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RESEARCH ARTICLES

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Accuracy of internal dynamics models in limb movements depends on stability

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Abstract This study investigated the ability to use an internal model of the environmental dynamics when the dynamics were predictable but unstable. Subjects performed goal-directed movements using a robot manipulandum while counteracting a force field, which created instability by assisting the movement in proportion to hand velocity. Subjects' performance was better on the last trial than on the first trial in the force field for all four movement directions tested: out, in, right and left. Subjects adapted to the force field primarily by increasing muscle co-contraction, compared to null field movements, during all phases of movement. This co-contraction generally declined for both the deceleration and stabilization phases during the course of the first 25 movements in each direction, but tended not to decrease significantly thereafter. Catch trials at the end of the learning period suggested that increased viscoelastic impedance due to muscle co-contraction was used to counteract the force field. Only in the case of outward movements were aftereffects observed that were consistent with formation of an accurate internal model of the force field dynamics. Stabilization of the hand for outward movements required less muscle co-contraction than for movements in other directions due to stability conferred by the geometry of the arm. The results suggest that the accuracy of an internal model depends critically on the stability of the coupled dynamics of the limb and the environment.

Keywords Arm · Co-contraction · Mechanical impedance · Muscles

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Introduction

The robust control of reaching with the arm not only requires the production of appropriate joint torques to move along a desired path, but also requires that there be sufficient mechanical impedance to ensure mechanical stability. Without stability, it would not be possible for the central nervous system to predict the path that the hand would follow and control of arm movements would be unreliable. However, humans clearly have the ability to control arm movements both reliably and predictably. This implies that our movements are stable.

Stable movement would be unremarkable if we lived in a world where all of our activities involved stable interactions with the environment. However, this is not the case. The instabilities associated with biped gait are obvious. It is perhaps less evident that a multitude of activities that we perform with our arms, not the least of which is feeding ourselves, require compensation for inherent instability. Activities performed with hand tools are prime examples (Rancourt and Hogan 2001). Since we learn to perform these activities successfully, it follows that we must be able to adjust the mechanical impedance of the arm to give us an adequate margin of stability. We have recently demonstrated that the central nervous system is able to control the stiffness of the arm to achieve directionally selective stability (Burdet et al. 2001). Differentially weighted co-contraction of antagonist muscles (Franklin et al. 2003) and selection of arm posture are the two principal means of selectively increasing stability (Milner 2002a), although the direction of applied force can also make a significant contribution in some circumstances (Franklin and Milner 2003).

The central nervous system is able to adapt to time-varying disturbances as long as they do not exceed the bandwidth or maximum force capability of muscles. For certain types of disturbances this is accomplished by learning to produce forces of approximately equal magnitude and oppositely directed to those engendered by the source of the disturbance. From recent studies which have investigated the adaptation process, a

consensus has emerged that the central nervous system acquires an internal dynamics model of the disturbing forces (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Gandolfo et al. 1996; Conditt et al. 1997; Flanagan and Wing 1997; Goodbody and Wolpert 1998; Krakauer et al. 1999; Thoroughman and Shadmehr 1999; Scheidt et al. 2000). It is clear from the way in which compensation for the disturbances is generalized that compensation does not simply entail memorization of a mirror-image force-time profile, but represents a computational process based on a model of the dynamics of the disturbance (Conditt et al. 1997; Goodbody and Wolpert 1998; Bhushan and Shadmehr 1999).

Most systematic investigations of motor learning have employed mechanically stable interactions with the environment. Adaptation to novel dynamics under stable conditions appears to involve the acquisition of an internal dynamics model through feedback error learning (Kawato 1990). However, it is unlikely that an internal dynamics model can be acquired in this way when the dynamics are unstable. This is because feedback error learning produces only reciprocal changes in muscle activation without co-contraction, which can cause the error to grow rather than decline when the error direction is not consistent from trial to trial (Franklin et al. 2003). In the case of adaptation to stable dynamics, changes in muscle activation patterns closely follow adaptive changes in joint torques, although there is excess agonist-antagonist muscle co-contraction, particularly in the early stages of learning (Thoroughman and Shadmehr 1999; Franklin et al. 2003). When dynamics are stable, reciprocal patterns of muscle activation are used to control the trajectory. However, co-contraction is often necessary to stabilize the limb at its final position (Feldman 1980). Trajectory control and stabilization of the final position should be considered as two separate processes. This becomes even more evident when the dynamics are unstable (Milner 2002b). As adaptation progresses, a decrease in co-contraction occurs whether the dynamics are initially stable or unstable (Milner and Cloutier 1993; Thoroughman and Shadmehr 1999; Franklin et al. 2003). It would appear that the central nervous system initially uses co-contraction to increase resistance to the disturbing effects of the novel dynamics and reduces co-contraction as knowledge of the dynamics improves.

Our previous investigation of adaptation to unstable dynamics employed a position-dependent force field (Burdet et al. 2001), which we referred to as a divergent field. We concluded that the central nervous system did not acquire an internal model of this force field, principally because the initial force direction could never be accurately predicted. However, since this is not the only type of unstable interaction that can be produced, it does not rule out the possibility that an internal dynamics model could be acquired for other unstable interactions. For example, a velocity-dependent instability, which consists of a predictable force but which has unstable interaction characteristics, could provide insight into whether instability, per se, limits the ability to acquire an internal dynamics model. In particular, a force field with the characteristics of negative damping assists movement in proportion to velocity. Adaptation to such a force field by means of an internal dynamics model could be achieved by modifying the normal pattern of reciprocal muscle activation, i.e., curtailing the activity of agonist muscles which propel the limb toward the target and subsequently increasing the activity of antagonist muscles to control the acceleration produced by the force field and to provide the force necessary to brake the movement. However, co-contraction might also be employed to provide lateral stability during the movement and would be needed to stabilize the limb at the final position. Changes in the patterns of muscle activation during adaptation and aftereffects following adaptation suggested that it was very difficult to form an accurate internal dynamics model of this type of force field and that both trajectory control and stabilization were achieved primarily by increasing the mechanical impedance of the arm.

Methods

Seven male subjects participated in this study. All were right-handed and performed the task with their right arm. All subjects gave informed consent prior to participating in the study. The protocol was approved by the institutional ethics review committee and conformed to the ethical standards set down in the Declaration of Helsinki.

Experimental setup

The subjects made goal-directed movements in the horizontal plane while holding the handle of a 2-degree-of-freedom serial-link robot manipulandum. The subject's arm was supported against gravity by means of a sling suspended from the ceiling, which cradled the arm near the elbow. The handle rotated freely about its central axis to prevent torque from being applied. A 6-degree-of-freedom load cell at the handle measured the force applied by the subject. Optical encoders on the shafts of the motors driving each link, measured shaft angle with a resolution of 0.0275°, permitting x and y handle position to be determined with a resolution exceeding 0.04 mm. Tachometers on the motor shafts measured shaft velocity. The apparatus is described in greater detail by Conditt et al. (1997) and Scheidt et al. (2000).

Protocol

Subjects moved the manipulandum handle back and forth between two targets. They performed two blocks of 144 movements each. The first trial of each block began from a position about 30 cm in front of the trunk, directly in line with the center of rotation of the shoulder. Movements alternated in direction with every second movement returning to the initial position. In the first block of trials, the first movement was towards a target located 25 cm

forward of the initial position, along a line through the shoulder. In the second block of trials, the first movement was towards a target located 25 cm to the right of the initial position. Subjects were instructed to move at the same peak velocity (75.0±5.6 cm/s) across trials and to stabilize the handle in the end target window. The start and end targets for each movement were displayed as 2-cm squares (in workspace coordinates) on a computer monitor situated above the manipulandum. The instantaneous position of the handle was displayed as a 0.6 cm square cursor (in workspace coordinates) on the monitor. A display of peak velocity was provided immediately after completion of the movement. It consisted of a horizontal bar, whose length was proportional to peak velocity, shown just above the target velocity window. If the peak velocity was too low, the bar was shown in red; if it was too high, the bar was shown in blue; and if it was within the target window, the bar was shown in green and a tone sounded. Trials were self-initiated, allowing subjects to pause between trials if they desired.

Subjects performed 20 practice movements in a null field (no external force), followed by 20 additional null field movements which were recorded. Subjects were then warned that a destabilizing force field would be activated, beginning with the next trial. For the next 100 trials the manipulandum was destabilized by a means of an assisting force field

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} B & 0 \\ 0 & B \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix} \quad (1)$$

with B=25 N/m s^{-1}. The force field was activated shortly after movement onset when the handle velocity exceeded a threshold of 1 cm s^{-1}. Following 100 trials, the force field was unexpectedly deactivated for one trial, then reactivated for the next two trials and again deactivated on the final trial. The two catch trials occurred for movements in opposite directions and were designed to investigate the nature of the feedforward adaptation to the force field, i.e., to provide evidence that would help to distinguish between adaptation by means of increased mechanical impedance and adaptation by the formation of an internal dynamics model. Since subjects were not provided with any information about the number of force field trials, they could not anticipate the catch trials.

Interpreting the results of catch trials is not straightforward, however, because of the possibility of voluntary intervention, i.e., modification of voluntary motor commands. Previous studies that have used catch trials have failed to address this issue. It has always been assumed that catch trial kinematics represent the consequences of executing the adapted motor commands while moving in the original mechanical environment. Although this is likely a valid assumption during the first 200–250 ms of the movement, it is unlikely to be the case later in the movement unless subjects are explicitly instructed and trained not to intervene (Hinder and Milner 2003). Furthermore, it is difficult to establish that subjects have not intervened. For example, EMG during movement would be expected to change whether or not voluntary motor commands were altered. This is because motoneurons receive input both from peripheral sensory receptors, e.g., muscle spindle primary afferents, and from descending commands. Assuming that the descending commands remain the same, changing the mechanical environment will result in altered kinematics which in turn will modify the sensory input to motoneurons and, hence, the EMG. Furthermore, EMG can be highly variable from trial to trial. A common test for voluntary intervention is the presence of an inflection in the velocity profile that indicates a reversal in the direction of acceleration (Hinder and Milner 2003). This is the criterion that was used in deciding whether subjects intervened during catch trials.

The activity of brachioradialis, biceps, triceps lateral head, triceps long head, anterior deltoid and posterior deltoid was recorded with active bipolar surface EMG electrodes (Delsys), which had a bandwidth from 20–450 Hz. Analog signals were acquired with a 16-bit A/D converter. All signals were acquired at 1,000 Hz, which was also the update rate for control of the robot manipulandum.

Analysis

The rms (root-mean-square) EMG was computed over acceleration, deceleration and stabilization phases of movement. The acceleration phase comprised the interval starting 150 ms prior to movement onset until peak velocity in the target direction. The deceleration phase comprised the interval from 40 ms prior to peak velocity in the target direction until the first velocity zero crossing. The stabilization phase comprised the interval from the end of the deceleration phase until 2 s had elapsed from movement onset.

Because the force field produced an assisting force in whichever direction the hand was moving, the force direction changed whenever the movement direction changed, initially resulting in a convoluted handpath. The handpath was characterized in terms of the total distance moved from the start location to the end location, i.e., the length of the curve representing the handpath. To determine whether there was an overall improvement in performance with practice, the path length to each target for the first movement after activation of the force field was compared with the path length for the final movement to that target. Final position as well as maximum deviation from a straight line path and path length during each phase of the movement were also compared. Since distributions were not normal and variances were unequal, the nonparametric Mann-Whitney U-test with a significance level of p<0.05 was used. The general tendency for each subject to improve performance was investigated by examining whether there was a significant trend to reduce path length with increased exposure to the force field. The first trial was considered as a stimulus event, comprising only reactive responses. In contrast, all subsequent trials

were expected to have a predictive component. Since the objective of the analysis was to determine whether these predictive responses would provide better compensation for the force field with practice, the first trial was excluded. Separate regression analyses were performed for trials 2–26 and 26–50 to determine whether improvement occurred during both the first and second half of the learning period. Performance was judged to have improved if the slope of the regression line was significantly less than zero ($p<0.05$).

To quantify changes in EMG patterns associated with adaptation to the force field, comparisons were made between the EMG prior to activation of the force field and at the end of the adaptation period for each subject. The rms EMG during each phase of the movement for five trials in each direction prior to activation of the force field was compared with the corresponding mean rms EMG for the final five trials in the force field. A nonparametric Mann-Whitney U-test with a significance level of $p<0.05$ was again used. To determine whether muscle activation decreased progressively during adaptation, similar regression analyses were carried out on rms EMG, as for path length. The regression was performed for each combination of subject, target direction, phase of movement and muscle.

To demonstrate that the changes in muscle activity after adaptation to the assisting force field were large enough to have produced at least a 10% change in mechanical properties, the mean rms EMG of the last five movements in the null field and of the last five movements in the force field were calculated for each subject, muscle, movement direction and movement phase. The percentage change in rms EMG relative to the null field was then determined, averaged across subjects and tested for significance from zero.

Co-contraction during the stabilization phase, following adaptation to the force field, was compared for the different movement directions. The EMG of each muscle was first rectified and low-pass filtered (second-order, zero-lag, Butterworth filter with a cutoff frequency of 20 Hz). For each trial, the mean baseline EMG during the interval 200–300 ms prior to movement onset was subtracted from each sample. For each subject, the maximum value of the EMG for each muscle across all trials was then determined and used to normalize the EMG for that muscle. The co-contraction for each pair of antagonist muscles (a,b) was defined as $EMG_a+EMG_b-|EMG_a-EMG_b|$. The absolute value term represents the net EMG, i.e., the part that does not cancel due to co-contraction. This was subtracted from the total EMG (EMG_a+EMG_b) to give a measure of the EMG due to co-contraction. The co-contraction was summed for each sample during the stabilization phase and the sum divided by the total number of samples to give a value between 0 and 2. The nonparametric Mann-Whitney U-test with a significance level of $p<0.05$ was used to determine whether differences between movement directions were significant.

Results

Handpath adaptation

Handpath length was used as the primary measure of performance. The handpaths of the first, second and final

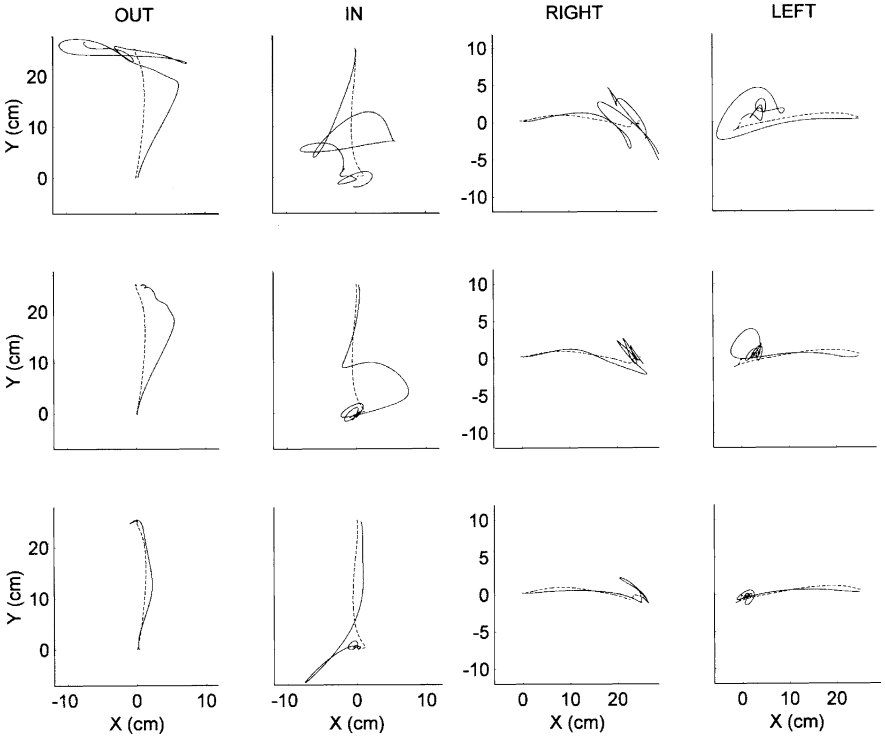

Fig. 1 Hand paths on the first trial (*top row*), second trial (*middle row*) and last trial (*bottom row*) in the assisting force field for each movement direction are shown as *solid lines*. The final movement in the null field prior to the activation of the force field is shown for comparison as a *dashed line*. All data is for the same subject

movements in the assisting force field are compared to null field movements in Fig. 1. The handpaths of movements in the null field were close to straight lines for all movement directions. The change in path length across trials is shown for the four movement directions in Fig. 2. There was little variation in path length across subjects for the null field movements, as is evident from the relatively small standard deviations. On average, the path length in the null field did not differ among movement directions and stayed consistently within 3 cm of the straight-line distance to the target. The handpath was markedly perturbed on the initial trials in the assisting force field, regardless of movement direction, although subjects were able to recover and stabilize the hand at the target (Fig. 1). Movements were generally characterized by large oscillations of the trajectory and a dramatic increase in the activation of all muscles compared with movements in the null field, particularly during the deceleration and stabilization phases of the movement (Fig. 3). The perturbing effect of the assisting force field more than doubled the path length on the first trial in any direction for most subjects. The effect was largest for the first outward movement, which occurred prior to any previous experience in the assisting force field (Fig. 2).

On subsequent trials, trajectories were less perturbed and the path length decreased (Fig. 1), while muscle activation was also generally reduced (Fig. 4).

Changes in path length were not a result of missing the target. There was no significant difference in the end position between the final null field movement and the final force field movement or between the first force field movement and the final force field movement across subjects for any movement direction. The mean distances from the start to end position for these comparisons ranged from 24.6 to 25.7 cm, indicating that movements inevitably ended within the end target window. The decrease in path length during adaptation to the force field was primarily the result of less movement during the stabilization phase. There was no significant difference in the path length of the acceleration phase or the deceleration phase, between the first force field movement and the final force field movement, for any movement direction. In contrast, the difference was significant for the stabilization phase for all movement directions. The mean changes in path length between the first and last movements in the force field were 52.3 cm (p=0.0017) for outward movements, 20.8 cm (p=0.035) for inward movements, 25.5 cm (p=0.006) for rightward movements and 17.1 cm (p=0.013) for leftward movements. Straightening of the handpath, as determined by the maximum deviation from a straight line path between start and end positions also occurred between the first and last movements in the force field. The reduction in maximum deviation was statistically significant for all phases of outward movements (p=0.0017). In contrast, it was only significant for the stabilization phase of rightward (p=0.013) and leftward (p=0.006) movements and for the acceleration phase of inward movements (p=0.048).

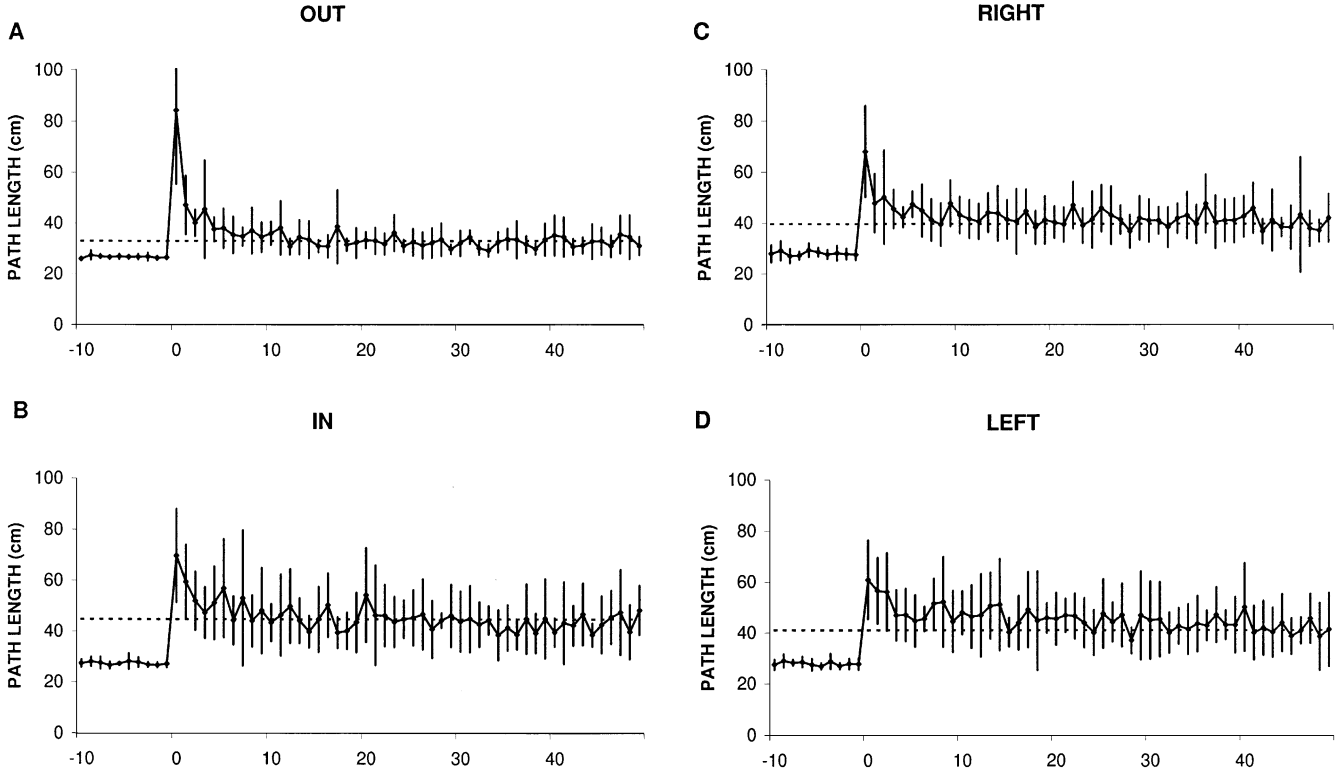

Fig. 2 The total hand path length is shown for each movement direction. The data represents the mean path length for the seven subjects with standard deviations. Trial 0 is the first trial in the assisting force field. All preceding trials represent movements in the null field. The *dashed line r*epresents the mean path length of the final five movements in the assisting force field

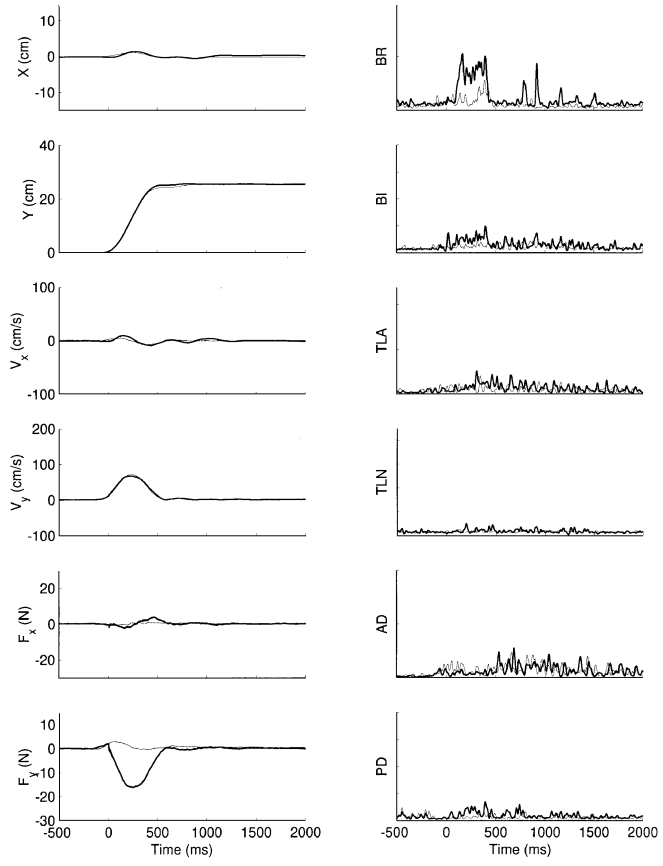

Fig. 3 Position, velocity and force on the first movement in the outward direction after activation of the force field are shown in the *left* panels (*dark solid line*). The average of the last five movements in the null field is shown for comparison (*light dotted line*). Rectified, low-pass filtered EMG for brachioradialis (*BR*), biceps (*BI*), triceps lateralis (*TRA*), triceps longus (*TRL*), anterior deltoid (*AD*) and posterior deltoid (*PD*) are shown in the *right* panels

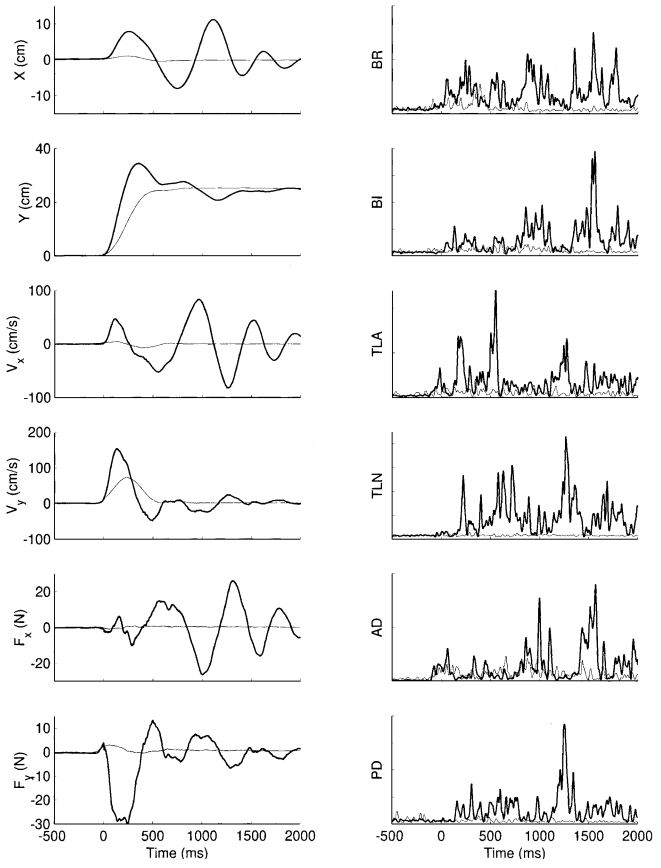

Fig. 4 Data are presented for the same subject and in the same format as Fig. 3 for the final outward movement in the assisting force field. EMG is plotted on the same scale as Fig. 3. The movement is well damped with kinematics similar to null field kinematics. Muscle activity was dramatically reduced during most phases of the movement

Path length in force field movements varied considerably more than for null field movements, both within and across subjects. After the first trial in a given direction there was a relatively large reduction in path length over the subsequent two to three trials in the force field. The path length generally continued to decrease over the next ten trials, after which it fluctuated but was not reduced further. In the case of movements to the left, the path length decreased more gradually, but appeared to change little after 25 trials. The path length after adaptation to the force field was shortest for outward movements and performance was more consistent across subjects (smaller standard deviation) than for the other movement directions (Fig. 2). Although the path length decreased significantly between the first and last trials in the force field for all directions, there was no clear indication that performance improved continuously. The slope of path length as a function of trial number for the first half of the learning period (trials 2–26 in the force field) was significantly less than zero ($p<0.05$) for 6/7 subjects in outward movements, for 4/7 subjects in inward and leftward movements and for 3/7 subjects in the rightward movements. During the second half of the learning period (trials 26–50 in the force field), the numbers decreased to 1/7 for outward movements, 2/7 for rightward and leftward movements and 3/7 for inward movements. This reinforces the general trend evident in Fig. 2 that most of the improvement in performance occurred during the first half of the learning period. The standard deviation in path length for trials 26–50 compared with the ten null field trials provides a good indication of the relative inconsistency in performance in the force field. The mean values across the seven subjects were 4.7 cm compared with 1.0 cm for outward movements, 8.5 cm compared with 1.6 cm for inward movements, 6.6 cm compared with 2.1 cm for rightward movements and 8.5 cm compared with 1.5 cm for leftward movements.

Force adaptation

Subjects generally applied the same force to the robot manipulandum, at movement onset, on the first trial in the assisting force field as for the previous null field movements (Fig. 5). There was no significant difference between the force applied on the last null field trial and the first force field trial for any movement direction. However,

on subsequent trials the force applied to accelerate the manipulandum was reduced. Most of the reduction occurred within three or four trials, although it did not reach its final level until after 5–15 trials, depending on the direction of movement. In the case of outward movement, the force was reduced from 2.5 N on the first trial in the force field to 1.7 N ($p<0.01$) by the fifteenth trial; for inward movements it was reduced from −1.7 to −1.2 N ($p=0.052$); for rightward movements it was reduced from 2.7 to 1.1 N ($p<0.0025$); for leftward movements it was reduced from −3.4 to −1.7 N ($p<0.013$).

The amount by which the force was reduced can also be inferred from catch trials. For outward movements, the mean peak force across subjects decreased from 3.9 N on null field trials to 2.2 N on catch trials ($p<0.0005$); for inward movements it decreased from −2.4 to −1.7 N ($p=0.033$); for rightward movements it decreased from 4.6 to 2.1 N ($p<0.0001$); for leftward movements it decreased from 5.8 to 2.7 N ($p=0.0035$). Although it is less straightforward to deduce how deceleration was achieved in the force field, the patterns of muscle activation can provide important insights.

Adaptation in muscle activity

Muscles were identified as agonists if they produced torque in the direction of acceleration in null field movements and showed a large change in activation prior to movement onset. Muscles which produced torque in the opposite direction to agonists were classified as antagonists. Although activation patterns for null field movements differed slightly from subject to subject, the majority of subjects used triceps lateralis and anterior deltoid as the principal agonists for outward movement, brachioradialis and posterior deltoid for inward movement, triceps lateralis and posterior deltoid for movement to the right and brachioradialis and biceps for movement to the left.

The patterns of muscle activation for the four movement directions, following adaptation to the force field are compared with those in the null field for one subject in Fig. 6. The changes in muscle activity differed from what would have been expected if muscle force had been adapted only to counterbalance the assistance provided by the force field. Had this been the case for outward movement, elbow extensor activity should have been replaced by elbow flexor activity. Although the activity of triceps lateralis was significantly lower than in the null field for most subjects, the activity of triceps longus was higher and the activity of anterior deltoid was lower for about half of the subjects (Fig. 7a). This suggests that after adaptation, biceps took over the role of shoulder flexor from anterior deltoid so that co-contraction of the biarticular muscles could provide increased stability. During deceleration, the activity of elbow flexors should have

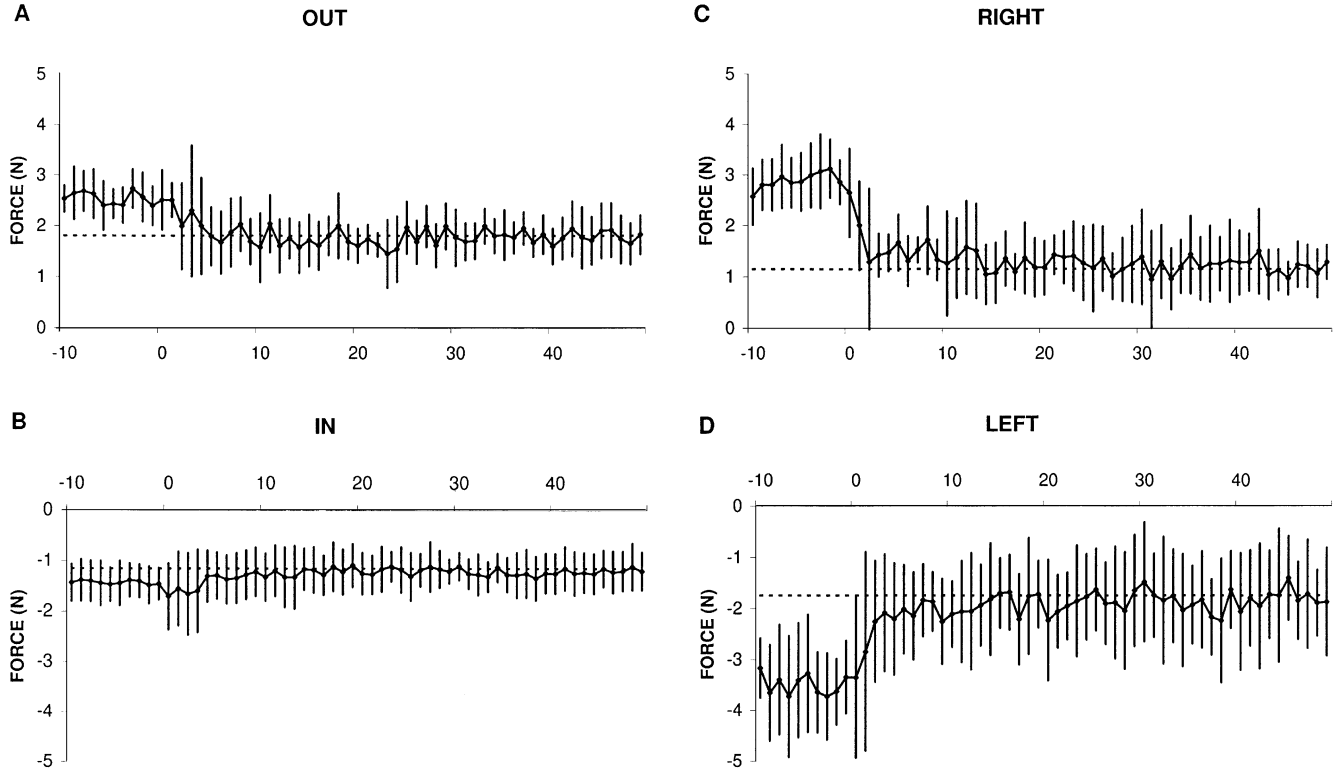

Fig. 5 The force in the target direction, applied at the onset of movement, is shown for each movement direction. The data represents the mean force for the seven subjects with standard deviations. Trial 0 is the first trial in the assisting force field. All preceding trials represent movements in the null field. The *dashed line* represents the mean force of the final five movements in the assisting force field

been considerably higher than in the null field. Although higher activity was observed for brachioradialis and biceps for all subjects, the activity of triceps lateralis and triceps longus was also generally higher (Fig. 7a), suggesting that co-contraction of elbow flexors and extensors was used to increase elbow stability. Activity of all elbow muscles was similarly elevated during the stabilization period, although the activity of anterior deltoid and posterior deltoid muscles was generally unchanged or lower when compared with the null field (Fig. 7a).

For the acceleration phase of movements in the other directions, similar changes in muscle activation were observed as in outward movement. In particular, there was an increase in the activity of triceps lateralis and triceps longus for inward and leftward movements, but generally no decrease in the activity of brachioradialis and biceps.

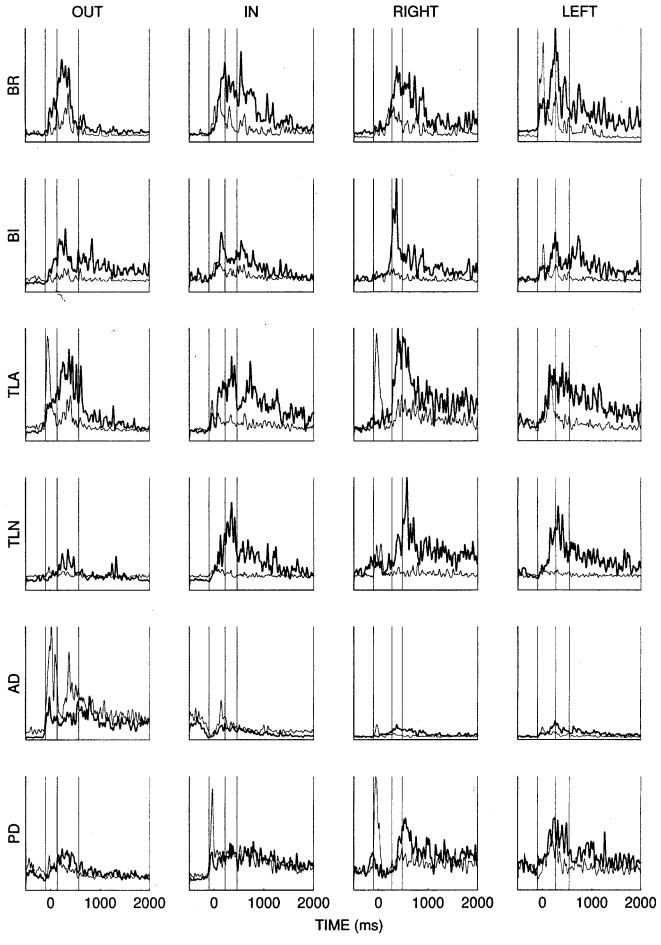

Fig. 6 Rectified low-pass filtered EMG for the six muscles of one subject is shown in columns for each movement direction. *Thick lines* represent the mean of the last five trials in the assisting force field. *Thin lines* represent the mean of the last five trials in the null field prior to activation of the force field. *Thin vertical lines* delineate the boundaries of the acceleration, deceleration and stabilization intervals. The EMG scale used for the four plots in each row, i.e., for one specific muscle, is the same and represents signal amplitude in units of electrical potential, e.g., volts. The scale for each row is different and was chosen so that the highest peak in any given row has approximately the same amplitude as the highest peak in every other row

On the other hand, there was an increase in the activity of brachioradialis and biceps and reduction in the activity of triceps lateralis, but not triceps longus for rightward movements. This indicates that there was always co-contraction of elbow muscles and biarticular muscles during acceleration. For inward and rightward movements there was little co-contraction of shoulder muscles during acceleration. However, for leftward movements posterior deltoid activity increased without a concomitant decrease in the activity of anterior deltoid. This suggests that co-contraction of both elbow and shoulder muscles was required to insure stability during leftward acceleration.

For the deceleration phase, an increase in torque, relative to null field movements, was required for all movement directions to counteract the assisting force field. The expected increase in activity was observed in the elbow muscles and biarticular muscles contributing to deceleration, although the activity of their antagonists increased, as well. In the case of the shoulder, a significant increase in the deceleration torque was required only for rightward and leftward movements. Consequently, the activity of the shoulder muscles contributing to deceleration increased only for these movement directions, i.e., anterior deltoid for rightward and posterior deltoid for leftward movements. Inward movements, like outward movements, showed little change in the activity of shoulder muscles in the deceleration phase. The results indicate, as in the case of inward movements, that viscoelastic mechanical impedance was increased by co-contraction of elbow and biarticular muscles to resist the force field during deceleration. The same pattern of increased co-contraction of elbow muscles and biarticular muscles observed in the deceleration phase of force field movements was maintained during the stabilization phase with additional co-contraction of shoulder muscles in some movement directions.

The changes in muscle activity described above were tested for significance, as described in the Methods (Mann-Whitney U-test). There were 56/72 cases, in Fig. 7, where four or more subjects showed a statistically significant increase in rms EMG for force field movements compared with null field movements. In 52 of these cases, the average increase in activity was greater than 100%. There were six cases where four or more subjects showed a statistically significant decrease in rms EMG. In four of these cases, the average decrease in activity was greater than 25%.

Regression analysis of the rms EMG in relation to trial number showed no definite trend for change in muscle activity in the acceleration phase of movements across subjects. However, activity generally decreased during the deceleration and stabilization phases. The number of subjects for which the slope of the relation between rms EMG and trial number was significantly less than zero for the deceleration and stabilization phases is shown for the first half of the learning period (force field trials 2–26 in each direction) in Fig. 8. In 18/24 cases (six muscles × four directions), four or more subjects showed a significant trend to decrease muscle activity as learning

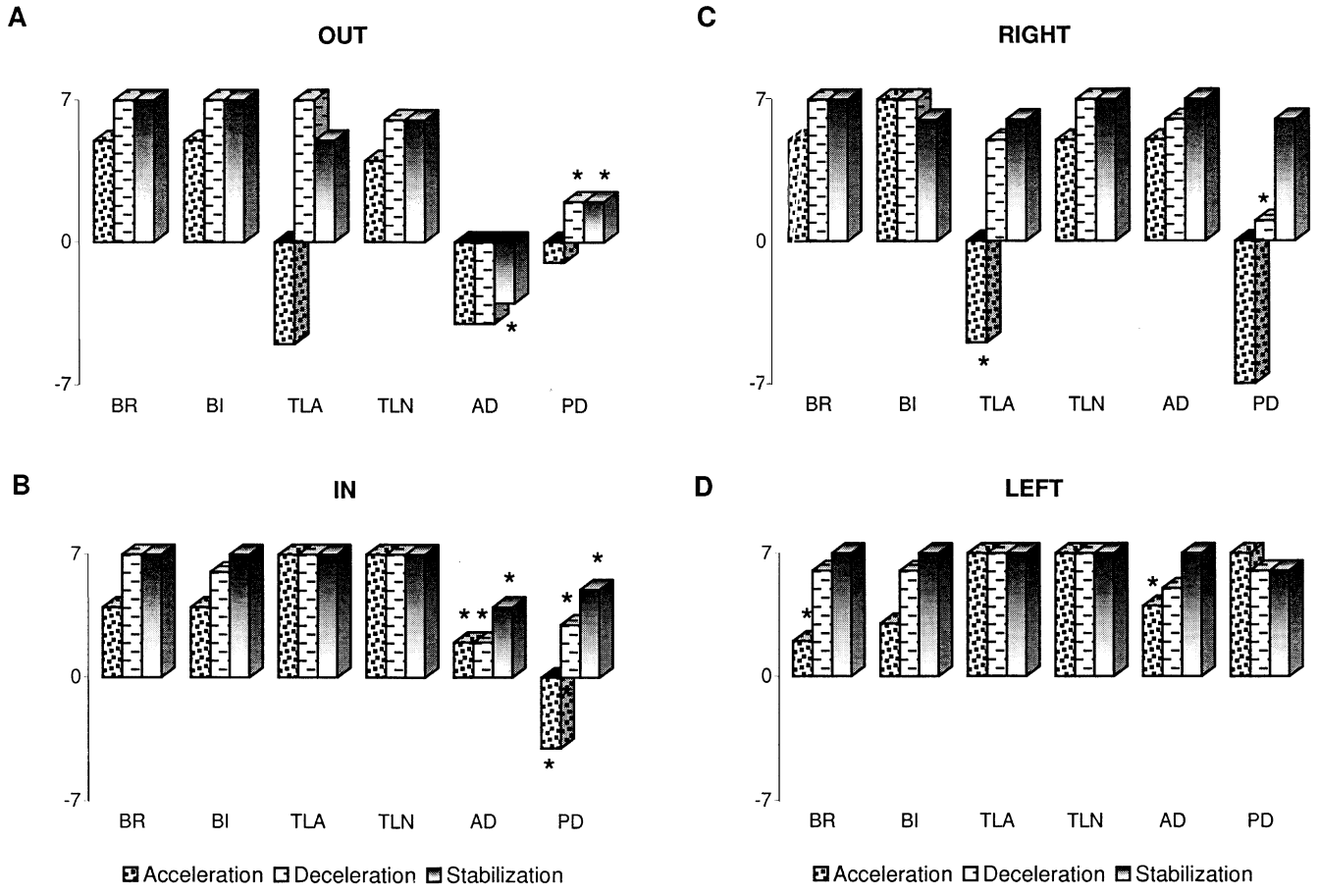

Fig. 7a–d The number of subjects whose rms EMG was significantly different in the last five trials in the assisting force field compared with the last five trials in the null field is shown for outward (**a**), inward (**b**), rightward (**c**) and leftward (**d**) movements. Results are given for each muscle and movement phase (acceleration, deceleration and stabilization). Positive values represent subjects whose activity was higher in the assisting force field than the null field. Negative values represent subjects whose activity was lower. *Asterisks* indicate cases where the opposite response was found for some subjects. In all cases, the number of subjects with the opposite response was less than or equal to that of the response which is shown

progressed for the deceleration phase and in 21/24 cases for the stabilization phase ($p<0.05$). This contrasts with 7/24 cases for the acceleration phase (not shown). For all directions of movement, the number of subjects for whom activity decreased in the stabilization phase was greater than or equal to the number for the deceleration phase. There was very little tendency to decrease muscle activity as learning continued over the next 25 trials (force field trials 26–50 in each direction). In only 1/24 cases for acceleration, 3/24 cases for deceleration and 5/24 cases for stabilization were there at least four subjects who showed a significant trend to decrease muscle activity ($p<0.05$). This suggests that most of the adaptation to the assisting force field occurred in the first half of the learning period.

Catch trials

Had adaptation to the assisting force field been based on the formation of an accurate internal dynamics model there would have been a large difference in the muscle torque needed during acceleration while the agonist muscles were being assisted by the robot manipulandum compared with deceleration where the antagonist muscles had to resist the assisting force field. Consequently, the torque impulse produced by antagonist muscles would have been much larger than that produced by agonist muscles. If subjects had formed a perfect inverse dynamics model of the force field, then on catch trials the hand should have reversed direction after about 200 ms, i.e., about 50 ms before peak velocity based on simulations.

A common feature of catch trials was an inflection in the velocity profile around 200–250 ms after movement onset, indicating that subjects intervened to accelerate at about the time that the hand would otherwise have reversed direction (Fig. 9 top). Often the initial velocity was very low and multiple inflections were apparent over an interval of twice the normal movement duration, indicating that several corrections were required to reach the target (Fig. 9 *bottom*). In four instances during outward catch trials (Fig. 10) and in one instance during rightward catch trials (not shown) there was a clear reversal in the direction of hand movement back toward the start position. In the rightward catch trial and in one of the outward catch

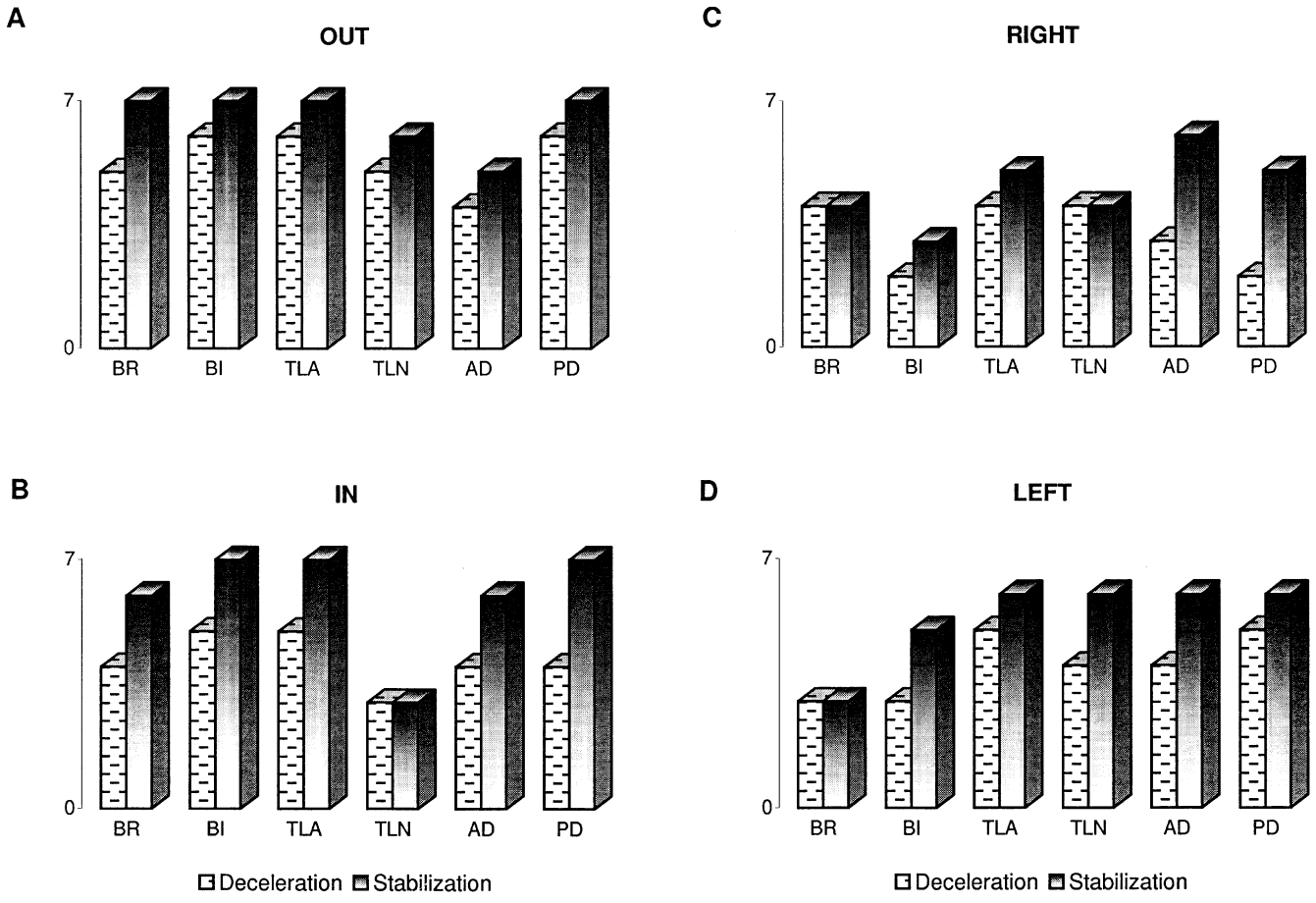

Fig. 8a–d The number of subjects for whom the slope of rms EMG was significantly less than zero over the first 25 trials in the assisting force field is shown for outward (**a**), inward (**b**), rightward (**c**) and leftward (**d**) movements. Results are given for each muscle in the deceleration and stabilization phases. Generally, the slopes were not significantly less than zero for the majority of subjects in the acceleration phase (not shown)

trials, the reversal was transient and the subjects subsequently resumed their movement toward the target, but in the other three outward catch trials the subjects stopped closer to the start position than the target position. However, in only one case did the reversal occur close to 200 ms after movement onset. In the other cases, the reversal occurred later, after the hand had moved farther. Simulations showed that if an inverse dynamics model only compensated for a portion of the assisting force and if the remainder of the compensation was provided by the viscoelastic impedance of the arm, then the greater the portion provided by the viscoelastic impedance the longer the latency before the hand reversed direction. This suggests that even for outward movements only one subject formed a truly accurate internal model of the force field.

The analysis of hand paths after adaptation suggests that movement was more stable in the outward direction than other directions. As an additional test of stability, we compared the total amount of co-contraction during stabilization, i.e., the sum of the co-contraction for the three pairs of antagonist muscles, between outward movements and movements in the other three directions for the final five trials in the assisting force field. Co-

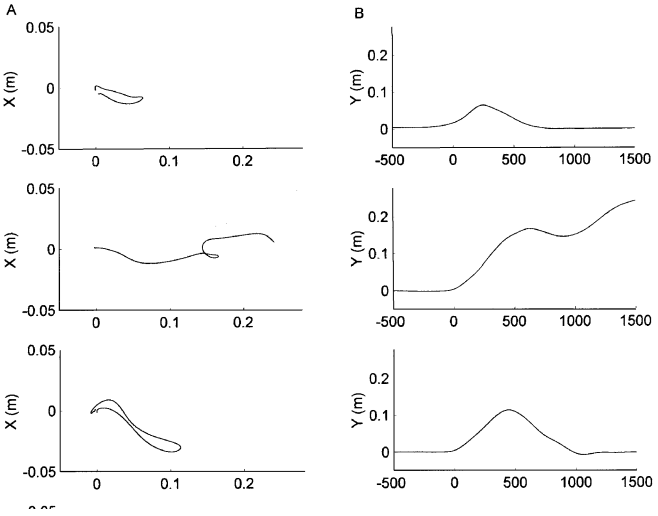

Fig. 9 Position (*top*) and velocity (*bottom*) records for a catch trial in the leftward (*solid*) and rightward (*dashed*) directions for different subjects. Note the prominent inflection soon after the first peak in the velocity profile, between 200 and 250 ms after movement onset, indicating a corrective movement. Velocity was slower for the rightward catch trial and there were inflections at regular intervals, indicating multiple corrective movements before the target was reached

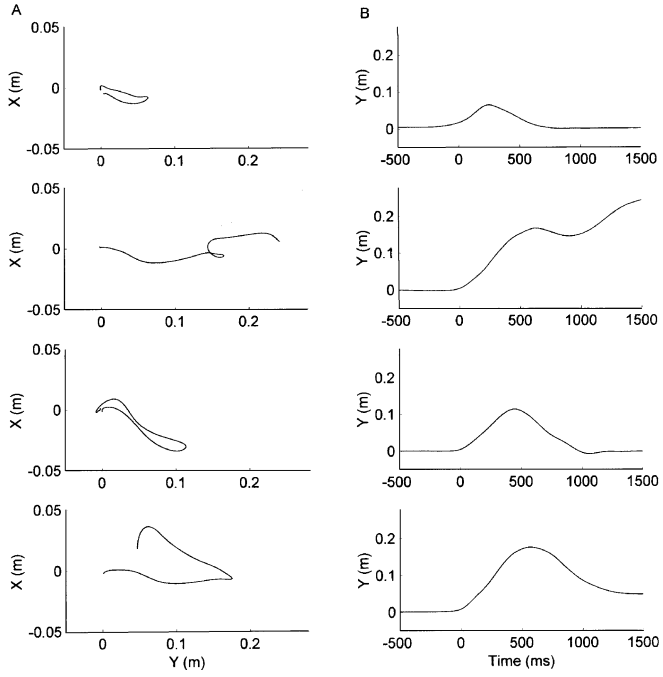

Fig. 10a, b Catch trials in the outward direction are shown for the four subjects whose hand path reversed direction before reaching the target. Hand path is shown in the *left* panel and *y*-position is shown as a function of time in the *right* panel. Note that for three of the subjects the hand returned to a position near the start position after reversal

contraction was calculated as described in the Methods. For all seven subjects, in the case of rightward movements, and for 6/7 subjects in the case of inward and leftward movements, co-contraction was greater than for outward movements ($p<0.05$). Co-contraction was elevated by about 200% for inward and rightward movements and 100% for leftward movements compared with outward movements. The need for less co-contraction during stabilization of outward movements provides further evidence that they were more stable. Thus, the formation of an accurate internal model of the assisting force field, as manifested by early reversal in movement direction during catch trials, would seem to require mechanical stability.

Discussion

This study showed that trajectory control in a velocity-dependent force field, which is inherently unstable, was achieved primarily by increasing the mechanical impedance of the arm through co-contraction of antagonistic muscles rather than by forming an accurate internal model of the force field dynamics. Stabilization at the final position also required an increase in co-contraction. Levels of co-contraction were reduced as adaptation progressed, particularly in the stabilization phase of the movement, but remained elevated relative to null field conditions after 50 movements to a given target. The length of the handpath and its trial-to-trial variability showed the greatest reduction for movements in the outward direction. There was less evidence of successful adaptation for movements in the other directions.

The present study attempted to determine whether impedance control played a more dominant role in adaptation to an assisting force field than the formation of an internal dynamics model. These two processes are analogous to the reciprocal and co-contraction commands which form the basis for the λ-model of equilibrium point control proposed by Feldman (1980). However, functionally they do not specify a controlled equilibrium position. Rather they represent two separate mechanisms for adapting to environmental dynamics (Franklin et al. 2003). Our earlier work, examining adaptation to unstable dynamics, focused on a situation where the force field was position dependent and impedance control was the only viable solution due to unpredictable features of the dynamics (Burdet et al. 2001; Franklin et al. 2003). This was not the case with the velocity-dependent assisting force field of the present study since the dynamics were predictable. Previous work on adaptation to velocity-dependent force fields showed that impedance control did play a role in the initial stage of learning (Thoroughman and Shadmehr 1999; Franklin et al. 2003) and though there was some evidence for residual co-contraction after adaptation, this was relatively insignificant. Various tests, including changes in muscle activation patterns, catch trials and stiffness measurement, suggested that the principal feature of adaptation was the formation of an accurate internal dynamics model of the force field. In the only previous study of adaptation to a stable force field, which found evidence of a significant role for impedance control, the gain of the force field was randomly varied, making the dynamics unpredictable (Takahashi et al. 2001). In contrast, we have demonstrated that even when the dynamics are predictable, subjects adapt to unstable dynamics by increasing the viscoelastic impedance of the arm through co-contraction of antagonistic muscle groups. We postulate that the increased mechanical impedance served two purposes. First, it compensated for the absence of an accurate internal model of the force field dynamics. This meant that subjects relied on the increased muscle impedance to oppose the assisting action of the force field rather than controlling acceleration by reciprocally activating the appropriate muscles. Reciprocal activation could potentially have been used both to control motion in the target direction and to control any lateral deviation. Second, it compensated for negative damping. The mechanical action of the assisting force field was equivalent to uniform negative damping. To avoid large oscillations about the final position, arising from the spring-like nature of muscles, it was necessary either to cancel oscillations by means of a strategy like pulse shaping (Singhose et al. 1997) or to increase the damping of the arm by increasing co-contraction of antagonistic muscle groups. Pulse shaping is a technique used to minimize oscillations about the final position during rapid positioning of flexible robots. It requires the generation of force pulses, which are controlled in terms of timing,

amplitude and duration to be precisely 180° out of phase with oscillations that would occur at the natural frequency thereby canceling the oscillations. Had such a strategy been exclusively used we would have expected to see bursts of activation interspersed with silent periods during movement followed by little or no activity at the final position. However, neither muscle in an antagonistic pair was ever silent at the final position, suggesting that co-contraction was important in damping oscillations about the final position during stabilization. There are currently no validated models of damping for multi-joint limbs. However, the results of Dolan et al. (1993) and Tsuji et al. (1995) suggest that the geometry of the endpoint viscosity of the arm is similar to that of the stiffness (Mussa-Ivaldi et al. 1985). Weiss et al. (1988) showed that joint viscosity was roughly proportional to the square root of joint stiffness for the ankle. Assuming that this is also the case for the elbow and shoulder and assuming that joint stiffness depends only on muscle activation and not on joint angle, when moving in the direction of the target, the viscosity of the arm would be much higher at the outward target than at the other targets. However, it would still require co-contraction to produce enough stiffness and damping to achieve a stable posture in the force field. Simulations based on the above assumptions suggested that co-contraction levels of about 30, 70 and 100% would be required to stabilize the hand at the outward, central and right targets, respectively. If the target were approached on an angle, then more co-contraction would be needed to provide lateral stability at the outward target, although not at the other targets. Given that the amount of co-contraction needed for stability was reduced with practice and that co-contraction levels dropped markedly once the target was reached (Fig. 6), it is almost certain that subjects also used an active control mechanism such as pulse shaping to reduce the reliance on damping from intrinsic muscle properties.

It might be argued that subjects did not perform a sufficient number of movements in the assisting force field to achieve complete adaptation and that with more practice the elevated levels of co-contraction, which were found in the deceleration and stabilization phases of the movement, would have disappeared. However, there was considerable variability in performance from trial to trial and there was no evidence that it was tending to decrease during the second half of the learning period. Therefore, there is no reason to believe that the performance of this subject group would have improved substantially with more practice. Since there was little change in muscle activity during the second half of the learning period, particularly during deceleration, it is doubtful that subjects were refining an internal dynamics model of the force field during this period. Nevertheless, the adaptations that did occur within the first 10–15 movements produced a significant reduction in oscillatory motion, indicating that they were effective in stabilizing the hand at the target position. The ability of subjects to reduce initial levels of contraction without compromising the stability of the stabilization phase suggests that the central nervous system begins with a large safety margin for stability, which is gradually reduced to minimize metabolic cost. The declining levels of co-contraction observed during the deceleration phase, on the other hand, suggest that subjects became less reliant on viscoelastic impedance to resist the force field, which may have been linked to formation of an internal model of the force field, however inaccurate.

Although the changes in activity of agonist muscles relative to null field movements, particularly for the acceleration phase, were generally consistent with the formation of an internal model of the force field dynamics, there was frequently also considerable co-activation of antagonist muscles as noted above. This, together with the consistent co-activation of single joint elbow muscles and biarticular muscles during deceleration, suggests that after producing a small force to initiate movement, subjects relied heavily on the viscoelastic impedance of the muscles to passively resist the force field until motion stopped. This increased impedance would also have served to attenuate oscillations around the final position that would otherwise have arisen from the negative damping property of the assisting force field. Only in the case of outward movements was there convincing evidence that an internal model of the force field dynamics also played a significant role in decelerating the movement. The reversal in movement direction, observed for four subjects, indicated that these subjects actively counteracted the force driving the arm toward the target as would be predicted from the formation of an inverse dynamics model. This return to the start position contradicts the equilibrium point hypothesis, which predicts equifinality, i.e., changing a velocity-dependent force should not affect the final position. The reasons are discussed in detail by Hinder and Milner (2003), who conducted a systematic study using a similar velocity-dependent load to investigate equifinality for single joint movements.

Reversal should also have been observed on catch trials for the other movement directions if subjects were employing an accurate internal model of the force field dynamics. However, the need for co-contraction to provide stability at the final position may have interfered with the development of the reciprocal pattern of muscle activation corresponding to an accurate internal model of the force field dynamics during movement. The predicted after-effects may have been masked by voluntary corrective movements, although early corrective movements likely indicate that subjects were more prepared to correct errors during catch trials because their internal model was less accurate than for outward movements. The formation of a more accurate internal model for outward movements is also supported by the shorter path length after adaptation to the force field than for movements in the other directions.

Previous studies have documented conditions under which either reciprocal muscle activation (internal dynamics model) or co-contraction of antagonistic muscles (impedance control) alone can account for observed adaptive responses (Thoroughman and Shadmehr 1999; Franklin et al. 2003). However, it was not clear whether

impedance control was related principally to unpredictability in the environmental dynamics, as shown by Takahashi et al. (2001), or to instability. The results of this study suggest that the accuracy of an internal model depends on the stability of the coupled dynamics of the limb and the environment. Even if the environmental dynamics are completely predictable, an accurate internal dynamics model can only be formed if the coupled dynamics of the limb and the environment is also sufficiently stable.

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