajectory is a straight line in a visually perceived coordinate frame.

Whereas Wolpert et al. (1995) state that their results are not easily explained by the minimization of dynamic variables, our findings suggest that two simultaneous optimization processes may indeed be taking place. Specifically, the control subjects minimized kinematic error rapidly, while the test subjects who moved in the channel also altered their performance with a time constant an order of magnitude slower than that exhibited by the controls. All but one test subject returned toward the “default” performance gradually, suggesting that a slow minimization of effort or other dynamic criteria likely occurred. These data are consistent with the idea that subjects were attempting to minimize hand-path errors during movement, while providing evidence for a slower, secondary process that is consistent with the optimization of effort or other dynamic criteria.

Are the systems that optimize kinematic performance distinct from those that optimize dynamic performance?

A recent study provides experimental evidence that the learning of novel kinematic transformations during reaching movements may be distinct from the learning of novel intersegmental dynamics (Krakauer et al. 1999). Specifically, Krakauer et al. had subjects perform supported, horizontal-plane, reaching movements from a central starting point to a series of peripheral (radial) targets displayed on a computer monitor. These movements were performed in 1) a rotated visual reference frame wherein subjects moved their hands to

targets while feedback of the hand movement was rotated 30° around the starting point (this 1st perturbation required subjects to learn a rotated spatial reference frame), and 2) an altered inertial configuration wherein subjects learned to move to the same targets as in 1 while the inertial configurations of their arms were altered by attaching a 1.5-kg mass 25 cm lateral to the forearm (this 2nd perturbation required subjects to learn to compensate for new intersegmental dynamics of the limb).

Krakauer and colleagues used the phenomena of consolidation and interference to evaluate how well subjects learned and retained novel motor tasks. Consolidation is observed when performance of a task improves more rapidly in one experimental session compared with performance in the same task on previous day(s). Interference refers to the observation that the learning of a second task within a short period of time after learning a first can often abolish consolidation of the first task. After showing that tasks performed exclusively in the rotated visual reference frame exhibit both consolidation and interference, and after showing that tasks performed exclusively with altered inertial configurations exhibit both consolidation and interference, Krakauer et al. found that learning of an altered inertial configuration immediately after learning a rotated visual reference frame *did not* interfere with consolidation of the newly learned reference frame. Furthermore, they found that the visual and dynamic transformations can be learned concurrently at the same rate as singly. These experimental results provide strong support for the hypothesis that the mechanisms involved in the learning of limb kinematics and limb dynamics are independent.

The results of Krakauer et al. are particularly pertinent to the current study in that they suggest why our control subjects exhibited a rapid loss of adaptation while our test subjects showed a slow, gradual loss. If we accept that the learning of kinematic and dynamic transformations occur by two independent processes, then it is reasonable to expect the processes to have different properties. Therefore the slow, gradual loss of adaptation exhibited by test subjects may be due to the action of a neuromotor mechanism optimizing some aspect of dynamic performance at a relatively slow rate, while the rapid loss of adaptation exhibited by control subjects was dominated by the action of a separate (and substantially faster) mechanism optimizing kinematic performance. By minimizing kinematic errors after adaptation, the channel constraint enables us to observe the action of a slower, secondary mode of neuromotor control that is usually obscured by the rapid minimization of hand-path errors.

What feedback signals influence the adaptive behaviors expressed by test and control group subjects?

The nervous system typically has several ways of assessing its own motor performance. Kinematic errors are transduced by both vision of the moving limb and by muscle spindle afferents which appear to signal a combination of both muscle fiber length and velocity (Houk and Rymer 1981). Dynamic performance may be estimated by Golgi tendon organs, which are accurate and sensitive sensors of muscle force. It is conceivable that dynamic performance could also be estimated indirectly by the slow-adapting, pressure-sensitive mechanoreceptors of the hand (Merkel receptors and Ruffini corpuscles) (Martin 1985), which respond continuously to enduring stimulation to the glabrous skin of the hand such as a steady skin indentation.

Based on the data obtained in the current study, we can speculate on which feedback modalities contribute to the adaptive behaviors expressed by the test and control groups of subjects. Specifically, the slow loss of adaptation of our test subjects was likely driven by Golgi tendon organs and/or hand mechanoreceptors since 1) vision does not appear necessary for the expression of both the rapid and slow loss of adaptation and 2) the sign of the slope of the relationship between time constant of disadaptation and penetration into the channel wall (Fig. 7) is not consistent with the hypothesis that small kinematic errors motivated the disadaptation observed within the channel. On the other hand, the rapid loss of adaptation of our control subjects was likely due to muscle spindle afferent feedback since these receptors are ideally tuned to unanticipated muscle stretches and,

potentially, to mismatches in the intended and actual movement velocities caused by the removal of the opposing channel wall.

There is, however, another possible control strategy that could describe control subject behavior in the null field movements following adaptation. Specifically we note that the mechanical channel dissociated dynamic performance from its usual kinematic consequence only while it was active. During the null field trials, control subjects not only experienced limb kinematics that deviated from the straight-line path, but they also experienced joint torques that deviated from those generated along the straight-line path in the perpendicular field and the channel environments. This is due in part to the acceleration of the limb inertia away from the intended trajectory. We cannot discount the possibility that subjects evaluate movement errors by comparing an estimate of the *expected* joint torques or muscle forces with those actually observed during movement.

Following this line of reasoning, our results would suggest that the motor commands (and the expectations they presumably give rise to) change rapidly when the mismatch between the expected and the actual sensory feedback is large (control subjects). The change observed in the motor commands of control subjects was consistent with recovery from adaptation, as well as with the minimization of error between expected and actual sensory feedback (visual and kinematic). Such behavior is in contrast to test subjects where the commands change much more gradually when the sensory mismatch is small. But here, change in motor commands was consistent with recovery from adaptation only, not with minimizing the error between expected and actual sensory feedback (force- or torque-related). Furthermore, while the possibility that the rate of learning may be dependent on the amplitude of sensory mismatch is intriguing, the proposition of such a unified mechanism is not easily reconciled with the observation that kinematic and dynamic transformations can be learned concurrently without interference (Krakauer et al. 1999). In summary, our data provide strong experimental evidence that both kinematic and dynamic criteria influence motor adaptation of arm movements to an external force field. However, kinematic-dependent factors appear to play a dominant role in the *rapid* loss of adaptation after restoring the original dynamics.

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FOOTNOTES

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