

# 35 Contributions of Vision and Proprioception to Accuracy in Limb Movements

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**ABSTRACT** We have studied movement errors in normal human subjects and in patients deafferented by large-fiber sensory neuropathy. In normals, movement extent and direction were subject to different sources of variable and systematic errors, suggesting that these parameters are programmed independent. Moreover, vision of the hand and the target were necessary to program direction accurately. These data suggest that the planning of reaching movements takes place in an extrinsic, hand-centered coordinate system.

In deafferented patients, simple movements aimed to visual targets showed large errors in direction and extent because of failure to compensate for directional variations in limb inertia. In movements with direction reversals, distinctive errors appeared because of failure to program elbow muscle contractions in accord with interaction torques produced at the elbow by variations in acceleration of the upper arm. Both inertial and reversal errors were substantially reduced when patients had recently had the opportunity to monitor movements of their arm visually. We conclude that the programming of accurate trajectories requires a frequently updated internal model of the state and properties of the limb by proprioceptive input. It is proposed that such internal models are critical for the transformation from extrinsic to intrinsic coordinates used to plan the joint angle changes and torques needed to execute the movement.

It is generally understood that the accuracy of limb movements depends largely on precisely calibrated feedforward commands that direct the hand to the target (Georgopoulos, 1986). Although vision and proprioception are both essential if movements are to be

accurate, the nature of the information provided by these two modalities is not fully understood. For example, it normally is taken for granted that vision simply provides information about the location of the target. Whether vision is needed also to determine the initial position of the hand is not known. Some investigators hypothesize that the relationship of the target to the limb is critical (Burnod et al., 1992; Flanders, Helms Tillery, and Soechting, 1992). For these authors, movement trajectories are driven by a motor error representing the difference between the intended final limb configuration and its initial configuration, determined proprioceptively. Whether the extent and direction of movement can, in fact, be programmed accurately by the comparison of visual information obtained from a target and information about arm configuration obtained proprioceptively has not been examined in any detail.

Significant insights into the role of proprioception in trajectory formation have been obtained by studying the motor deficits of patients with large-fiber sensory neuropathy (Rothwell et al., 1982; Sanes et al., 1985; Forget and Lamarre, 1987; Forget and Lamarre, 1990; Ghez et al., 1990). In these patients, the selective degeneration of large-diameter afferent fibers may abolish completely all sense of joint position as well as stretch reflexes. Studies of such patients have documented the importance of proprioceptive input for the regulation of steady-state force and for detecting and correcting trajectory errors due to mechanical perturbations (Rothwell et al., 1982; Sanes et al., 1985). Evidence from such studies suggests that loss of proprioception does not alter or impair the strategies that subjects use to make single-joint movements: Like intact controls, deafferented patients produce move-

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ments or forces of different magnitudes by scaling a stereotyped pattern of contraction in agonist and antagonist muscles (Rothwell et al., 1982; Sanes et al., 1985; Forget and Lamarre, 1987). Nevertheless, it is generally agreed that proprioceptive information is essential for the correct calibration of motor commands (Paillard and Brouchon, 1974) and that motor learning might be impaired in deafferentation (Rothwell et al., 1982). However, the aspects of trajectory control that require such learning remain undefined.

The studies described in this chapter examine how visual and proprioceptive information about the limb contributes to accuracy of planar hand movements. We first address the question of whether extent and direction are explicitly planned features of reaching movements. We approach this question by analyzing the sources of variability of movement endpoints and by defining how vision of the limb alters systematic trajectory errors in movements made without visual feedback. We then examine the trajectory deficits exhibited by deafferented patients to determine how proprioceptive information contributes to accuracy. Patients are found to demonstrate extent and direction errors that vary with movement direction, as do normals, but in exaggerated form. Finally, we consider the role of proprioceptive input in more complex movements requiring precise coordination of elbow and shoulder joint motions. Our findings indicate that proprioceptive input plays a critical role in motor planning by updating an internal model of biomechanical characteristics of the limb.

### *Methods*

Subjects were 11 neurologically intact individuals between the ages of 28 and 42 years and 3 patients with large-fiber sensory neuropathy. All three patients (MA, age 42; GL, age 54; and CF, age 60) had virtually complete loss of position, vibration, and discriminative touch sensation in both upper extremities, including elbow and shoulder, and tendon reflexes were absent. On the other hand, pain, temperature, and coarse touch sensations were preserved. Somatosensory evoked potentials from upper as well as lower extremities were absent. Sensory nerve conductions were slowed, a finding consistent with a loss of large-diameter afferent fibers. Muscle strength and electromyography were, however, normal. Although the degree of sensory loss in the upper extremities was

roughly similar for the three patients, lower-extremity involvement was most severe in patients GL and CF, who were wheelchair-bound. Patient MA, on the other hand, could walk, albeit with a wide base.

The results reported here were obtained using two tasks in which subjects faced a vertical computer screen and moved a hand-held cursor on a horizontal digitizing tablet. In general, the tablet was at shoulder level and the subject's arm was supported in the horizontal plane by a sling suspended from the ceiling. This was done to counter the effects of gravity and to simplify biomechanical analyses. For selected experiments, however, the tablet was at waist level. The first task was a simple reaching task in which the computer screen was used to display the position of the cursor on the tablet along with two circles, indicating a starting and a target location. At the beginning of a trial, subjects were to position the cursor in the start circle. Then, after an unpredictable time, a go tone was presented, and subjects were to move the cursor to the target with a single, uncorrected movement. Knowledge of results (KR) generally was provided by displaying the hand path on the screen after the movement although, in some experiments, the errors made with and without KR were compared. Targets in different directions and at different distances from the starting position were presented in a pseudorandom order. To prevent the correction of errors detected visually and to identify errors related to the planning of movement, the screen cursor was blanked after presentation of the tone. Each subject's hand and arm were hidden from view by a drape and a two-way mirror. The influence of information about the location and properties of the limb was analyzed in certain experiments by allowing each subject to see his or her limb at rest or during movements. Data consisted of hand positions sampled by the computer at 200 Hz.

In the second task, subjects viewed the computer screen that now displayed one of six possible straight-line segments, in pseudorandom order, along with the cursor. They were instructed first to position the cursor at one end of the line. On presentation of an auditory cue, they were to move the cursor straight to the end of the line and return to the origin in a single uninterrupted movement. The cursor was again blanked during the movement to prevent visual corrections. The instructions stressed that the outward and return motion should overlap and that movement reversals should be sharp and without discernible pause between

the outward and inward segments. Movements were to be carried out at a comfortable speed.

During these reversal movements, the arm and forearm were supported in the horizontal plane by a low-inertia brace equipped with ball-bearing joints under the shoulder and elbow joints. Joints distal to the elbow were immobilized with a thermoplastic splint attached to the brace, and the scapula was immobilized with straps to restrict movement to the shoulder and elbow. Precision, single-turn, linear potentiometers (Beckman Instruments) were used to monitor the elbow and shoulder joint angles. The tip of a magnetic pen, controlling the screen cursor, was attached to the end of the hand splint, 1 cm above the digitizing tablet. Surface electromyographic (EMG) activity from biceps, brachioradialis, and triceps was recorded with active electrodes (Liberty Mutual, Inc.). EMG and potentiometer signals were sampled at 1000 Hz and were acquired by a Macintosh computer equipped with external A/D converters (MP-100 Biopacq).

## Results

We begin our analysis by presenting results obtained in normal subjects. We then analyze the changes in trajectory formation in deafferented patients.

**INDEPENDENTLY PLANNED EXTENT AND DIRECTION**  
Despite the absence of visual feedback, movements made by intact subjects were reasonably accurate, their endpoints clustering around the appropriate targets. As in studies of planar hand movements performed with vision, hand paths were nearly straight and trajectory profiles were bell-shaped (figure 35.1A). In general, endpoint distributions had elliptical shapes whose major axes were oriented in the directions of the movements; however, the eccentricity of these ellipses decreased with distance (figure 35.1B). Thus, while extent variability was fairly large for small movements, relative extent variability decreased progressively with distance. In contrast, directional variability was essentially constant and unaffected by distance. The fact that extent and directional variability were differently influenced by target distance suggests that these two features of the response were specified by distinct mechanisms.

The straight hand paths and the scaling of peak accelerations implies that both the directions and extents of the movements were largely specified by the

time of movement initiation. There were, however, systematic differences in the scaling of velocities (figure 35.1C) and accelerations for movements in different directions. To explore this directional dependency, we presented subjects with targets in 24 directions at a constant distance from a common starting position. As illustrated for one subject in figure 35.2B, peak accelerations varied markedly with movement direction, and acceleration vectors formed an ellipsoidal shape. Accelerations in the 60° and 240° directions were more than twice as large as for movements in the 150° and 330° directions.

Why should accelerations vary with the direction of the movement? In our convention and with the hand's initial position in the midline, the 150° direction corresponded approximately to the axis of the forearm, whereas the 60° direction was perpendicular to it. Because the inertial load at the hand is greatest in the direction of the forearm and lowest at right angles to it, we hypothesized that the systematic differences in acceleration resulted from directional variations in inertia. To test this idea, we used the standard equations of motion of a two-link manipulator and morphometric data from each subject to compute the directional variations in inertia at the hand (Hogan, 1985). As has been demonstrated by Hogan (1985), inertia at the hand varies with direction, forming an elliptical contour whose major axis is oriented in the direction of the forearm (see figure 35.2B). This means that if a constant force were to be applied at the hand, the resulting initial accelerations would show a corresponding directional variation but rotated 90°. The resulting contour is referred to as a *mobility ellipse*. It can be seen in figure 35.2B that the directional variations in acceleration closely match the changes in initial acceleration due to the inertial anisotropy (compare solid lines fitted to points and dotted lines representing the computed mobility ellipse). Although movements in the directions of lowest inertia are slightly hypermetric, movement extents showed much less directional variation than the accelerations. This is because differences in hand acceleration were largely compensated by directional variations in movement time. It should be noted that these variations in movement time were substantial and ranged, across subjects, from 150 to 300 ms for average movement times of approximately 400 ms.

These findings indicate that subjects do not program the magnitude of the force they use to accelerate the hand at the onset of movement to take into account

# Control JG

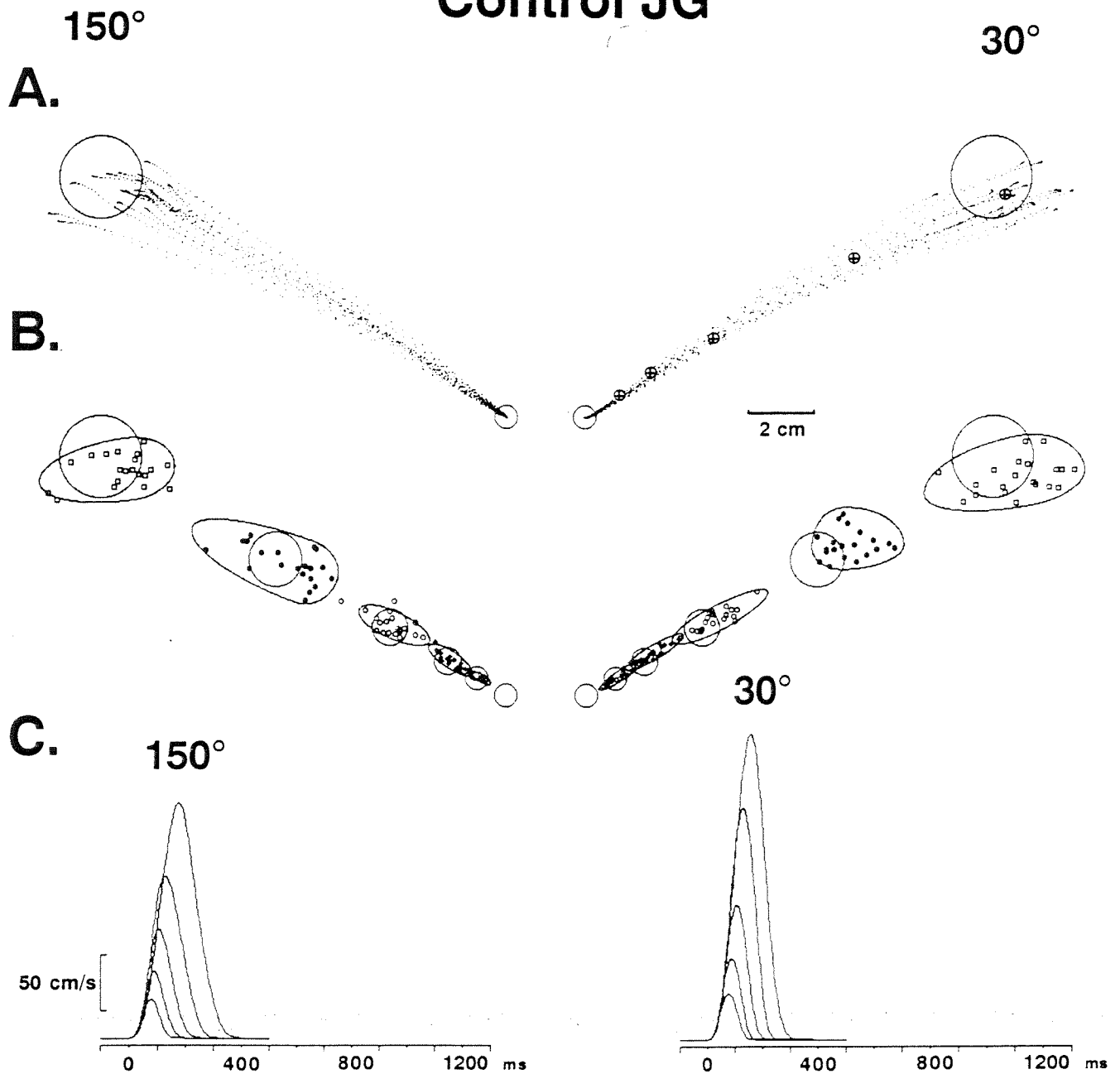


FIGURE 35.1 Hand paths are nearly straight, and tangential velocities of movements scale with target distance. Control subject made 20 movements to targets at five distances in two directions presented in pseudorandom order. Tablet was at waist level. (A) Hand paths to the most distant targets (19.6 cm) in the two directions (150° and 30°) plotted at 20-ms intervals. Note that the centers of the endpoint distributions of movements to nearer targets (small circles with

crosshair) lie along the slightly curved paths to the most distant target at 30°. (B) Endpoint distributions. Each distribution is surrounded by a contour whose orientation was computed by the method of principal components and whose size and shape is based on the interquartile range in each of the major axes. Small circles show target locations. (C) Tangential velocities of movements.

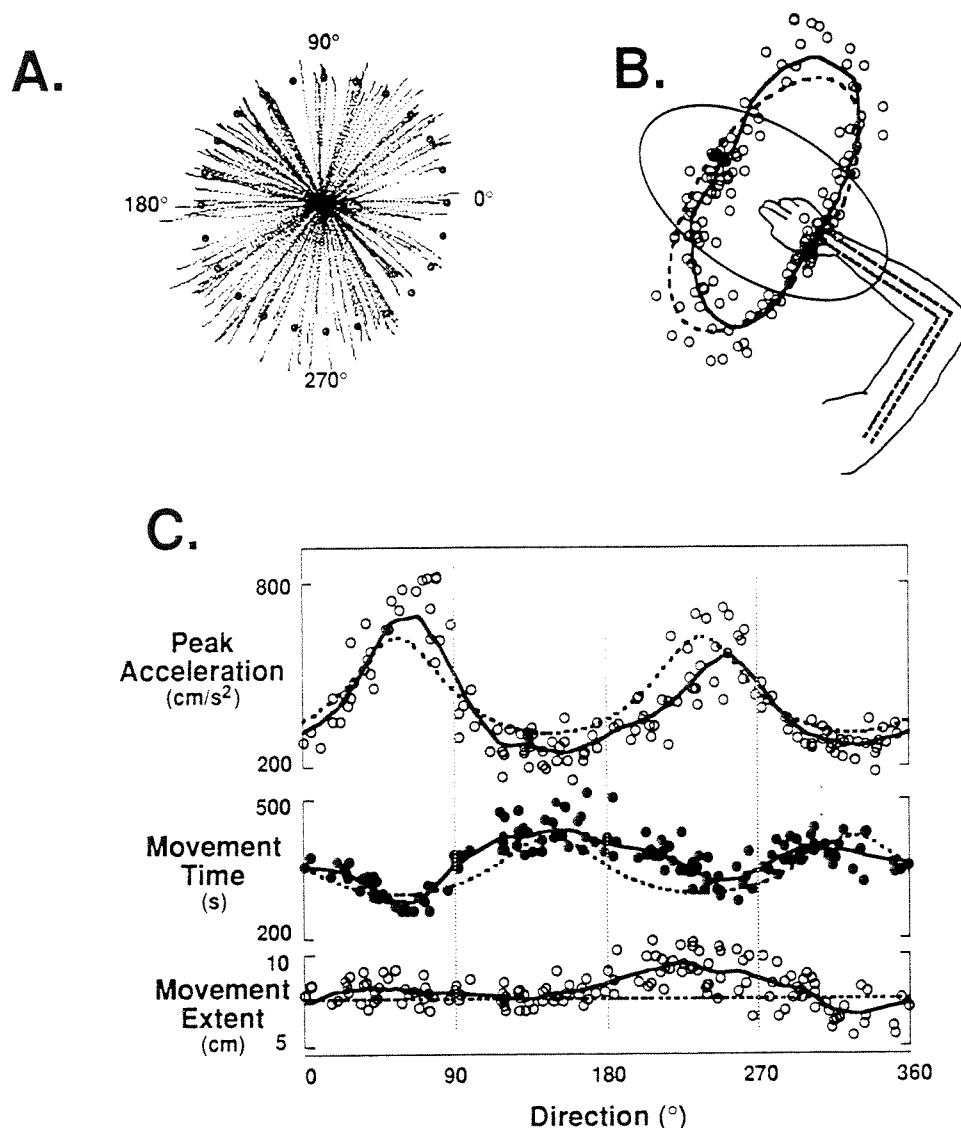


FIGURE 35.2 Subjects compensate for variations in inertial resistance by modulating movement time. (A) Hand paths of movements (six per target) aimed to targets in 24 directions at 7.5 cm from a central starting position (plotted at 5-ms intervals). (B) Solid ellipse represents inertial resistance of the tip of the hand to force applied in different directions. Dashed ellipse represents mobility of the hand. The small circles show the directions and magnitudes of peak accelerations for movements in (A) in a polar format, with the origin at the index finger of the hand. The solid curve is a

LOWESS fit to these points (Cleveland, 1979). (C) Scatter plots and fitted solid lines show peak acceleration, movement time, and movement extent as a function of direction for the movements in (A). Dashed line on peak acceleration is predicted peak acceleration for a constant force applied to the hand in all directions. Dashed line on movement time represents predicted movement time under the assumption that trajectories have invariantly shaped velocity profiles. Dashed line on movement extent indicates target distance.

directional differences in limb inertia.<sup>1</sup> Instead, they adapt movements to these differences by adjustments in movement time. Although it is not inconceivable that neural mechanisms could vary movement time to compensate for expected variations in load, it does not seem likely that such control could be as precise as

observed here. It is more plausible that the variation in movement time for different directions occurs because, as suggested by several groups (Bizzi et al., 1984; Feldman et al., 1990), the nervous system does not specify directly the precise kinematic features of the movement. Rather it specifies a virtual trajectory whose im-

plementation lags behind the actual trajectory by a delay that reflects the biomechanical properties of the physical plant. This lag would be expected to be greater for directions in which resistive forces are greater. Whether the resulting compensation for differences in inertia occurs purely because of the biomechanical characteristics of the muscles and joints

(Bizzi et al., 1984) or because of feedback mechanisms—as envisaged, for example, in the lambda model of Feldman and coworkers (1990)—remains to be determined.

PLANNED MOVEMENT IN A HAND-CENTERED COORDINATE SYSTEM Although directional errors were gen-

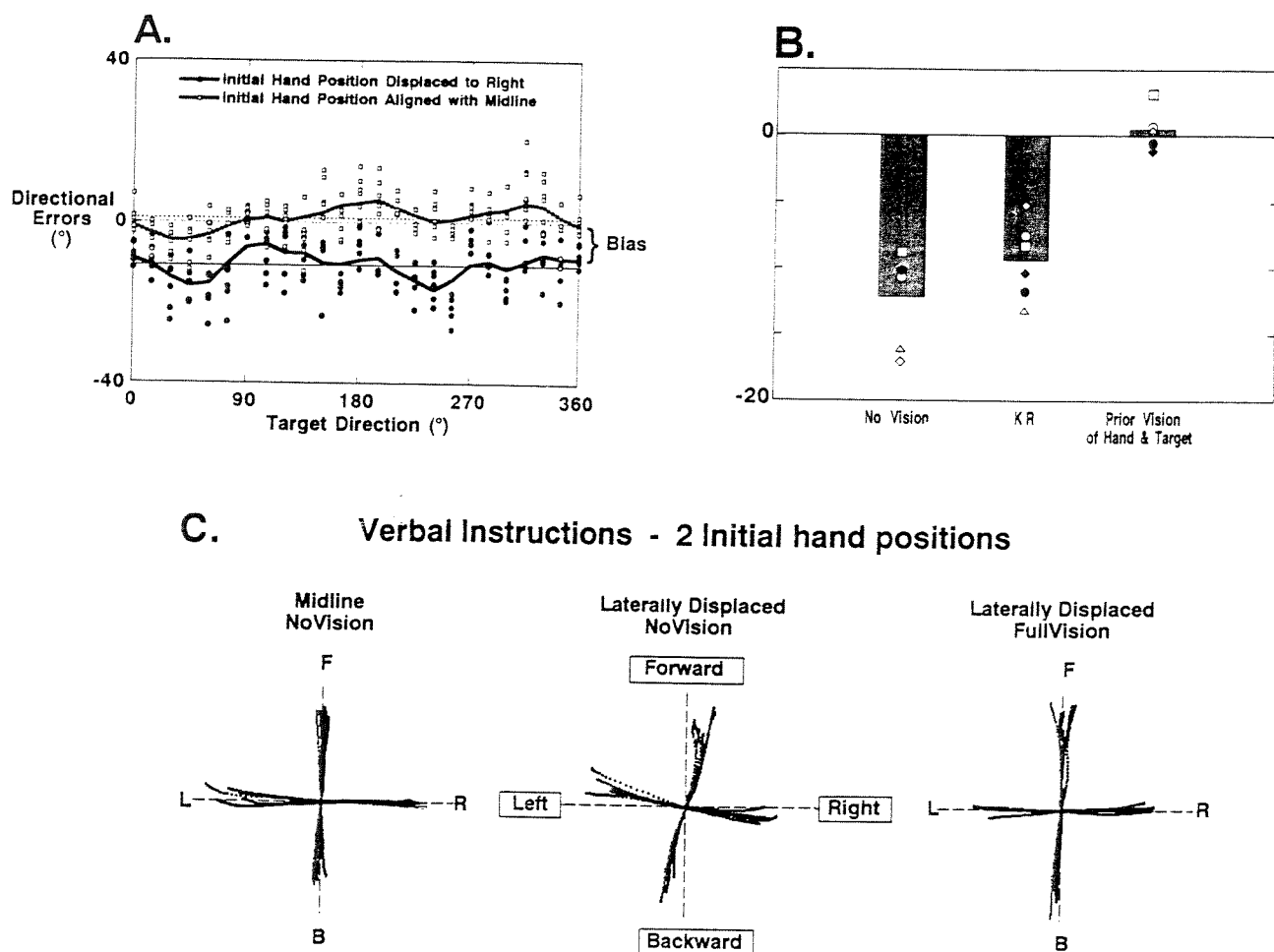


FIGURE 35.3 Deviations of the initial position of the hand from the midline produce directional biases that can be corrected only by vision of the hand relative to the target. A) Directional errors for movements to 24 radially arranged targets with starting positions of the hand in the midline (open circles) and displaced 44 cm to the right (filled circles). Clockwise errors are negative; counterclockwise errors are positive. Fitted lines are computed, as previously, by LOWESS. In both initial positions, the elbow angle was approximately  $90^\circ$ . With the hand in the midline, the forearm segment angle was approximately  $140^\circ$  and, with the hand in the lateral position, the forearm segment angle was nearly  $90^\circ$  relative to the mediolateral axis. B) Mean direc-

tional errors for movements from the displaced initial position under three conditions: No vision, without vision of the hand or knowledge of the results (KR); KR, without vision of the hand but with KR; and prior vision, in which subjects were allowed to see their hand and target before movement but there was no KR. Bars are mean directional errors of six subjects whose individual means are shown by different symbols. C) Hand paths for movements in four directions and two initial positions when subject was given the verbal instruction to move the hand in the directions indicated. No-Vision indicates subject was allowed no vision of the hand throughout block; in FullVision, subject was allowed to see the hand during movement.

erally small, even when movements were performed without visual feedback, this was true only when the initial position of the hand was near the subject's midline. Figure 35.3A shows the relationships of directional errors to target direction for two initial hand positions. For both positions, there are small systematic variations in directional errors for different target directions.<sup>2</sup> In addition, however, lateral displacement of the initial hand position (in this case, by extending the initial shoulder angle and maintaining the same elbow angle) produced a directional bias that shifted the directions of all responses clockwise by an average of 11°.

Comparisons of movements from a wide variety of initial positions showed that the magnitude of this directional bias varied systematically with the mediolateral distance of the hand from a plane through the body midline. It was, however, relatively unaffected by variations in anteroposterior location of the initial position of the hand. Similarly, directional bias was identical for movements of varying extents.

These directional biases were remarkably robust, present in all subjects, and surprisingly resistant to learning. Thus, they were only minimally reduced in movements made with KR (i.e., display of hand path after each movement) in comparison to movements without KR (figure 35.3B). In contrast, the bias always disappeared when subjects were allowed to visualize the location of their hand relative to targets placed directly in the workspace (see figure 35.3B).

The directional biases did not, however, depend on the presence of a visual display. Indeed, the same clockwise bias was evident when subjects were verbally instructed to move the hand directly forward, directly backward, to the left, or to the right from different initial positions (figure 35.3C). As in the experiments with targets presented on a computer monitor, this bias disappeared when each subject was allowed to view his or her hand during the movement. These directional biases therefore represent transformational errors related, perhaps, to distortions in the subjects' representation of the location of their hand in peripersonal space. Whatever the precise geometry of subjects' representation of peripersonal space, the finding of directional biases that are independent of movement extent lends further support to the hypothesis that extent and direction are planned independently. The fact that these errors are corrected by viewing the hand in relation to the target indicates that this information can-

not be derived correctly from proprioceptive input alone.

#### ROLES OF PROPRIOCEPTIVE INFORMATION IN THE PLANNING AND EXECUTION OF MULTIJOINT MOVEMENTS

*Prevention of inertial errors by vision of the limb's response to a prior motor command* The directional biases just described emphasize that proprioception does not provide sufficient information about limb configuration for neural controllers to compute hand direction accurately. What, then, is the function of proprioceptive information in programing movements? If it plays a role in "calibrating" motor commands or updating an internal representation of the limb, what aspects of the limb are represented? To answer these questions, we studied movements performed by three patients deprived of proprioceptive sensation because of large-fiber sensory neuropathy but with intact motor function (see under Methods). We examined the effects of visual feedback by comparing movements with and without vision of the screen cursor. If proprioceptive sensation functioned solely by correcting movements through negative feedback, performance would be expected to improve only when movements were performed when the cursor was displayed on the screen. Vision of the limb by itself would be expected to have little, if any, effect because targets were not displayed in relation to the limb and thus error information, needed for feedback, was not readily available. However, if vision served to improve programing (e.g., by updating a subject's internal model of his or her arm), vision of the arm should improve performance, and this improvement should persist for some time when vision was no longer available.

In contrast to the straight and accurate movements made by controls, movements of deafferented patients were highly curved, and endpoint errors were greatly increased (compare figure 35.4A, B with figure 35.1A and B). Nevertheless, the normal scaling strategy for producing movements of different extents was preserved (figure 35.4C). The hand paths of movements in different directions showed a striking dependence of both extent and direction errors on the direction of the movement (figure 35.5A, no vision; compare to control paths in figure 35.2A). The variations in movement extent corresponded closely to directional variations in

## Patient MA

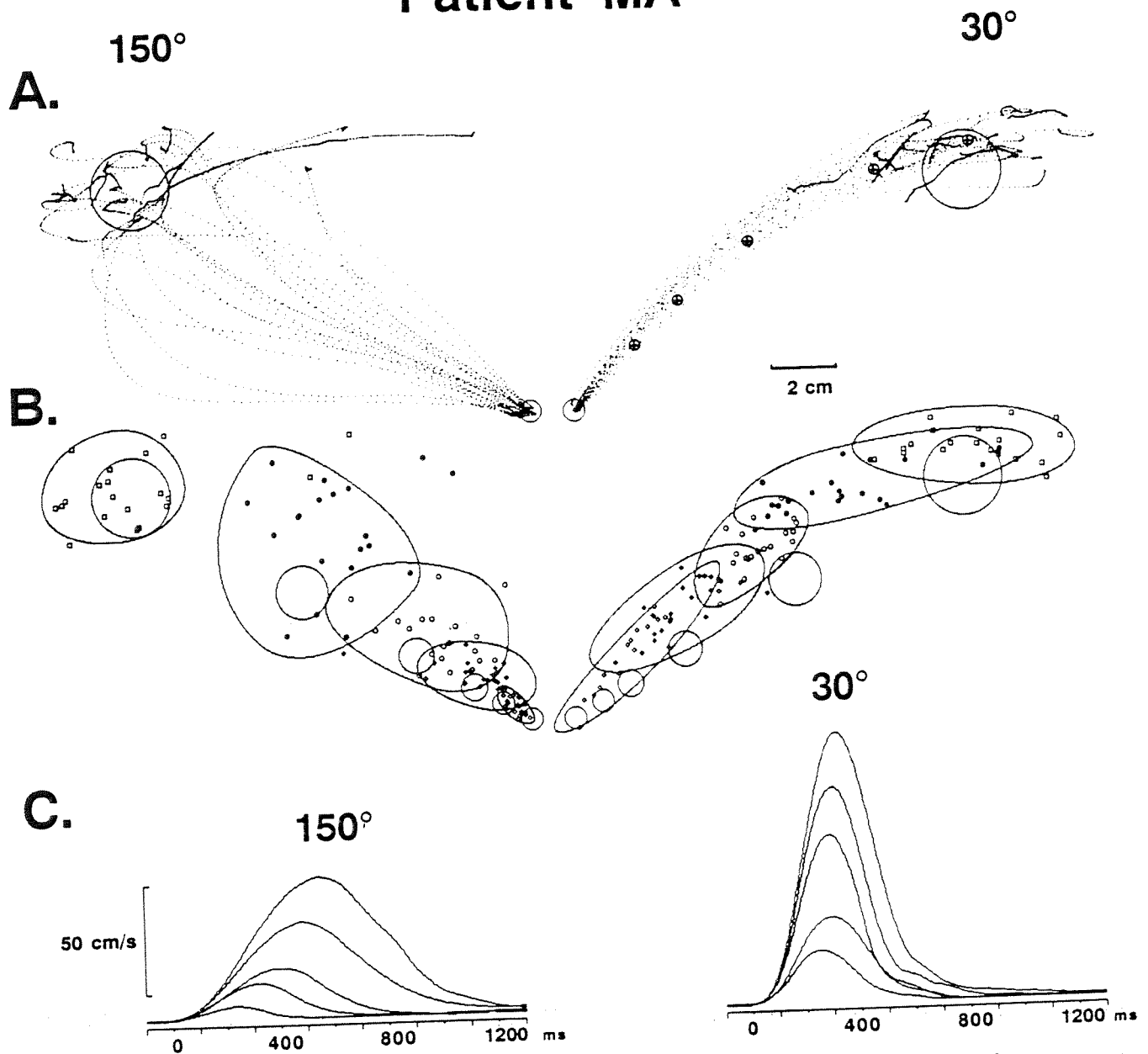


FIGURE 35.4 (A) Hand paths, (B) endpoint distributions, and (C) tangential velocities of movements to targets in two directions in patient MA (as per figure 35.1). Note the consistent curvature of movements to 30°, which were performed principally by external rotation of the shoulder, and

the fact that the endpoint distributions of movements to nearer targets, shown by small circles with a crosshair, all lie along the paths to the most distant target. See text for further comments.

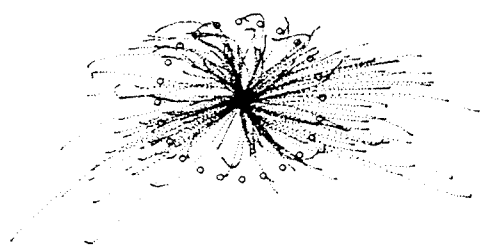
inertia. Thus, whereas in controls variations in movement extent show little or no dependence on inertial variations in peak acceleration (figure 35.5B, left), in the patients the two parameters were highly correlated (figure 35.5B, right, no-vision condition). Correspond-

ingly, variations in movement time were negatively correlated with inertial variations in acceleration in controls (figure 35.5C, left) but not in the patients (figure 35.5C, right, no-vision condition). Thus, a significant cause of the patients' errors in movements per-



## A. Successive Trials

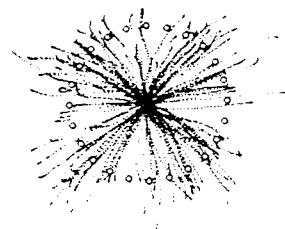
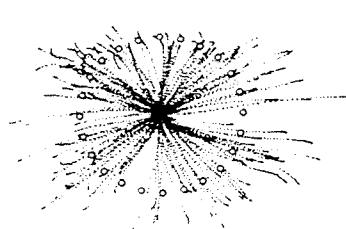
### No Vision of hand



## Alternate Trials

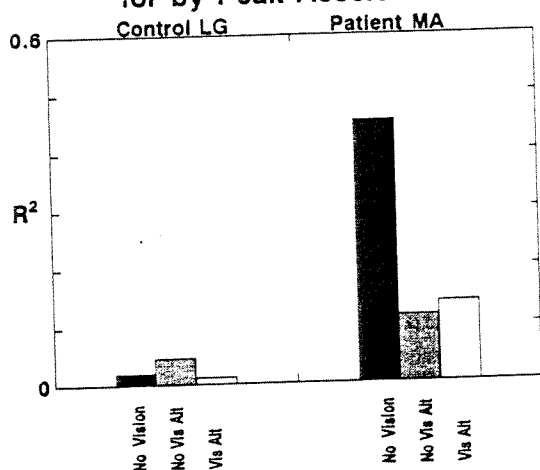
No Vision of hand

Vision of hand



4 cm

## B. Extent Variance Accounted for by Peak Acceleration



## C. Movement Time Variance Accounted for by Peak Acceleration

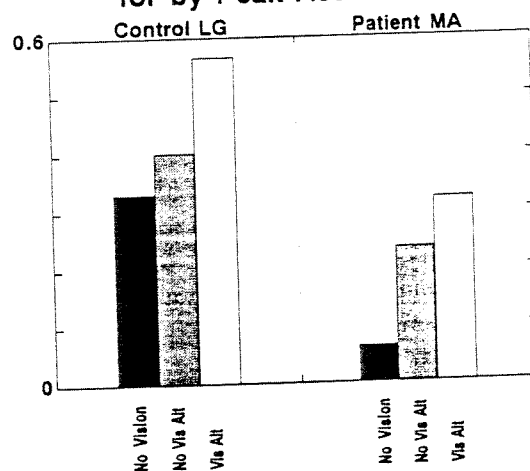


FIGURE 35.5 Vision of the hand prior to or during movement reduces inertial errors. (A) Hand paths for movements made in 24 directions by patient MA under three conditions. The left plot shows hand paths when the subject could not see her hand at all. The middle and right plots show movement during a session in which trials were presented alternately with no vision of the hand and with vision of the hand. Paths plotted every 20 ms. (B) Squared correlation coefficient ( $r^2$ ) between peak acceleration and movement extent for movements made by a control subject (LG) and deafferented subject (MA) in the three conditions described in (A). (C) Squared correlation coefficient ( $r^2$ ) between peak acceleration and movement time for movements made by a control subject (LG) and deafferented subject (MA) in the three conditions described in (A).

in these alternating blocks, with movements performed in blocks of trials in which all movements were made without vision. Hand paths of responses made by patient MA with and without vision of the limb in the alternating block are plotted separately in figure 35.5A (center and right), and errors are analyzed separately in parts B–D. The paths are straighter and less hypermetric in low-inertia directions in both alternate vision blocks compared with the block performed without vision (see figure 35.5A, left). In both sets of alternate

formed without vision was the failure to compensate for variations in limb inertia by modifying movement time according to movement direction.

Whereas vision of the limb produced little change in the errors made by controls, it produced a remarkable improvement in the patients, and this effect outlasted the presence of vision information. This was ascertained by allowing patients to see their limb on alternate trials with randomized directions. We then compared movements performed with and without vision

vision responses, movement extent becomes substantially less dependent on acceleration (see figure 35.5B), whereas movement time develops a significant dependence on initial acceleration, as in the control (see figure 35.5C). Thus, vision of the limb either during or before movement improves accuracy by allowing patients to adapt their motor commands to inertial and other mechanical properties of the limb.

Errors were also decreased when patients simply viewed their limb between trials during a period of immobility. However, in all patients, this improvement was less than when they were allowed to see their limb in motion during a preceding response. Viewing the limb in motion provides information about the limb's dynamic response to a preceding neural command, information that cannot be obtained simply from a static view of the limb. It is likely that this information allows subjects to recalibrate dynamic internal models of their limb and that these models are critical for the programming process (Atkeson, 1989; Jordan and Rumelhart, 1990; Morasso and Sanguineti, 1992). Interestingly, however, the improvement provided by vision was short-lived and lasted only 5 to 10 trials (approximately 1 minute). This suggests that in control subjects, the huge amounts of information provided by proprioception are critical to recalibrating continuously the internal limb representations.

*Proprioceptive information is needed to control interaction torques* The prominent and variable curvature of their hand movements (see figures 35.4, 35.5) suggests that

patients also had difficulty coordinating elbow and shoulder motions. This was confirmed by comparing the time of directional changes in joint motion in three-dimensional movements performed by patients and controls (Sainburg, Poizner, and Ghez, in press).

Incoordination of elbow and shoulder movements was particularly striking when patients attempted to reverse the direction of their hand movements. Because direction reversals are associated with high angular accelerations that, in turn, produce large interaction torques, we suspected that failure to synchronize joint motions might reflect a failure to control this aspect of limb biomechanics (Hollerbach and Flash, 1982; Schneider et al., 1989).

To characterize the effects of interaction torques on the coordination of elbow and shoulder, we used a task that allowed these torques to be varied systematically (Sainburg et al., 1992). Each subject was to move his or her hand along a straight target line and, at the end of the line, to reverse direction and return to the point of origin. Directions were selected so that the shoulder angular excursion would increase progressively over six target directions (figure 35.6). The lengths of the target paths were adjusted to maintain the elbow angular excursion nearly constant; the arm was supported in the horizontal plane to eliminate the effects of gravity.

Whereas controls always reversed direction sharply, patients could do so only for directions in which shoulder excursions were minimal. The sharp reversals in controls corresponded to nearly synchronous direction reversals of the shoulder and elbow joints. In patients, as shoulder excursions increased, hand paths devel-

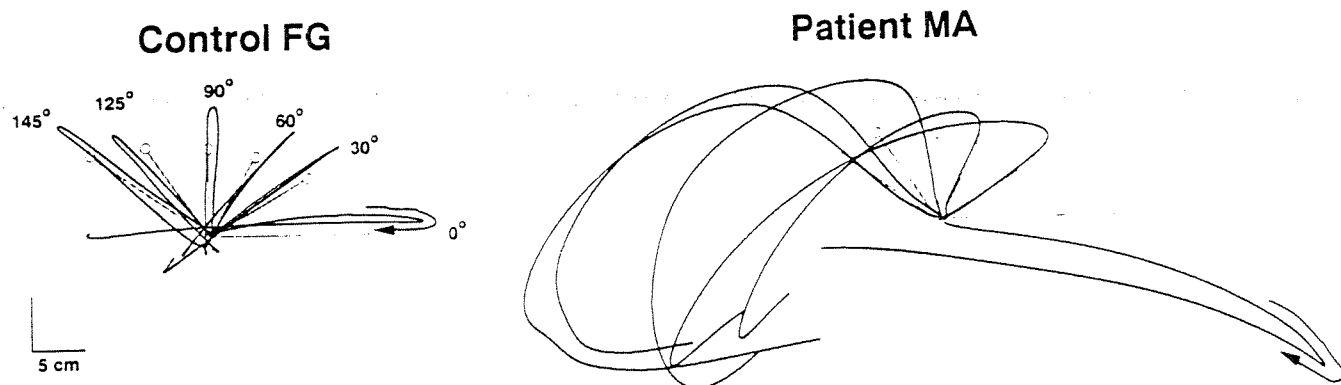


FIGURE 35.6 Deafferented patients are unable to reverse direction abruptly. Sample hand paths of movements performed by control subject (left) and patient (right) are

drawn over the corresponding target lines (gray). Circles at the end of each line are shown for clarity and did not exist in the actual visual presentation to the subjects.

oped a marked medial deviation because the elbow reversed direction prematurely.

To determine whether the premature elbow flexion could have resulted from a failure to counter an inter-

action torque produced by shoulder deceleration, we next computed the torques acting on the elbow (Winter, 1990). Using a modification of the method introduced by Hoy, Zernicke, and Smith (1985), we sub-

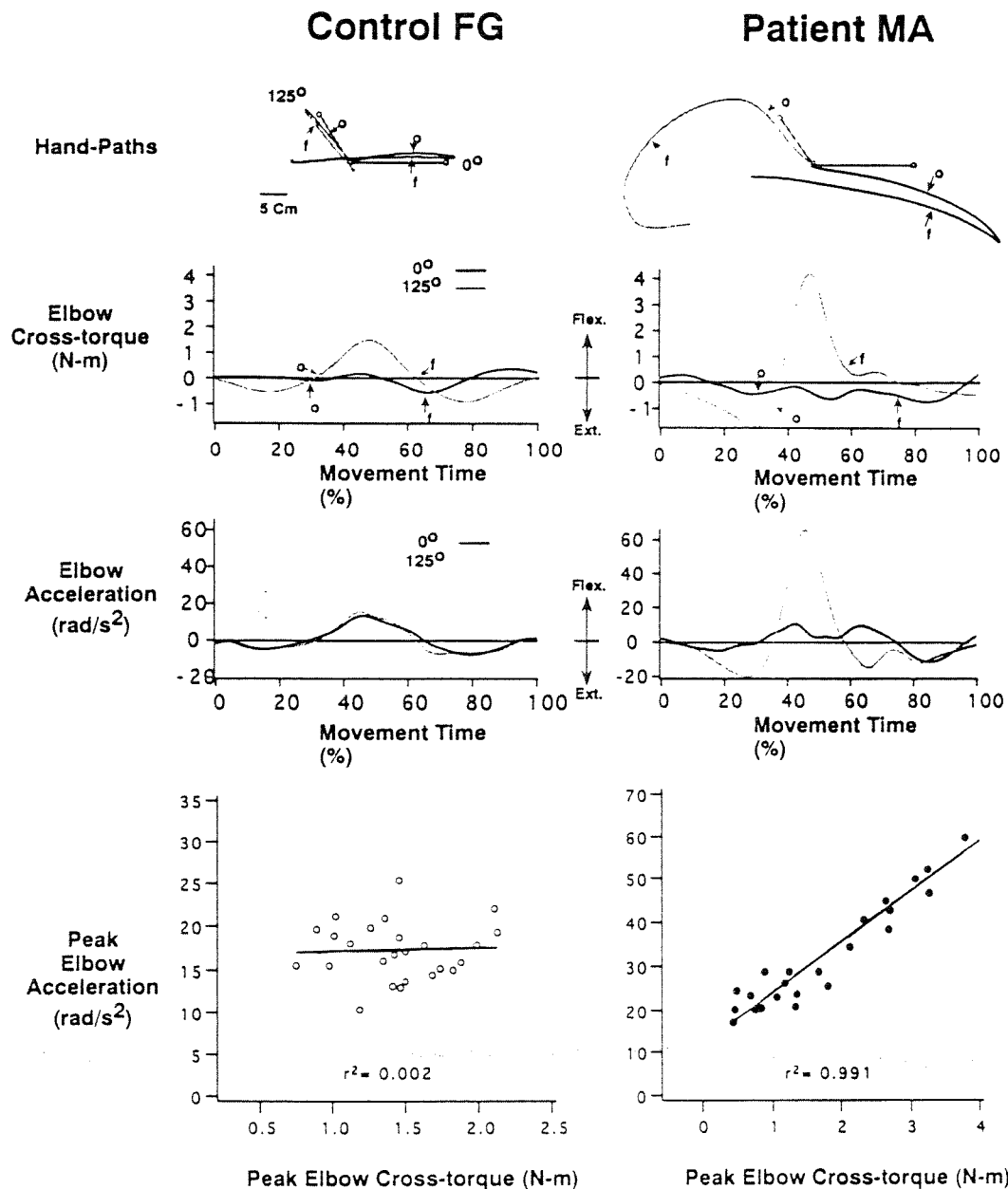


FIGURE 35.7 Reversal errors are produced by cross-torques acting at the elbow. (Top) As in figure 35.6, the hand paths (solid lines) are drawn over the targets (gray lines) for movements in the 0° and 125° directions performed by a control subject (left) and a patient (right). Elbow joint cross-torque profiles are shown for the movements illustrated at top. Elbow joint angular acceleration profiles also are shown. Initiation (o) and final (f) points of the flexor acceleration phase

of elbow joint motion are marked by arrows in all graphs in plots of cross-torques and elbow accelerations. At bottom, peak elbow flexor acceleration is plotted against peak flexor cross-torque for all movements performed by control subject (left) and by patient (right). Note the absence of correlation in the movements performed by control subject ( $r^2 = .002$ ), whereas correlation is high in the movements performed by patient ( $r^2 = .911$ ).

divided the torques acting at the elbow into three components, which we termed *self-torque*, *cross-torque*, and *residual torque* (Cooper, Martin, and Ghez, in press).<sup>3</sup> The self-torque at the elbow represents the torque required to overcome the inertial resistance of the forearm and, as such, varies with elbow angular acceleration alone. The cross-torque is the interaction torque produced at the elbow by motions at other joints. The residual torque represents the inverse of the summed cross- and self-torques; thus, it includes the effects of active muscle contraction as well as the elasticity and viscosity of muscles and connective tissue elements (Hoy, Zernicke, and Smith, 1985).

This partitioning of joint torques showed that for hand directions with significant shoulder excursions, the cross-torque acting on the elbow during movement reversals was indeed in the flexor direction. It was small or negligible for movements at 0° and 30° but increased progressively for movements at 60°–145° for both controls and patients. In controls, elbow angular accelerations remained independent of cross-torque across directions, whereas in the patients, elbow accelerations were closely correlated with cross-torques (figure 35.7).

Controls were able to control elbow acceleration in spite of varying cross-torques by varying the timing and degree of activation of elbow flexors and extensors. Thus, when cross-torque was low, as in the 0° movements, biceps and brachialis EMG recordings became active prior to the onset of flexor acceleration, while the triceps that had been extending the forearm became silent. In contrast, at 125° and 145°, biceps and brachialis were silent. Flexor acceleration was initiated by the cross-torque from the shoulder, which was then modulated by triceps activation. In contrast, patients were unable to modulate substantially the timing of elbow muscle activation across directions. Instead EMG recordings of elbow muscles showed that they attempted to regulate movement trajectory by increasing joint stiffness through cocontraction of flexors and extensors. This was not a successful strategy, however, perhaps because the loss of stretch reflexes may substantially alter the functional stiffness of muscles (Sanes and Shadmehr, in press).

These results confirm and extend the observations of Smith and Zernicke and their colleagues and demonstrate a critical role of proprioceptive input in compensating for interaction torques (Smith and Zernicke, 1987; Koshland and Smith, 1989a,b). Interestingly, as

was the case for inertial errors, vision of the limb enabled the patients to improve interjoint coordination significantly. Pilot data in two patients indicates that when they could see their limb in motion, the patients were better able to synchronize elbow and shoulder reversals. Similarly, the timing and patterns of biceps and triceps activation were better adapted to the direction of movement. The compensation provided by vision of the limb was, however, far from complete, and interaction torques still produced significant distortions in the hand paths. This suggests that vision cannot fully compensate for the loss of proprioception in ensuring interjoint coordination.

Several factors may account for this. First, it is possible that muscle proprioceptors contribute to interjoint coordination in part through feedback mechanisms operating directly through spinal connections (Smith and Zernicke, 1987; Koshland and Smith, 1989a,b; Nichols, 1989; Soechting and Lacquaniti, 1989; Lacquaniti, Borghese, and Carrozzo, 1991). Indeed, while classical physiological studies have emphasized their monosynaptic connections, recent experiments suggest that both Ia and Ib receptors have extensive connections with interneurons acting on a variety of motoneuron groups (Baldissera, Hultborn, and Illert, 1981). Second, somatosensory receptors may provide more high-frequency information concerning limb dynamics than is available through vision. Third, the amount of information that can be processed in parallel by somatosensory channels may be much greater than through vision (Gordon and Ghez, 1992). It remains for future experiments to decide among these alternatives.

### Conclusions

The finding that extent and direction variability have different determinants supports the idea that extent and direction represent explicitly planned dimensions of reaching movements (Rosenbaum, 1980; Bonnet, Requin, and Stelmach, 1982; Bock et al., 1990; Gordon et al., in press; Gordon, Ghilardi, and Ghez, in press B). This is equivalent to stating that reaching movements are specified vectorially as suggested by the results of unit-recording studies in motor cortex (Georgopoulos, 1986). Because different factors independently influence errors in extent and direction, our data suggest that these two features of the hand path are programed by channels operating relatively independently. This principle, which we found to govern

the specification (or programming) of single-joint movements (Favilla, Hening, and Ghez, 1989; Ghez, Hening, and Favilla, 1990), therefore appears to extend to multijoint movements as well (see also Favilla et al., 1990).

Our finding that the initial planning of extent and direction does not take into account limb geometry and inertia implies that essential aspects of trajectory planning take place in an extrinsic coordinate system. The nature of the systematic directional errors made by normal subjects further suggests that this system is centered at the initial position of the hand. Whether a shoulder-centered system, suggested by the work of Soechting and coworkers (see Flanders et al., 1992, for discussion), represents a task-specific alternative or whether it represents a later stage in processing is not clear at present. It should be noted that this representation of target location in extrinsic space eventually will have to be transformed into its equivalent in intrinsic coordinates, where muscles or joint torques are represented explicitly.

We envisage that processes related to the extent channel adaptively set a temporal profile of descending activation (Ghez, 1979; Ghez et al., 1983; see also Gottlieb et al., 1992) according to the type of load (viscous, elastic, etc.) that the subject expects. The extent channel appears to use visual information about target distance to scale the activation profile according to a calibration rule. The direction channel would specify the relative changes in joint angle at the elbow and shoulder corresponding to movements in a particular direction (Mel, 1991). Movements planned in this way would not be perfectly straight. Moreover, one would expect to find similar errors related to incorrect specification of relative joint angle changes for movements at different distances. Such consistent curves should result in movement endpoints to nearer targets distributed along the curvature of the paths to the most distant target. Such corresponding patterns occurred frequently in deafferented patients (e.g., figure 35.4, 30° movements) but were noted also in normal subjects (e.g., figure 35.1, 30° movements) (see also Gordon, Ghilardi, and Ghez, in press).

Our findings indicate that, although trajectories are adjusted to reach targets at different distances by a simple scaling rule, significant aspects of movement kinematics are emergent properties of the system and are not controlled explicitly. Thus, our results provide support for the view that descending mechanisms spec-

ify a virtual trajectory that is distinct and leads the actual trajectory of the limb (Kelso and Holt, 1980; Bizzi et al., 1984; Flash, 1987; Feldman et al., 1990). Thus, the detailed shape of the acceleration profile and movement duration appears to arise from the interplay of descending control signals, segmental mechanisms, and muscle properties with inertial and other biomechanical characteristics of the limb. However, the existence of inertial extent errors is difficult to explain if one assumes a simple equilibrium control system. A clue may lie in the large lags that appear to exist between virtual and actual trajectories (which must be at least as great as the difference in movement time between movements in low- and high-inertia directions). This suggests that central mechanisms need to provide a terminal control signal cocontracting agonist and antagonist muscles to ensure that the final position be achieved without oscillations. Such a clamping system at the end of movement has been proposed by others in the context of single-joint movements (Ghez, 1979; Ghez et al., 1983; Feldman, 1986; Feldman et al., 1990; Gottlieb, 1992). Errors in setting the parameters or the timing of this terminal clamping command may be responsible for the inertial errors in normals and in patients.

The occurrence of direction-dependent biases that are corrected by vision of the hand and target demonstrates the importance of knowledge of the initial position of the hand in the planning of movement direction. Our findings further suggest that proprioceptive information does not provide the static cues necessary to specify correctly a direction of movement that will reach an arbitrary target in space. The fact that directional biases (and the corresponding underestimate of the distance of the hand from the midline) are similar in intact and deafferented subjects strongly suggests that this aspect of initial state information arises from other sources, especially vision of the hand in relation to the target.

The remarkable trajectory errors made by patients with large-fiber sensory neuropathy indicate that proprioceptive information is critical if accuracy is to be achieved. The function of such information, however, is not limited to the correction of errors through feedback; in addition, it operates by generating and recalibrating internal models of the mechanical properties of the limbs (Atkeson, 1989; Jordan and Rumelhart, 1990; Ghez, Hening, and Gordon, 1991; Morasso and Sanguineti, 1992). These internal models appear to be

essential for the transformation of direction and extent information into an intrinsic coordinate system of muscles or joint torques. Vision of the limb in motion allowed the patients to reduce substantially inertial errors in movement extent as well as the curvature and directional errors that we presume are due to uncontrolled interaction torques. It seems plausible that these dynamic properties of the limb are computed from the information about the limb's response to centrally monitored voluntary commands.

Our results suggest that representations of the dynamic properties of the limb are especially crucial for achieving accurate control over interaction torques that develop during multijoint movements. The dramatic breakdown of this control during movement reversals in deafferented patients attests to this. Because of delays inherent in transmission and in excitation-contraction coupling, it is difficult to imagine that the normal control of such interaction forces could be accomplished through feedback mechanisms alone. Instead, failure of feedforward control mechanisms that depend on a proprioceptively updated internal model of the limb are more likely to account for the reversal errors seen in patients. Hence, it appears that the motor systems predict interaction torques and control their effects so as to achieve the kinematic results required by the behavioral task. In such a system, internal models would provide the means for predicting the unfolding scenario of goal-directed movements. These internal models may also be critical for interpreting corollary discharge information and errors that arise in the course of such movements.

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## NOTES

1. It should be noted that the similarity between the distribution of acceleration vectors and the mobility ellipse indicates only that the major source of variability in peak acceleration is the variation in limb inertia. This suggests that the forces at the hand were actually constant or independent of direction. However, in a different task situation, direct measurements of forces at the onset of movements in different directions (Shadmehr, Mussa-Ivaldi, and Bizzi, in press) indicated that force at the hand showed directional variations that were *not* matched to limb inertia but appeared to be explained by the stiffness fields of the arm. Similarly, the patterns of activation of elbow and shoulder muscles initiating targeted movements

in different directions from different initial positions cannot be accounted for simply by assuming that subjects direct either the force or the acceleration precisely in the direction of the target (Karst and Hasan, 1991a). It is difficult to compare our data with either of those studies because the tasks were somewhat different and neither errors nor response trajectories were reported in the published material.

2. The occurrence of systematic directional errors that varied with movement direction resulted in a distribution of movement directions with four distinct peaks. Although similar from subjects to subject, neither the errors nor the peaks in the distributions can be completely explained on the basis of inertial anisotropy. One hypothesis that appears attractive and that we currently are testing is that these systematic directional errors reflect errors in the selection of elbow and shoulder muscle activation patterns. Indeed, recent work by Karst and Hasan (1991a,b) indicates that for horizontal plane movements such as the ones studied here, movements are initiated with one of four stereotypical patterns. Like the peaks in direction distributions for our subjects, those patterns depend on the forearm segment angle.
3. The inertial moment ( $I_f$ ), center of mass ( $r_f$ ), and mass ( $m_f$ ) of the forearm segment were computed from regression equations that include body weight and segment length (Winter, 1990).

Torque Component	Formula
Residual torque	$(I_f + m_f r_f^2 + m_f r_{ie} r_f \cos \theta_e) \ddot{\theta}_i$ $+ (I_f + m_f r_f^2) \ddot{\theta}_e + m_f r_{ie} r_f \sin \theta_e \dot{\theta}_i^2$
Self-torque	$-(I_f + m_f r_f^2) \ddot{\theta}_e$
Cross-torque	$-(I_f + m_f r_f^2 + m_f r_{ie} r_f \cos \theta_e) \ddot{\theta}_i$ $-(m_f r_{ie} r_f \sin \theta_e) \dot{\theta}_i^2$
	where $\theta_e$ = elbow angle $\theta_i$ = shoulder angle $r_{ie}$ = upper arm length

## REFERENCES

- ATKESON, C. G., 1989. Learning arm kinematics and dynamics. *Annu. Rev. Neurosci.* 12:157-183.
- BALDISSERA, F., H. HULTBORN, and M. ILLERT, 1981. Integration in spinal neuronal systems. In *Handbook of Physiology: Sec. 1. The Nervous System: Vol. 2. Motor Control* part 1. V. B. Brooks, ed. Bethesda, Md.: American Physiological Society, pp. 509-595.
- BIZZI, E., N. ACCORNERO, W. CHAPPLE, and N. HOGAN, 1984. Posture control and trajectory formation during arm movement. *J. Neurosci.* 4:2738-2744.
- BOCK, O., M. DOSE, D. OTT, and R. ECKMILLER, 1990. Control of arm movements in a 2-dimensional pointing task. *Behav. Brain Res.* 40:247-250.
- BONNET, M., J. REQUIN, and G. E. STELMACH, 1982. Specification of direction and extent in motor programming. *Bull. Psychon. Soc.* 19:31-34.

- BURNOD, Y., P. GRANDGUILLAUME, I. OTTO, S. FERRAINA, P. B. JOHNSON, and R. CAMINITI, 1992. Visuomotor transformations underlying arm movements toward visual targets: A neural network model of cerebral cortical operations. *J. Neurosci.* 12:1435-1453.
- CLEVELAND, W. S., 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74:829-836.
- COOPER, S. E., J. H. MARTIN, and C. GHEZ, 1993. Differential effects of localized inactivation of deep cerebellar nuclei on reaching in the cat. *Soc. Neurosci. Abstr.* 19:1278.
- FAVILLA, M., J. GORDON, M. F. GHILARDI, and C. GHEZ, 1990. Discrete and continuous processes in the programming of extent and direction in multijoint arm movements. *Soc. Neurosci. Abstr.* 16:1089.
- FAVILLA, M., W. HENING, and C. GHEZ, 1989. Trajectory control in targeted force impulses: VI. Independent specification of response amplitude and direction. *Exp. Brain Res.* 75:280-294.
- FELDMAN, A. G., 1986. Once more on the equilibrium-point hypothesis ( $\lambda$  model) for motor control. *J. Mot. Behav.* 18:17-54.
- FELDMAN, A. G., S. V. ADAMOVICH, D. J. OSTRY, and J. R. FLANAGAN, 1990. The origin of electromyograms—explanations based on the equilibrium point hypothesis. In *Multiple Muscle Systems: Biomechanics and Movement Organization*, J. M. Winters and S. L.-Y. Woo, eds. New York: Springer-Verlag, pp. 195-213.
- FLANDERS, M., S. I. HELMS TILLERY, and J. F. SOECHTING, 1992. Early stages in a sensorimotor transformation. *Behav. Brain Sci.* 15:309-362.
- FLASH, T., 1987. The control of hand equilibrium trajectories in multi-joint arm movements. *Biol. Cybern.* 57:257-274.
- FORGET, R., and Y. LAMARRE, 1987. Rapid elbow flexion in the absence of proprioceptive and cutaneous feedback. *Hum. Neurobiol.* 6:27-37.
- FORGET, R., and Y. LAMARRE, 1990. Anticipatory postural adjustment in the absence of normal peripheral feedback. *Brain Res.* 508:176-179.
- GEORGOPOULOS, A. P., 1986. On reaching. *Annu. Rev. Neurosci.* 9:147-170.
- GHEZ, C., 1979. Contributions of central programs to rapid limb movements in the cat. In *Integration in the Nervous System*, H. Asanuma and V. J. Wilson, eds. Tokyo: Igaku-Shoin, pp. 305-320.
- GHEZ, C., J. GORDON, M. F. GHILARDI, C. N. CHRISTAKOS, and S. E. COOPER, 1990. Roles of proprioceptive input in the programming of arm trajectories. *Cold Spring Harb. Symp. Quant. Biol.* 55:837-847.
- GHEZ, C., W. HENING, and M. FAVILLA, 1990. Parallel interacting channels in the initiation and specification of motor response features. In *Attention and Performance: XIII. Motor Representation and Control*, M. Jeannerod, ed. Hillsdale, N.J.: Erlbaum, pp. 265-293.
- GHEZ, C., W. HENING, and J. GORDON, 1991. Organization of voluntary movement. *Curr. Opin. Neurobiol.* 1:664-671.
- GHEZ, C., D. VICARIO, J. H. MARTIN, and H. YUMIYA, 1983. Sensory motor processing of targeted movements in motor cortex. In *Motor Control Mechanisms in Health and Disease*, J. E. Desmedt, ed. New York: Raven, pp. 61-92.
- GORDON, J., and C. GHEZ, 1992. Roles of proprioceptive input in control of reaching movements. In *Children with Movement Disorders, Medicine and Sport Science: 36*. H. Forssberg and H. Hirschfeld, eds. Basel: Karger, pp. 124-129.
- GORDON, J., M. F. GHILARDI, S. E. COOPER, and C. GHEZ (in press). Accuracy of planar reaching movements: II. Systematic extent errors resulting from inertial anisotropy. *Exp. Brain Res.*
- GORDON, J., M. F. GHILARDI, and C. GHEZ (in press). Accuracy of planar reaching movements: I. Independence of direction and extent variability. *Exp. Brain Res.*
- GOTTLIEB, G. L., 1992. Kinematics is only a (good) start. *Behav. Brain Sci.* 15:749.
- GOTTLIEB, G. L., M. L. LATASH, D. M. CORCOS, T. J. LIUBINSKAS, and G. C. AGARWAL, 1992. Organizing principles for single joint movements: V. Agonist-antagonist interactions. *J. Neurophysiol.* 67:1417-1427.
- HOGAN, N., 1985. The mechanics of multi-joint posture and movement control. *Biol. Cybern.* 52:315-331.
- HOGAN, N., 1988. Planning and execution of multijoint movements. *Can. J. Physiol. Pharmacol.* 66:508-517.
- HOLLERBACH, J. M., and T. FLASH, 1982. Dynamic interactions between limb segments during planar arm movement. *Biol. Cybern.* 44:67-77.
- HOY, M. G., R. F. ZERNICKE, and J. L. SMITH, 1985. Contrasting roles of inertial and muscle moments at knee and ankle during paw-shake response. *J. Neurophysiol.* 54:1282-1294.
- JORDAN, M. I., and D. E. RUMELHART, 1990. *Forward Models: Supervised Learning with a Distal Teacher (Occasional Paper No. 40)*. Cambridge, Mass.: Center for Cognitive Science.
- KARST, G. M., and Z. HASAN, 1991a. Initiation rules for planar, two-joint arm movements: Agonist selection for movements throughout the work space. *J. Neurophysiol.* 66:1579-1593.
- KARST, G. M., and Z. HASAN, 1991b. Timing and magnitude of electromyographic activity for two-joint arm movements in different directions. *J. Neurophysiol.* 66:1594-1604.
- KELSO, J. A. S., and K. G. HOLT, 1980. Exploring a vibratory system analysis of human movement production. *J. Neurophysiol.* 43:1183-1196.
- KOSHLAND, G. F., and J. L. SMITH, 1989a. Mutable and immutable features of paw-shake responses after hindlimb deafferentation in the cat. *J. Neurophysiol.* 62:162-173.
- KOSHLAND, G. F., and J. L. SMITH, 1989b. Paw-shake response with joint immobilization: EMG changes with atypical feedback. *Exp. Brain Res.* 77:361-373.
- LACQUANITI, F., N. A. BORGHESE, and M. CARROZZO, 1991. Transient reversal of the stretch reflex in human arm muscles. *J. Neurophysiol.* 66:3:939-954.
- MEL, B. W., 1991. A connectionist model may shed light on neural mechanisms for visually guided reaching. *J. Cogn. Neurosci.* 3(3):231.

- MORASSO, P., 1981. Spatial control of arm movements. *Exp. Brain Res.* 42:223-227.
- MORASSO, P., and V. SANGUINETI, 1992. Equilibrium point and self-organization. *Behav. Brain Sci.* 15:781-782.
- NICHOLS, T. R., 1989. The organization of heterogenic reflexes among muscles crossing the ankle joint in the decerebrate cat. *J. Physiol. (Lond.)* 410:463-477.
- PAILLARD, J., and M. BROUCHON, 1974. A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. *Brain Res.* 71:273-284.
- ROSENBAUM, D. A., 1980. Human movement initiation: Specification of arm, direction, and extent. *J. Exp. Psychol. [Gen.]* 109:444-474.
- ROTHWELL, J. L., M. M. TRAUB, B. L. DAY, J. A. OBESO, P. K. THOMAS, and C. D. MARSDEN, 1982. Manual motor performance in a deafferented man. *Brain* 105:515-542.
- SAINBURG, R. L., M. F. GHILARDI, F. FERRACCI, H. POIZNER, and C. GHEZ, 1992. Deafferented subjects fail to compensate for interaction torques during multi-joint movements. *Soc. Neurosci. Abstr.* 18:647.
- SAINBURG, R. L., H. POIZNER, and C. GHEZ, 1993. Loss of proprioception produces deficits in interjoint coordination. *J. Neurophysiol.* 70:2136-2147.
- SANES, J., and R. SHADMEHR (in press). Organization of motor control and postural stiffness of deafferented humans. *Can. J. Physiol. Pharmacol.*
- SANES, J. N., K.-H. MAURITZ, M. C. DALAKAS, and E. V. EVARTS, 1985. Motor control in humans with large-fiber sensory neuropathy. *Hum. Neurobiol.* 4:101-114.
- SCHNEIDER, K., R. F. ZERNICKE, R. A. SCHMIDT, and T. J. HART, 1989. Changes in limb dynamics during the practice of rapid arm movements. *J. Biomech.* 22:805-817.
- SHADMEHR, R., F. A. MUSSA-IVALDI, and E. BIZZI (in press). Postural force fields of the human arm and their role in generating multi-joint movements. *J. Neurosci.*
- SMITH, J. L., and R. F. ZERNICKE, 1987. Predictions for neural control based on limb dynamics. *Trends Neurosci.* 10:123-128.
- SOECHTING, J. F., and F. LACQUANITI, 1989. An assessment of the existence of muscle synergies during load perturbations and intentional movements of the human arm. *Exp. Brain Res.* 74(3):535-548.
- WINTER, D. A., 1990. *Biomechanics and Motor Control of Human Movement*. New York: Wiley.