

# Loss of Proprioception Produces Deficits in Interjoint Coordination

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## SUMMARY AND CONCLUSIONS

1. We analyzed the performance of a simple pantomimed gesture in 2 patients with large-fiber sensory neuropathy and 11 control subjects to determine how proprioceptive deafferentation disrupts unconstrained multijoint movements. Both patients had near-total loss of joint position, vibration, and discriminative touch sensation in the upper extremities. Muscle strength remained intact.

2. Subjects performed a gesture similar to slicing a loaf of bread. In this gesture, the hand first moves outward from the body, reverses direction sharply, and then moves back toward the body. Accurate performance requires precise coordination between the shoulder and elbow joints during movement reversals. Movements were performed under two conditions: with eyes open and with eyes closed. Three dimensional shoulder, elbow, wrist, and hand trajectories were recorded on a WATSMART system.

3. When control subjects performed the gesture with their eyes closed, their wrist trajectories were relatively straight and individual cycles of motion were planar. Movements reversed direction sharply, such that outward and inward portions of the wrist path were closely aligned. Corresponding to this spatial profile, the reversals in movement direction at the shoulder joint, from flexion to extension, and at the elbow joint, from extension to flexion, were synchronous.

4. In contrast, when deafferented patients performed the gesture with their eyes closed, their wrist trajectories were highly curved and individual cycles were severely nonplanar. The wrist paths showed a characteristic anomaly during the reversal in movement direction, when elbow joint movement became transiently locked. Correspondingly, the movement reversals at the shoulder and elbow joints were severely temporally decoupled.

5. When patients were able to view their limbs during performance of this gesture there was significant improvement in the linearity and planarity of movements. However, the patients remained unable to synchronize the movements at the shoulder and elbow joints to produce spatially precise wrist paths.

6. We conclude that loss of proprioception disrupts interjoint coordination and discuss the hypothesis that this interjoint coordination deficit results from a failure to control the interaction forces that arise between limb segments during multijoint movements.

## INTRODUCTION

It is widely recognized that proprioceptive input from muscles, joints, and other receptors is necessary for the accurate control of movement and posture. Indeed, patients with large-fiber sensory neuropathy, in whom axons carrying this information to central structures degenerate, show prominent disorders of motor control. However, despite a great deal of research in animals and human subjects, the precise contribution to motor control made by proprioception remains incompletely understood. Studies in patients with large-fiber sensory neuropathy have primarily focused

on the control of single-joint movement. It has been shown, for example that patients deprived of proprioceptive feedback are unable to adjust their movements in the face of unexpected loads, nor can they maintain a steady joint angle without vision (Rothwell et al. 1982; Sanes et al. 1985). On the other hand, these patients are able to program and execute isolated movements of the finger (Rothwell et al. 1982), wrist (Sanes et al. 1985), or elbow (Forget and Lamarre 1987) relatively accurately, although with increased variability. Electromyographic (EMG) studies have shown that this variability in the amplitude of movement reflects variability in the timing of agonist and antagonist muscle activation (Forget and Lamarre 1987).

Recently, however, it has been shown that loss of proprioception results in large systematic errors in multijoint movements attributable, at least in part, to impaired motor programming (Ghez et al. 1990; Gordon et al. 1990). Patients deafferented by large-fiber sensory neuropathy were shown to make large errors in direction and extent while movement paths were curved instead of being straight. These systematic errors were so severe as to give rise to motor scotomas, regions of space into which patients' hand trajectories rarely entered, despite the presence of targets. Errors in movement extent varied systematically with the direction of movement in accord with variations in the inertial field of the hand, which, for planar movements of the hand, has an elliptical distribution. While control subjects adjusted the duration of acceleration and deceleration to compensate for directional variations in inertia, this compensation did not occur in deafferented patients (Ghez et al. 1990; C. Ghez, J. Gordon, and M. F. Ghilardi, unpublished data). The errors in direction and extent were substantially reduced when patients were able to view their arm before moving, indicating that the deficit that occurred without vision was, to a large degree, the result of defective feedforward control.

The special difficulty shown by deafferented patients in controlling limb inertia emphasizes the greater difficulty in achieving accurate control of the hand in multijoint compared with single-joint movement. In multijoint movements, the shape of the hand path is dependent not only on the angles through which each joint moves during the course of motion, but also on the temporal relations between individual joint movements. Consequently, both the time and degree of activation of muscles acting at all joints need to be precisely coordinated to achieve spatial accuracy.

Another factor that complicates the control of multijoint movement is that motion of any limb segment produces forces at all other mechanically coupled segments (Hasan 1991). For example, in reaching movements forces varying with angular velocities and accelerations of the shoulder

produce significant torques at the elbow. These torques vary with the direction of movement. Even in movements of moderate speed they become large enough to displace the limb (Hasan 1991; Sainburg et al. 1992; Smith and Zernicke 1987). Therefore, during multijoint movements in three-dimensional space, neural control signals must not only take account of the variable effects of gravity and limb inertia, but also the mechanical interactions that occur between limb segments. Hollerbach and Flash (1982) demonstrated through simulations that without this compensation, linear movement paths would become curved and inaccurate. Such control is likely to be achieved by coordinating the muscle actions upon a given limb segment with the interaction torques acting upon that segment.

Thus the production of spatially accurate multijoint movements requires temporally precise patterns of muscle activity. Precision in muscle timing may also be important in controlling limb interaction torques (Sainburg et al. 1992). This control is likely to present a particular problem for deafferented patients given their known difficulty in accurately timing agonist and antagonist muscle contraction even in single-joint movements. We therefore hypothesized that the curvature and directional errors of multijoint movements in these patients could reflect impairments in inter-joint coordination.

To address this question we compared the spatial and the temporal profiles of three-dimensional, unconstrained arm movements made by patients with large-fiber sensory neuropathy with those of control subjects. Specifically, we explored the role of proprioception in the temporal coordination between multiple joints. For this analysis, we expanded recently developed computer graphic techniques (Kothari et al. 1992; Poizner et al. 1986) that allow simultaneous numeric and graphical display of three-dimensional trajectories. In a pilot study, patients with large-fiber neuropathy and normal control subjects performed a variety of visually modeled gestures, including slicing bread, rolling down a car window, hammering a nail, and unlocking a door. In all these gestures, the deafferented patients' limb trajectories were severely distorted relative to those of control subjects. We chose to focus this study on the slice gesture because this movement has certain readily definable task requirements for spatial precision: hand movement must be straight and planar and successive motions must overlap one another. In addition, this task requires precise coordination between the shoulder and elbow joints for accurate performance. This is a geometrical consequence of the sharp reversal in movement at the most outward point in each cycle of movement. To reverse hand direction by 180°, it is necessary that both shoulder and elbow joint angular motions reverse direction simultaneously. Our findings indicate that the patients' performance deficit in this task arises in large part from an inability to coordinate the motions of elbow and shoulder joints. Some of these results have been previously presented in abstract form (Sainburg et al. 1991).

## METHODS

### *Subjects*

Subjects were 11 neurologically normal adults (9 females and 2 males, aged 24–46 yr), and 2 patients (*MA* and *CF*) with severe

large-fiber sensory neuropathies affecting both upper extremities, as well as their trunks and lower extremities. In both patients, the disease is of undetermined etiology and has not progressed for several years.

*Patient MA*, a right-handed woman, was 46 years old at the time of testing. Her errors in a planar reaching task are described elsewhere (Ghez et al. 1990; C. Ghez, J. Gordon, and M. F. Ghilardi, unpublished data). Her symptoms began in 1985 with painful dysesthesias and loss of sensation in the right arm as well as clumsiness of previously skilled movements. Her disease progressed over a period of 6 months to involve both sides of the body and the lower part of the face, but has remained stable since then. She was hospitalized in 1986 for evaluation when the diagnosis of large-fiber sensory neuropathy was made.

At the time of her initial evaluation, she was found to have marked loss of position and vibratory sensation in all four extremities. The arms were more affected than the legs and the right more than the left. Nerve conduction studies showed an absence of sensory responses in medial, ulnar, and radial nerves bilaterally, as well as in the right sural nerve. EMGs, motor responses, and conduction were, however, normal. Sensory evoked potentials from the upper extremities were absent, but were present from the lower extremities. Apart from an increase in cerebrospinal fluid protein with oligoclonal bands, laboratory and brain imaging studies failed to reveal any malignancy or any CNS pathology.

The disease has not progressed significantly over the 6 years since her hospitalization. Although *patient MA* is able to walk, her gait is unsteady and she is unable to maintain balance with her eyes closed. She has difficulty performing any task requiring fine coordination, such as buttoning her clothes and bringing food to her mouth with a fork or spoon. Her difficulties in locomotion and manipulation are markedly accentuated in the dark, when she can not see.

At the time of our study, the patient showed a reduction in tactile and pinprick sensation in the lower part of the face and both arms. Position sensation was absent in the digits and wrist. At the elbow and shoulder, she could only detect the occurrence of movement and sometimes its direction at the extreme end of the joint's range of motion. Vibration sensation was normal along the vertebral column, but absent in the digits, wrist, and elbow and was markedly reduced at the shoulder. Strength was mildly reduced through the upper extremity muscles, compatible with decreased use.

The second patient *CF* is a left-handed man who was 63 years old at the time of testing. During the course of an acute febrile illness in 1989, he developed acute sensory loss and ataxia progressing over a period of ~1 week. He was hospitalized and diagnosed as having an acute ganglioneuritis of unknown origin. Over the ensuing 3 years, there has been no clinical recovery, nor any further degradation in his neurological status.

Over the 3 years since his hospitalization, the patient has continued to show severe sensory loss and incoordination in his movements but no significant weakness. He suffers from the same difficulties in manipulating objects and feeding himself as *MA* and, as with *MA*, his difficulties are accentuated in the dark or when his eyes are closed. His lower extremities are however considerably more severely affected, and he is unable to walk or independently propel a manual wheelchair.

At the time of testing, he was unable to detect motion of the digits, wrist, elbow, or of any joints of the lower extremities. At the shoulder, he could only detect movement at extreme angular displacements. The patient was unable to detect movement when the experimenter produced combined elbow and shoulder movements of the same magnitude and speed as those produced in the slicing gesture. Similarly, vibratory sensation was absent at the fingers, wrist, elbow, and shoulder and was reduced below the lumbosacral spine to the toes. Vibratory sensation was intact



FIG. 1. Schematic illustration of the slice gesture as performed by a control subject.

above the clavicle. Two-point discrimination was absent throughout both upper extremities and mildly reduced over the face. Detection of pin pricks, temperature, and subjective sense of sharpness was intact throughout the face, body, and extremities. Detection of touch was intact throughout, although the ability to localize tactile stimuli over the upper and lower extremities was very poor. Strength was normal through the shoulder, elbow, and wrists, and mildly reduced through the fingers. Deep tendon reflexes were absent. Plantar responses were flexor.

Data were collected in one session for each control subject, in three sessions over an 8-month period for *MA*, and in one session for *CF*.

### Tasks

Subjects were seated in a firm armless chair, facing the experimenter. The deafferented subjects' trunks were supported to prevent loss of balance. Subjects were instructed to perform a gesture, similar to slicing a loaf of bread with a knife, as performed in front of them by an examiner. Figure 1 illustrates the gesture as performed by a control subject. The gesture to be imitated consisted of a series of cyclic back and forth motions of the hand in which the hand was to return to its original position after each cycle of movement. Subjects were urged to maintain their hand in a single plane and to keep their movements smooth and straight. All subjects used their dominant hand and first performed the movement with their eyes closed (no vision condition) and then with their eyes open (vision condition). Five movements consisting of three to six cycles each were collected under each condition during each session.

### Three-dimensional data acquisition and computer graphic analysis

Three-dimensional data were recorded using a WATSMART system (Northern Digital). Two optoelectronic cameras directly sensed the positions of three infrared-emitting diodes placed on the limb segments of the subjects. A microcomputer synchronized

the sequential activation of the diodes with the digitizing of the camera signals. The infrared-emitting diodes were strapped to the subject's limb segments at consistent positions that were referenced to the following bony landmarks: acromial process of the scapula (shoulder), lateral epicondyle of humerus (elbow), and the ulnar styloid process (wrist). Data were sampled at 100 Hz and low-pass filtered with a modified Butterworth filter using a cutoff frequency of 8 Hz. The two-dimensional positional data from each camera were then reconstructed into three dimensions.

The data were analyzed on a Silicon Graphics IRIS 4D/80GT workstation with customized software for the interactive manipulation and dynamic display of the reconstructed trajectories (Kothari et al. 1992; Poizner et al. 1986). All trajectories were edited graphically to remove portions of movement related to the subjects raising and lowering their hands at the beginning and end of movement trials. The three-dimensional trajectories were differentiated twice to obtain tangential velocity and acceleration of each limb segment over time. Individual cycles of motion, each representing an individual "slice" of movement, were analyzed separately.

The angular orientations of the upper arm and of the forearm segments and the angle of flexion and extension of the elbow were computed. The parameters chosen were the upper arm elevation and yaw angles. Figure 2 illustrates the elbow and upper arm angles in relation to our three-dimensional coordinate system. Angular elevation is measured in a vertical plane and yaw in a horizontal plane, relative to the anterior direction (see Soechting and Terzuolo 1986).

### Spatial accuracy

We used measures of linearity of individual wrist and elbow motions and planarity of individual cycles of motion to assess the accuracy of task performance. Linearity was computed separately for outward and inward portions of each cycle (divided at the minimum of the wrist tangential velocity). Major and minor axes of each half-cycle of movement were then calculated. The major axis of a trajectory segment was defined as the maximum distance between any two coordinate points, whereas the minor axis was defined as the largest distance, perpendicular to the major axis,

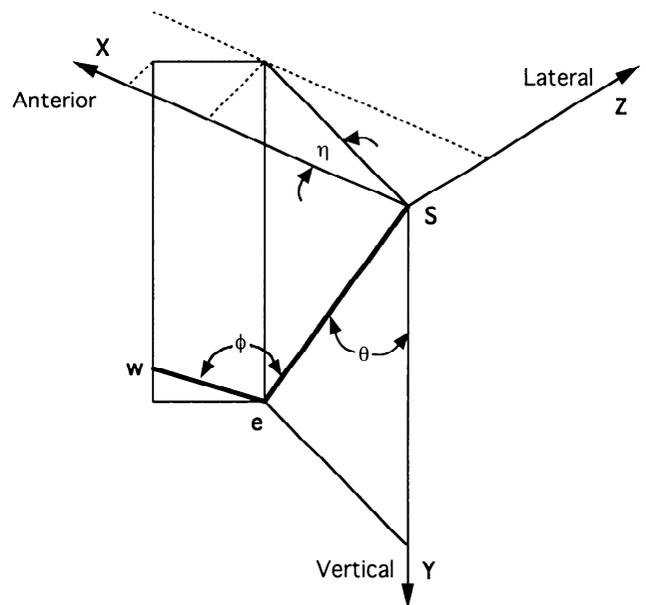


FIG. 2. Upper arm orientation angles. The two upper arm orientation angles are illustrated relative to our 3-dimensional coordinate system. Upper arm yaw ( $\eta$ ) and elevation ( $\theta$ ), as well as the anatomic elbow joint angle ( $\phi$ ) are shown. Modified from Soechting and Terzuolo (1986).

between any two coordinates. The ratio of the major to minor axis of each half-cycle of movement was taken as the measure of movement linearity. A ratio of one characterizes a circular path, whereas larger values indicate progressively more linear paths.

To assess the planarity of individual cycles of the movements, the best fitting plane of wrist motion was computed with a least-squares fit of the series of wrist coordinates to the plane equation. The SD of the distances of individual coordinates from this plane was also calculated. This SD was then normalized to the amplitude of the movement (length of major axis). The resultant ratio was inverted to provide a measure of the degree of deviation from trajectory planarity, such that high values indicate that the path remained in a single plane, whereas low values indicate deviation from planarity.

### Statistics

The Mann-Whitney  $U$  was used to test the significance of differences between data sets. This nonparametric test was chosen due to the small sample sizes when comparisons were made between subgroups of data within a single subject's movements. This test was also used for analysis of larger sample sizes to obviate the need for assumptions regarding population distributions required in parametric tests. To reduce the probability of type I errors, we divided the  $\alpha$  value (0.05) by the number of tests (14). Thus, we used an  $\alpha$  value of 0.001, which provided a stringent and conservative test for our analysis.

## RESULTS

### *Deafferentation impairs the spatial precision of movement*

When performed by control subjects, the slicing gesture consisted of a stereotyped sequence of four to seven forward and backward motions of the hand. We first describe the features of the gesture performed without vision and later examine the effects of vision of the limb on performance.

The characteristic features of these movements are illustrated in Fig. 3, which shows individual cycles of movement taken from a single gesture performed by a control subject (*top*) and by the two deafferented patients, *MA* (*middle*) and *CF* (*bottom*). The lefthand panels of Fig. 3 show a three-dimensional view of the shoulder, elbow, and wrist paths. Stick figure representations of the arm and forearm show successive limb positions every 40 ms during the outward portion of the cycle. To enhance the clarity of this illustration, stick figures are not shown for the return portion of the trajectory. The righthand panels of Fig. 3 plot the wrist paths individually for each cycle. The second cycle of the gesture, corresponding to the three-dimensional view at the left, is shown in bold. Each cycle is composed of an outward and an inward phase during which the wrist moves first away from and then back toward the subject's body axis. At the midpoint of the movement cycle, the wrist trajectory reverses direction.

In the control subjects, wrist paths of individual cycles are very similar to one another: outward and inward segments are linear and closely aligned, remaining in a narrow plane. Movements are terminated near their starting position, as demonstrated by the close alignment of the stick drawings in Fig. 3. Reversals in direction, at the most outward point, are sharp. In contrast, the wrist paths of deafferented patients are variable, curved and nonplanar. At the end of each cycle of movement, the wrist is distant from where it was at the start of the cycle. While the wrist paths of control subjects show sharp reversals in direction between

the outward and inward segments of the trajectory, such reversals are blunted in the patients. However, the movement reversals between cycles (i.e., from inward to outward portions of the wrist trajectory) are sharp for both control subjects and patients.

Figure 4 shows the group means of movement linearity and planarity for all cycles of motion sampled in the control subjects (150 cycles) and for each deafferented subject separately (*MA*: 50 cycles; *CF*: 33 cycles). Medians are indicated by open circles. In control subjects and in both patients, elbow trajectories were curved. This is a geometric consequence of the fact that the upper arm rotates around a single joint, the shoulder. Control subjects' wrist trajectories were both more linear ( $U = 6,815$ ,  $P < 0.001$ ) and more planar ( $U = 2,843$ ,  $P < 0.001$ ) than their elbow trajectories. In deafferented patients, the wrist paths were both less linear ( $U = 814.5$ ,  $P < 0.001$ ) and less planar ( $U = 182$ ,  $P < 0.001$ ) than those of control subjects. Moreover, the patients' wrist trajectories were significantly less linear ( $U = 4,371$ ,  $P < 0.001$ ) and less planar ( $U = 826$ ,  $P < 0.001$ ) than their elbow trajectories. Thus, in contrast to control subjects, the movements of the deafferented patients' forearms were less linear and planar than those of their upper arms.

### *Deafferentation produces discrete trajectory anomalies during reversals in movement direction*

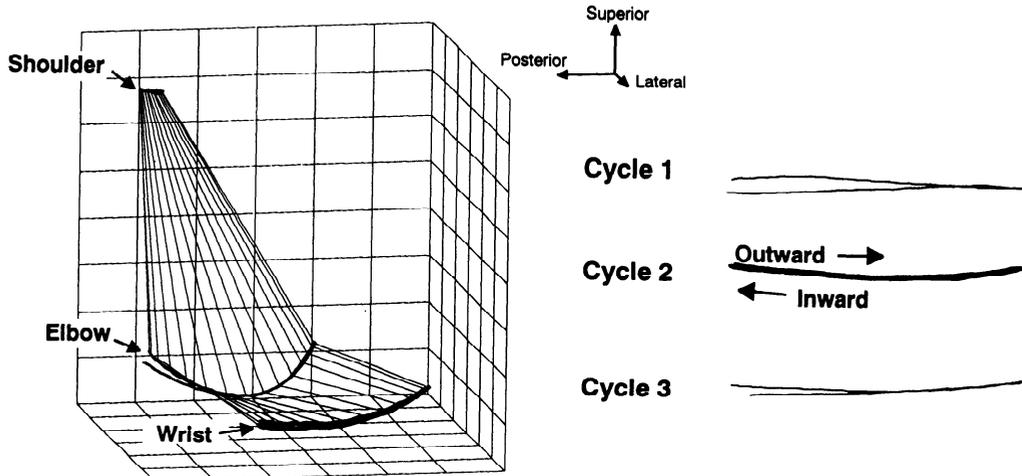
To characterize the spatial distortion in the patients' limb trajectories that occurred at direction reversals, we partitioned each cycle of movement into three phases: outward, reversal, and inward phase (Fig. 5). The outward phase began with the onset of outward acceleration of the wrist and ended at peak wrist deceleration. The reversal phase (shading in Fig. 5) was defined as starting at the peak deceleration of outward movement and ending at the peak acceleration of the inwardly directed movement. The inward phase began at the peak acceleration of inward movement and continued until the end of the cycle.

As can be seen in the example shown in Fig. 5, in control subjects the direction of wrist movement reverses sharply, so that inward and outward paths are closely aligned. This sharp direction reversal corresponds to a single minimum in both the tangential velocity and acceleration of the wrist. In contrast, movements of the patients show a pronounced widening of the wrist path during the reversal phase with a resulting spatial separation of inward and outward paths (Fig. 5, *bottom left*). This spatial distortion corresponds to a discrete anomalous peak in wrist tangential velocity and acceleration (Fig. 5, *bottom right*). A similar peak occurred in 96% of the reversal phases of all cycles of movement sampled in *MA* and in 100% of all cycles of movement sampled in *CF*. However, only 3% of the 150 cycles of movement sampled in control subjects had acceleration peaks within the reversal phase.

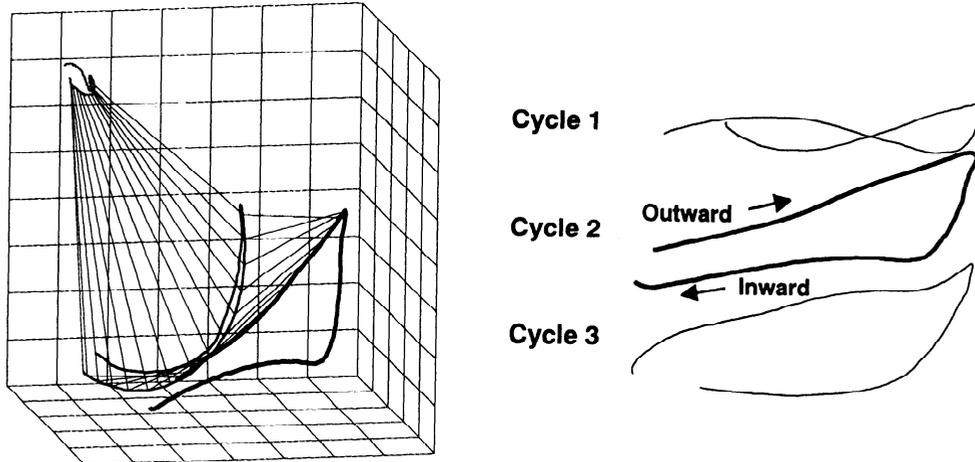
### *Reversal phase anomaly in the wrist path reflects transient locking of the elbow joint in extension*

We next sought to characterize the changes in joint kinematics that gave rise to the spatial errors in wrist trajectories during the reversal phase of movement in the patients. Figure 6 shows ensemble averages of the changes in elbow angle (*bottom*) and elbow angular velocity (*top*) for all move-

### Control: 1



### Deafferented: MA



### Deafferented: CF

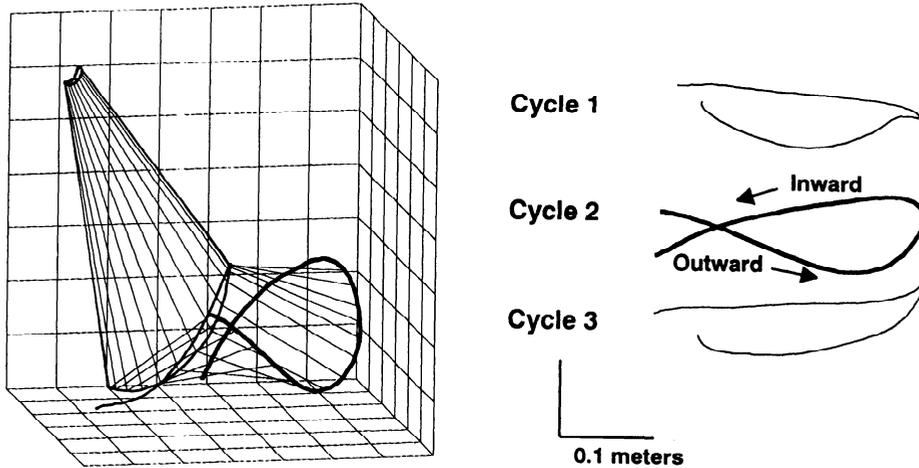


FIG. 3. *Left*: 3-dimensional limb trajectories. A single cycle of a movement trial performed by *control 1* (*top*) and the two deafferented patients: *MA* (*middle*) and *CF* (*bottom*). Shoulder, elbow (gray), and wrist paths are shown. Stick figures represent limb positions at the beginning and end of each movement cycle. *Right*: parasagittal views of successive cycles of the wrist path. The second cycle of each movement (bold) corresponds to the 3-dimensional view shown on the *left*.

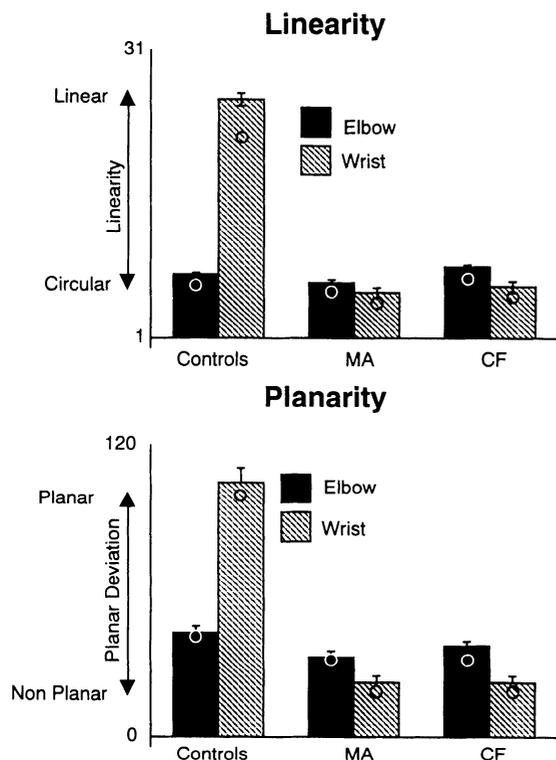


FIG. 4. Movement linearity and planarity. Mean linearity and planarity measures are shown for all 150 cycles of movement sampled across all 11 control subjects, all 50 cycles sampled from *MA*, and all 33 cycles sampled from *CF*. Error bars represent SEs. Open circles depict the median values for these measures. In contrast to the deafferented patients' trajectories, control subjects' wrist trajectories (▨) are more linear and planar than their elbow trajectories (■).

ment cycles in each deafferented patient (*solid*) and in all control subjects (*dashed*). In these averages, individual cycles were synchronized with the initiation of elbow flexion (at the zero-crossing of the elbow angular velocity).

In control subjects, the elbow extends during the outward phase of movement and flexes during the inward phase. The transition from elbow extension to flexion occurred smoothly. In the patients, on the other hand, the transition from extension to flexion is interrupted by a transient reversal in the slope of the elbow angular velocity (Fig. 6, *top*). This reversal effectively locks the elbow at or near peak elbow extension (Fig. 6, *bottom*) for an average of 90 ms in *CF* and 120 ms in *MA*. Thus, while intact subjects can smoothly reverse the direction of elbow movement during the slicing gesture, the deafferented patients cannot. Instead, when the hand is to reverse direction, the elbow joint becomes transiently locked.

#### Deafferentation impairs interjoint coordination

Deafferentation is known to disrupt the temporal precision with which antagonistic muscles are sequentially activated during rapid force pulses (Gordon et al. 1987) and during single joint movements (Forget and Lamarre 1987). We therefore, hypothesized that the spatial distortion of the wrist paths in deafferentation might result in part from an impairment in the temporal coordination of shoulder and elbow motions. To test this hypothesis, we examined the temporal relationship between shoulder joint and elbow

joint movements during the slicing gesture. It should be noted that the characterization of movements at the shoulder is significantly more complex than at the elbow. The elbow is a simple hinge joint with a single axis of rotation, whereas the shoulder comprises five distinct articulations, each with multiple axes of rotation. Motions at the shoulder can, however, be characterized by the elevation (orientation relative to a vertical axis passing through the shoulder) and yaw (orientation relative to a horizontal axis passing through the shoulder) angles of the upper arm segment (see Fig. 2). We therefore plotted the changes in elbow angle against both upper arm elevation and upper arm yaw during each cycle of movement. We expected that in control subjects, the sharp reversal in the spatial path of the wrist would be produced by simultaneous reversals at the shoulder (flexion to extension) and elbow joints (extension to flexion).

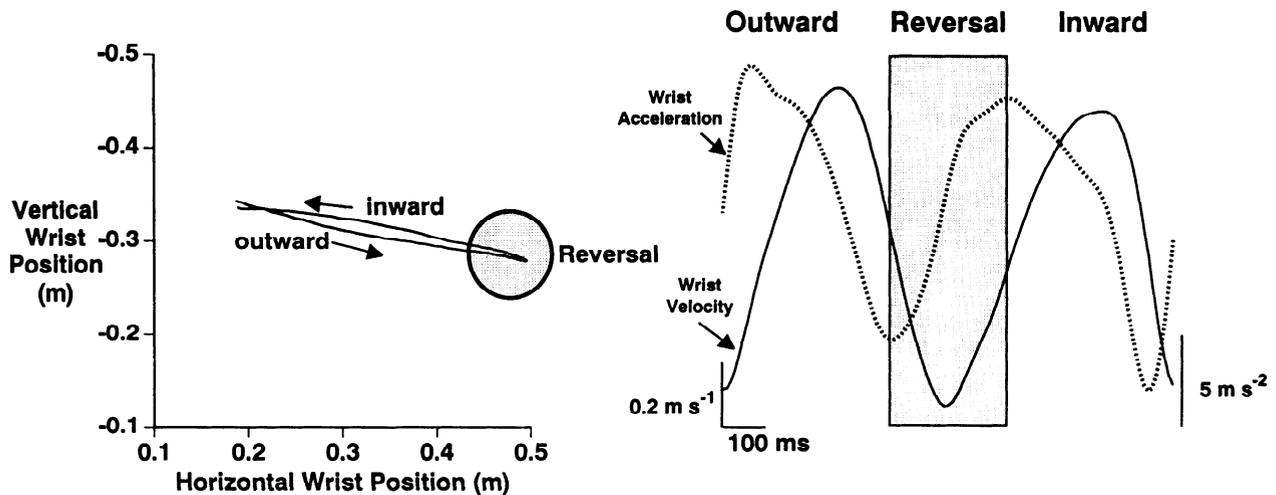
Figure 7 presents examples of such plots for five consecutive cycles from a control subject (*top*) and from each patient (*MA: middle, CF: bottom*). In the control subject, increases and decreases in elbow angle occur synchronously with increases and decreases in both upper arm elevation and yaw. Elbow and shoulder joint movements reverse direction simultaneously. In deafferented patients, however, the elbow angle remains stationary for a brief interval once its maximal value is achieved (the observed locking noted earlier). While upper arm elevation or yaw continue to increase, resumption of elbow flexion does not typically occur until after the upper arm angles reverse direction. Thus, the temporal decoupling of shoulder and elbow rotations represents the joint angle counterpart of the spatial distortions in the reversal phase of the patient's wrist trajectories.

The combined effect of moving the various degrees of freedom at the shoulder joint is a displacement of the distal end of the humerus, i.e., the elbow point itself. Accordingly, the minimum in the elbow tangential velocity within the reversal phase of movement represents the reversal in direction of upper arm movement in three-dimensional space. To quantify the degree of temporal coordination of shoulder and elbow, we therefore computed the time difference between this minimum and the reversal in direction of the elbow angle. We refer to the value of this time difference as "interjoint coupling interval."

Figure 8 shows superimposed records of the elbow angular velocities of all movement cycles aligned with the minimum in elbow tangential velocity (vertical line in Fig. 8). In control subjects (*top*), all elbow angular velocity traces cross zero close to the time that the elbow tangential velocity reaches minimum (arrow at vertical line). Figure 9 shows the distribution of time differences between the zero crossings in elbow angular velocities and the minima in elbow tangential velocities (interjoint coupling interval). This coupling interval, an index of the temporal coordination between elbow and shoulder joint movement, averaged  $10.76 \pm 8.1$  (SD) ms in the control subjects.

On the other hand, in the patients, the zero crossings of the elbow angular velocity occurred at a variable time relative to the elbow tangential velocity minima (Fig. 9, *MA: middle and CF: bottom*). Elbow angle reversed an average of  $136 \pm 88$  ms in *MA* and  $98 \pm 66$  ms in *CF* before the reversal of shoulder joint movement. However, the range of timing in elbow flexion initiation was as early as 350 ms

## Control



## Deafferented: MA

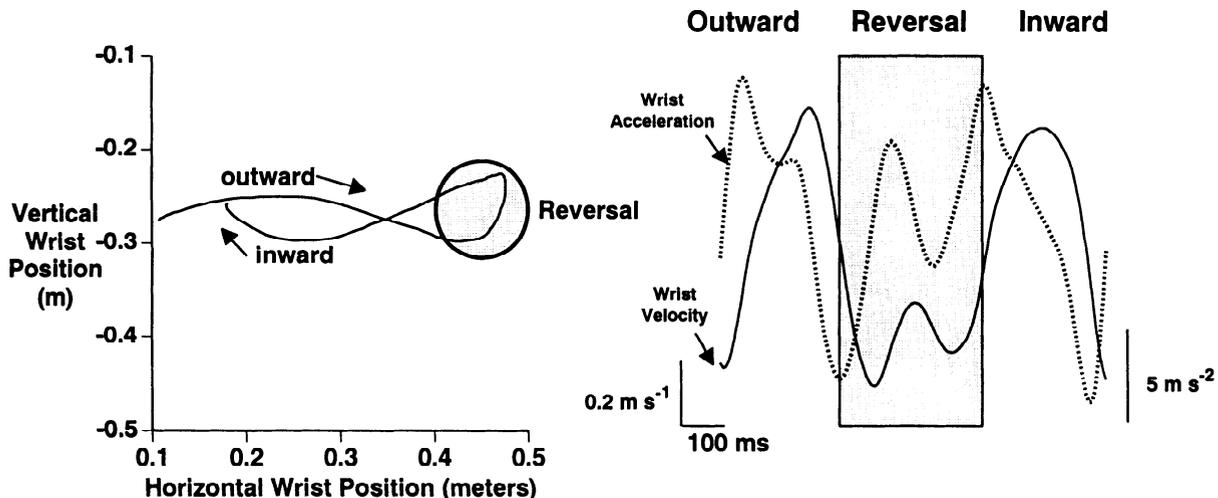


FIG. 5. Phases of the movement cycle. A parasagittal projection ( $X$ - $Y$  plane) of the wrist trajectories of typical movement cycles from *control 2* (top) and *MA* (bottom) is shown on the left. The corresponding temporal profile of each trajectory, including wrist tangential velocity (—) and acceleration (----) is shown on the right. Each cycle has been subdivided into outward, reversal, and inward phases. The reversal phase has been shaded in both the spatial (left) and temporal (right) profiles of the wrist trajectories.

before and as late as 140 ms after the reversal in shoulder joint rotation in the deafferented patients. Thus, whereas in normal subjects elbow flexion is initiated quite precisely some 10 ms before the reversal in shoulder joint motion, in the deafferented patients the two reversals are severely desynchronized.

### *In deafferentation, spatial precision and interjoint coordination improve with vision of the limb*

It is known that deafferented patients are able to use visual information to partially compensate for errors in reaching (Ghez et al. 1990). Therefore, we asked whether vision of the moving limb could also improve the spatial precision and temporal coordination of the three-dimen-

sional multijoint slicing gesture. Figure 10 shows the effects of vision on spatial precision (top and middle) and interjoint coordination (bottom). The spatial distortion that resulted from deafferentation was reduced when the movement was performed with vision. The patients' wrist paths became more linear ( $U = 2,601$ ,  $P < 0.001$ ) and more planar ( $U = 657.5$ ,  $P < 0.001$ ), when they viewed their limb during performance of the gesture. These improvements corresponded to a large decrease in the interjoint coupling interval during the reversal phase of motion ( $U = 2,129.5$ ,  $P < 0.001$ ).

No significant difference in either movement planarity ( $U = 12,039.5$ ,  $P = 0.964$ ) or linearity ( $U = 42,602$ ,  $P = 0.055$ ) occurred between the vision and no vision conditions in control subjects. Similarly, there was no significant

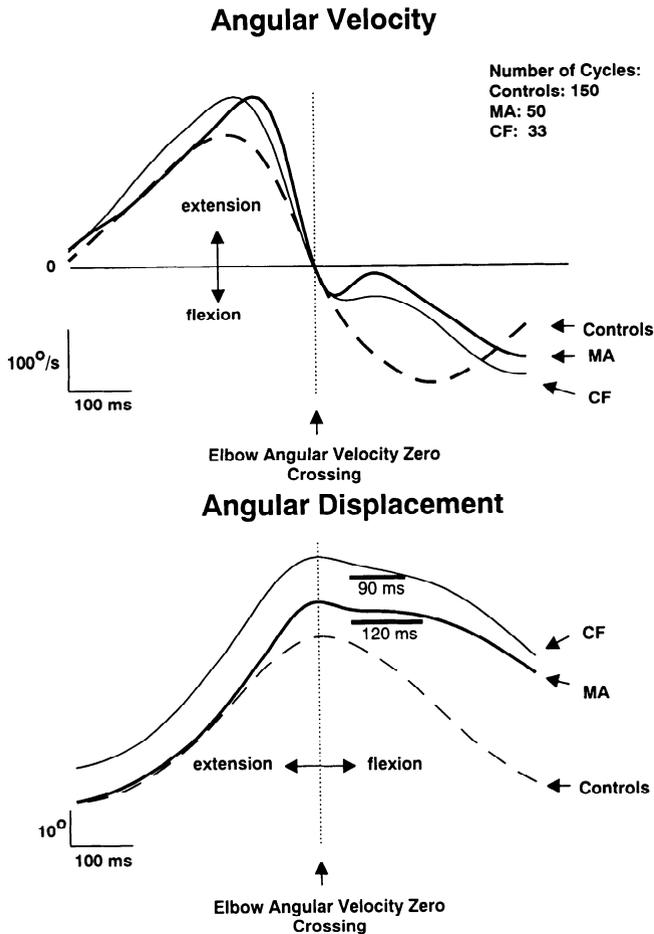


FIG. 6. Elbow joint kinematics. Ensemble averages of elbow joint angular velocity (*top*) and elbow angular displacement (*bottom*) profiles are shown for all cycles of movement sampled across 11 control subjects (-----) and each deafferented subject (—). Data has been synchronized to the elbow angular velocity zero crossing marked by the vertical line in both plots. Four hundred milliseconds to each side of this event were sampled. Horizontal bars represent the duration in which the elbow angular velocity remained less than the value at the slope reversal (beginning of the bar) in the deafferented patients.

difference in the interjoint coupling interval ( $U = 8,007.5$ ,  $P = 0.350$ ). The mean interjoint coupling interval was  $10.76 \pm 8.1$  ms when movements were performed without vision and  $10.5 \pm 7.93$  ms when performed with vision.

When able to view their limbs during movements, deafferented patients were still unable to perform spatially precise multijoint movements. Their wrist trajectories remained significantly less linear ( $U = 2,601$ ,  $P < 0.001$ ) and less planar ( $U = 657.5$ ,  $P < 0.001$ ) than the trajectories of the control subjects. As when performing with eyes closed, the spatial deficit under vision conditions corresponded to significant interjoint decoupling in deafferented subjects compared with control subjects ( $U = 1,461.5$ ,  $P < 0.001$ ). Thus, while vision reduced interjoint decoupling in deafferentation, it did not enable the patients to synchronize elbow and shoulder motions enough to produce as spatially precise wrist trajectories as control subjects.

DISCUSSION

The results reported here demonstrate that the performance of unconstrained multijoint movements is pro-

foundly impaired in patients who have lost proprioceptive sensation in the limbs. We analyzed the performance of a visually modeled gesture that required precise coordination between shoulder and elbow joint movements. Instead of a series of linear back and forth motions of the hand within a single plane, the patients' hand-paths were curved, non-planar and showed a characteristic anomaly at movement

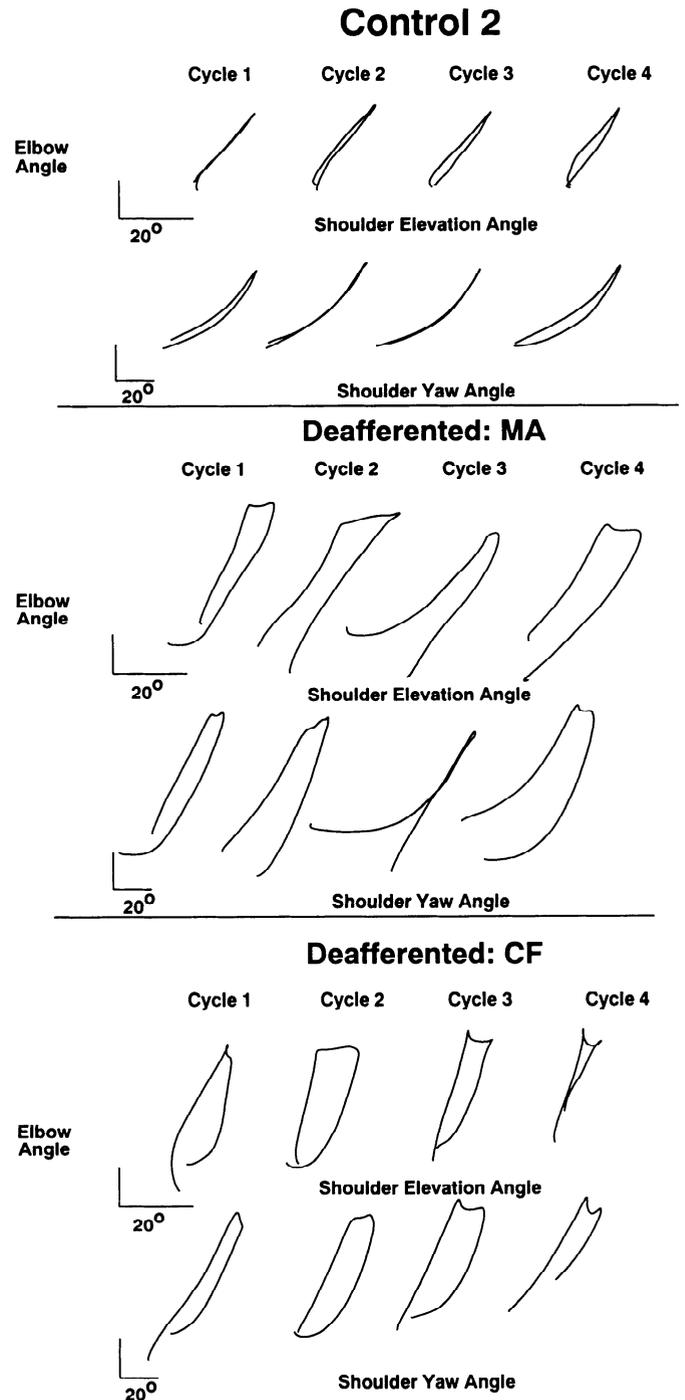


FIG. 7. Coupling of elbow and shoulder motions. The upper arm elevation angle was computed as the angle between the upper arm and the vertical axis. The horizontal angle, or yaw, was computed relative to the anterior/posterior axis. The elbow flexion/extension angle has been plotted against the upper arm elevation (*top*) and yaw (*bottom*) angles for individual cycles of a four cycle movement from control 2 (*top*), MA (*middle*), and CF (*bottom*).

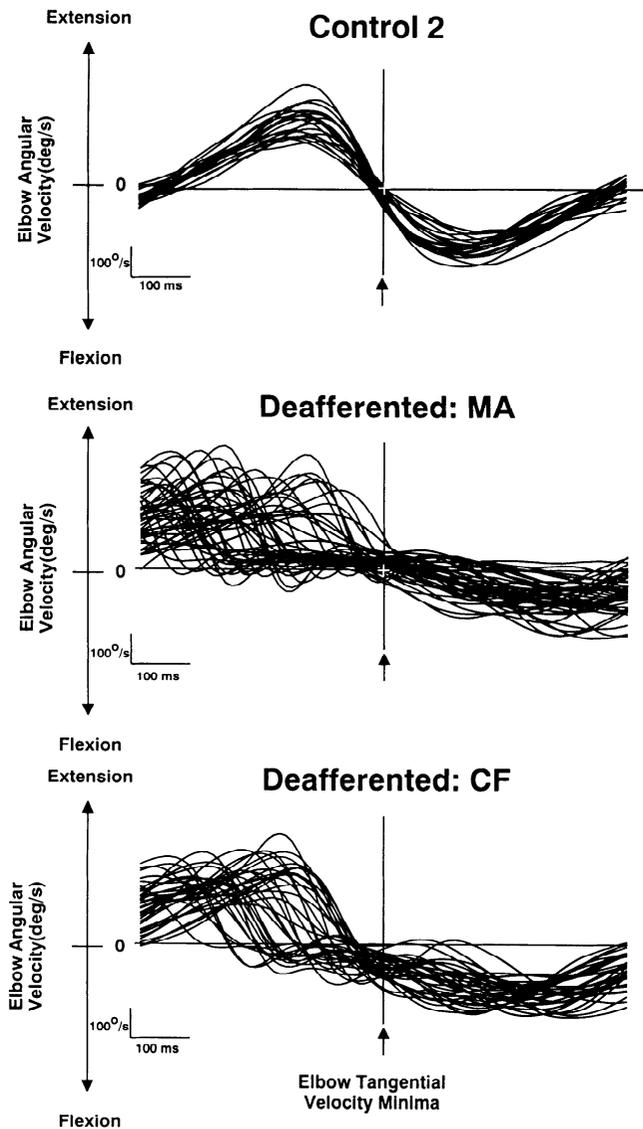


FIG. 8. Temporal coordination between shoulder and elbow joint movements. Elbow angular velocity profiles from successive cycles of motion are overlapped from 2 control subjects (*top*), from *MA* (*middle*), and from *CF* (*bottom*). Data have been synchronized to the elbow tangential velocity minimum within the reversal phase of movement. Four hundred milliseconds of data to each side of this event were selected. Thus, time zero (arrows) on the abscissa represents the reversal phase elbow tangential velocity minima. The zero value on the ordinate represents the elbow angular velocity zero crossing. Above the horizontal line represents elbow extension, and below this line represents elbow flexion. The cross hairs represent temporal synchrony between these two events.

reversals. This anomaly was associated with a decoupling in the timing of the normally synchronous reversals of angular motions at the shoulder and elbow joints. When the patients were allowed to view their limbs during movement, both the linearity and planarity of their movements improved. This indicates that vision can provide some of the information normally supplied by limb proprioceptors. Nevertheless, even when they could see their limbs, the reversals of joint motions remained severely decoupled and the hand paths remained significantly distorted. Thus, limb proprioceptors must provide critical information necessary for interjoint coordination.

Both visual and proprioceptive inputs are known to con-

vey information about the state and configuration of the limb needed to program movements (Flanders et al. 1992; Ghez et al. 1990; Polit and Bizzi 1979), and both can be used to correct errors introduced by externally applied perturbations (Rothwell et al. 1982; Sanes et al. 1985). However, the dynamic response properties of muscle proprioceptors may provide unique information about the temporal characteristics of evolving limb movements that is not available through vision. The present findings suggest that this input is critical for neural control systems to coordinate the timing of muscle actions at different joints, and is necessary to make spatially precise movements.

The hypothesis that proprioceptive input is needed for the precise timing of muscle contractions in different muscle groups agrees with the results of prior studies of single-joint movements in deafferented patients. Although movements and isometric force pulses may be, on average,

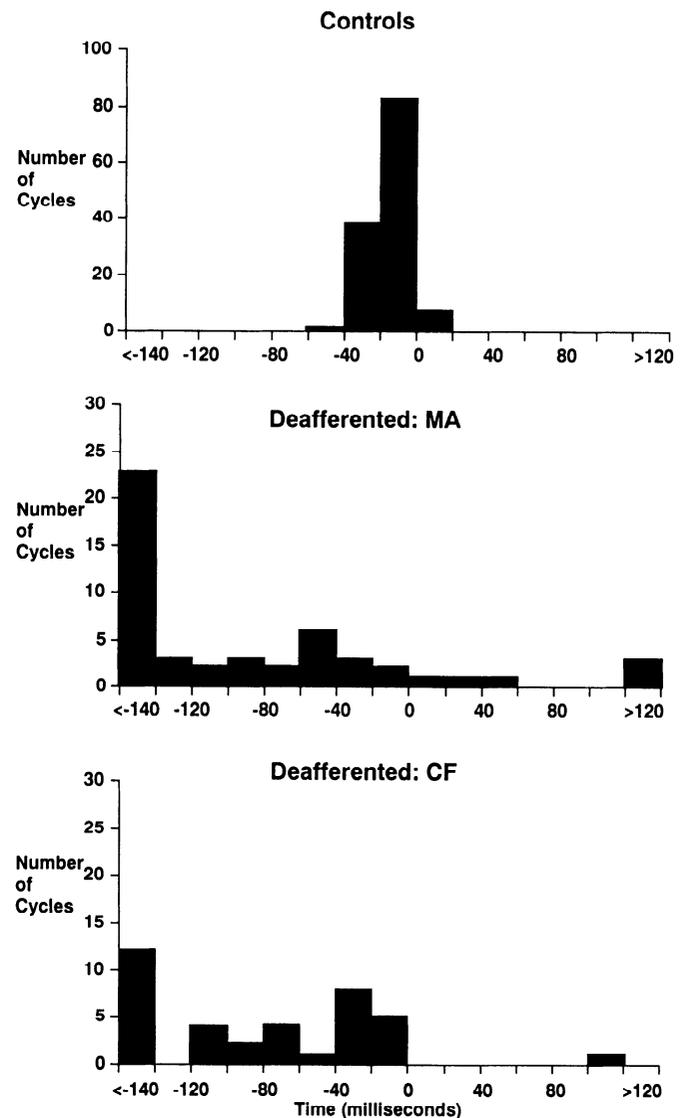


FIG. 9. Histograms of the time differences between the reversal phase elbow tangential velocity minimum and the elbow angular velocity zero crossing. Values of less than zero represent elbow angular velocity zero crossing prior to the tangential velocity minima. Data from all 150 cycles of movement from 11 control subjects (*top*), 50 cycles from *MA* (*middle*), and 33 cycles from *CF* (*bottom*) are shown.

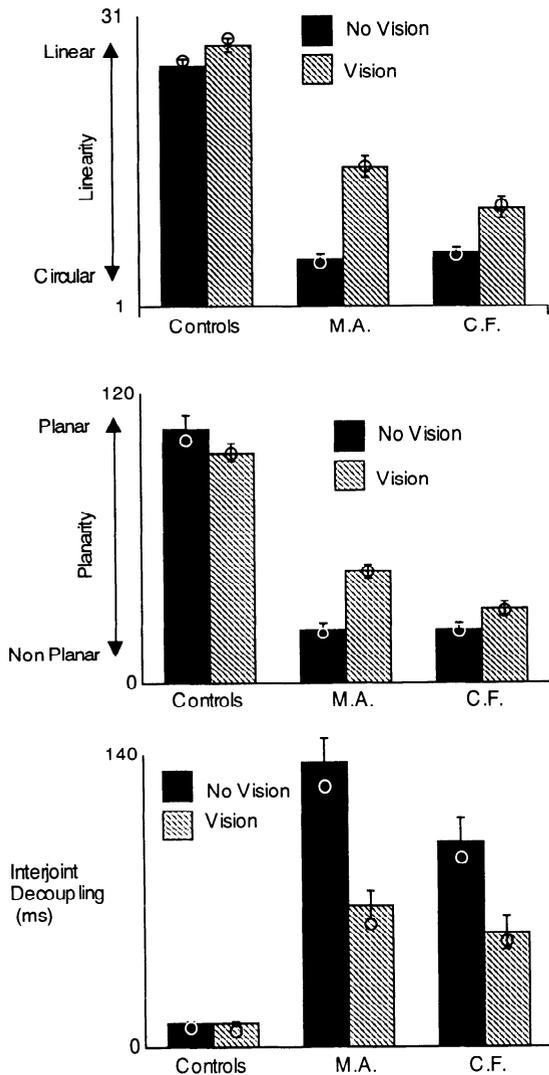


FIG. 10. Effects of vision on movement accuracy and interjoint coordination. The mean measures of wrist trajectory linearity (*top*) and planarity (*middle*) are shown for all cycles of movement sampled over 11 control subjects and for each deafferented subject: *MA* and *CF*. The mean interjoint decoupling time, measured as the absolute value of the time difference between the minimum in tangential elbow velocity and the zero crossing in elbow joint angular velocity within the reversal phase is also shown (*bottom*). Median values are depicted as open circles. Values are compared between no vision (■) and vision (▨) conditions for control subjects and each patient, separately. Error bars, SE.

correctly scaled, their trajectories and endpoints are highly variable (Forget and Lamarre 1987; Gordon et al. 1987; Kelso and Holt 1980; Rothwell et al. 1982; Sanes et al. 1985). These variable errors are associated with increased variability in the timing of agonist and antagonist muscle activation. In both intact subjects and deafferented patients, rapid movements are produced by the sequential activation of agonist and antagonist muscles manifest in EMG recordings as a triphasic pattern of activity. Whereas in normal subjects the antagonist burst is timed precisely to occur at the peak velocity (Forget and Lamarre 1987; Sanes et al. 1985) or the peak rate of change of force (Gordon et al. 1987), in patients this temporal precision is markedly degraded. Thus, in single-joint movements, increased variability in the onset of antagonist activation produces inaccur-

acy in movement extent by increasing the variability in the onset of movement or force deceleration.

In multijoint movements, however, in addition to any increase in variability there are remarkable trajectory and endpoint errors that vary systematically with the direction of movement. In a prior study, some of these errors were shown to reflect a failure to adapt motor commands to the more complex inertial characteristics of the multisegment limb (Ghez et al. 1990). In the present study, the anomalous elbow joint movement disruption at the reversal of outwardly but not of inwardly directed movements is another direction-dependent trajectory error that also appears to reflect biomechanical properties of the limb.

Qualitative assessment of the dynamic interactions likely to occur during the slicing gesture suggest that the elbow anomaly reflects a failure to control interaction forces that develop during the movement. As noted earlier, during unconstrained multijoint movements, motion of any limb segment produces forces that act on all other segments (Hasan 1991; Hasan and Stuart 1988; Hollerbach and Flash 1982; Hoy and Zernicke 1986; Schneider et al. 1989). The rotational counterparts of these forces with respect to the joints of the limb are generally referred to as interaction torques (Hasan 1991; Hollerbach and Flash 1982; Smith and Zernicke 1987). Hollerbach and Flash (1982) described these interactions for a two-segment, rigid-body system in some detail.

The unconstrained nature of the movements in the present study, although allowing for a kinematic analysis, precluded a quantitative analysis of joint dynamics. This was primarily because the movements of the deafferented subjects were highly variable with respect to movement direction, orientation relative to gravity, trajectory shape, and joint kinematics. However, a qualitative assessment of the expected limb dynamics during this task is useful in considering the possible dynamic interactions that may have contributed to the reversal phase errors in the patients. Such a discussion requires an idealization of the limb movements in our task.

Assuming, for simplicity, that the movements were limited to the shoulder and elbow joints and that they were confined to a plane, two main classes of interaction torques act at each joint. One is proportional to the squared angular velocity of the other joint. The other is proportional to the angular acceleration of the other joint. In addition, acting only at the shoulder, there is a component proportional to the product of the angular velocities of each joint, or Coriolis torque (Hollerbach and Flash 1982). At direction reversals, when the anomalous motion occurred, joint angular accelerations, and therefore acceleration-dependent interactions, are greatest. At such reversals, joint velocities approach zero and velocity-dependent interaction torques become negligible. Gravitational torques may have contributed to the variability of the patients' movements, because the magnitude and direction of this torque varies with the orientation of the limb segments to the line of gravity. This orientation, which the patients were unable to monitor under the no vision condition, was quite variable.

The direction of the interaction torque acting at the elbow during the reversal phase is consistent with the hypothesis that it was responsible for the anomalous elbow motion

in the deafferented patients. At the beginning of the reversal phase, the deceleration of shoulder flexion would be expected to produce a flexor torque at the elbow joint when the elbow angle is  $>90^\circ$ . Failure to take account of this torque (e.g., by reducing or delaying the activation of elbow flexor muscle activity or by activating extensors) should therefore result in premature flexion of the elbow relative to the extension of the shoulder joint. This is what was observed in the deafferented patients.

The hypothesis that the reversal phase disruption in elbow joint movement resulted from inadequately controlled interaction torques acting at the elbow joint is supported by two additional factors. First, the effect of uncompensated interaction torques should, in principle, be greater at the elbow than at the shoulder joint because the inertia (which dampens these effects) is greater at the shoulder (as it moves both arm and forearm) than at the elbow (moving just the forearm). Second, the fact that the disruption did not occur during reversals in which the hand was close to the body is also consistent with our hypothesis. This is because the magnitude of the acceleration-dependent interaction torque acting at the elbow varies with the cosine of the elbow angle.<sup>1</sup> This torque is largest in midcycle when the elbow joint is fully extended. It is smallest between cycles when the elbow joint approximates  $90^\circ$ . Thus, the perturbation produced by this torque should be greatest at midcycle reversals and smallest during the movement reversals between cycles.

In more recent experiments, we further tested the hypothesis that interjoint coordination deficits in deafferented patients result from a failure to control joint interaction torques (Sainburg et al. 1992, 1993). In those experiments, subjects were to move their hand straight out and back, as in the movements studied here. However, the arm was supported in the horizontal plane and movements were performed in different directions from a common starting position. The paths that subjects were to produce required variable amounts of shoulder excursion but similar elbow excursions. Control subjects produced straight paths with overlapping out and back segments. Regardless of the direction of movement, they were able to maintain elbow accelerations invariant and to synchronize the reversals at the shoulder and elbow joints. In contrast, the patients' movements showed reversal errors that were similar to those reported here, but that increased with the amount of shoulder excursion. The patients were unable to maintain invariant

elbow accelerations across movement directions, resulting in large interjoint coordination deficits in those movements with large shoulder excursions. Dynamic analysis of joint torques and EMG recordings of elbow muscles showed that control subjects adapted their patterns of muscle activation to variations in interaction torques, while the patients' muscle patterns remained relatively invariant across movement direction. The patients' elbow joint accelerations during movement reversals directly reflected the amplitude of the interaction torques produced by different shoulder motions. It is likely that the interjoint coordination deficits in the present study also reflect a failure of the patients to incorporate these mechanical interactions into movement commands.

Proprioceptive information, thus appears necessary to control limb interaction torques. However, the feedback delay in neural circuits combine with the latencies in excitation-contraction coupling make feedback mechanisms inefficient to prevent significant errors due to interaction torques (Hasan 1988, 1991; Karst and Hasan 1991a,b). The high loop gain required for such control would introduce instability into a system with such long feedback delays (Houk and Rymer 1981). This is because the delivery of a corrective response would occur when the response was no longer appropriate to the mechanical condition of the limb. The correction would introduce further error into the system, which would stimulate new, but similarly ineffective responses. However, feedforward control mechanisms, which predict errors based upon the responses of an internal model to output commands, could bypass problems of feedback delay. In addition to providing temporal information during the course of movements, proprioceptive input may allow calibration and updating of an internal model of the limb. Such a model could then be used to modify output commands during evolving limb movements.

In support of this hypothesis, Ghez et al. (1990) demonstrated that deafferented patients were able to use feedforward mechanisms based on visual information to improve the accuracy of their limb movements. The trajectory errors that these patients made during multijoint reaching movements were improved when they were able to view their limbs during movement. The same improvement occurred when vision of their limbs was occluded on subsequent trials, even though target directions were randomized. Thus, prior visual information about the configuration and/or properties of the limb allowed patients to program subsequent movements more accurately. Ghez et al. (1991) thus hypothesized that proprioceptive information operates during limb movements to update an internal model of the limb that is used to plan and execute limb movements.

The results of the present study provide new insights into the role of proprioceptive information in the temporal control of muscle actions during multijoint limb movements. Although previous work has focused on the roles of proprioceptive inputs in regulating muscle actions at individual joints, the present study suggests that information arising from the movements of other joints is equally or more important. Indeed, loss of proprioception disrupts the ability to make spatially precise three-dimensional, multijoint arm movements and a loss in the ability to coordinate movements about multiple joints. Further experiments will have

<sup>1</sup> Joint torque equation for the elbow joint in a two-segment model is given by  $R_2 - (I_2 + m_2 r_2^2) \ddot{\theta}_2 - \dot{\theta}_1 (I_2 + m_2 r_2^2 + m_2 L_1 r_2 \cos \theta_2) - \dot{\theta}_1^2 (m_2 L_1 r_2 \sin \theta_2) = 0$ , where subscript 1 and 2 refer to the upper arm and forearm segments, respectively;

I is limb segment inertia;  
 m is limb segment mass;  
 r is distance from proximal joint to limb segment center of mass;  
 L is limb segment length;  
 $\theta_1$  is shoulder angle;  
 $\theta_2$  is elbow angle (the  $180^\circ$  complement of the anatomic elbow joint angle); and  
 R is residual torque, defined as that component of the joint torque that is not attributable to interaction forces. Hollerbach and Flash (1992) refer to this term as "net joint torque," while Schneider et al. (1989) refer to a corresponding term as "generalized muscle moment."

to be done to clarify the roles of proprioceptors in controlling limb interaction torques and to determine whether proprioceptive input assures interjoint coordination through feedforward, as well as feedback mechanisms.

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