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Accuracy of planar reaching movements

II. Systematic extent errors resulting from inertial anisotropy

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Abstract This study examines the source of direction-dependent errors in movement extent made by human subjects in a reaching task. As in the preceding study, subjects were to move a cursor on a digitizing tablet to targets displayed on a computer monitor. Movements were made without concurrent visual feedback of cursor position, but movement paths were displayed on the monitor after the completion of each movement. We first examined horizontal hand movements made at waist level with the upper arm in a vertical orientation. Targets were located at five distances and two directions (30° and 150°) from one of two initial positions. Trajectory shapes were stereotyped, and movements to more distant targets had larger accelerations and velocities. Comparison of movements in the two directions showed that in the 30° direction responses were hypermetric, accelerations and velocities were larger, and movement times were shorter. Since movements in the 30° direction required less motion of the upper arm than movements in the 150° direction, we hypothesized that the differences in accuracy and acceleration reflected a failure to take into account the difference in total limb inertia in the two directions. To test this hypothesis we simulated the initial accelerations of a two-segment limb moving in the horizontal plane with the hand at shoulder level when a constant force was applied at the hand in each of 24 directions. We compared these simulated accelerations to ones produced by our subjects with their arms in the same position when they aimed movements to targets in the 24 directions and at equal distances from an initial position. The magnitudes of both simulated and actual accelerations were greatest in the two directions perpendicular to the forearm, where inertial resistance is least, and lowest for movements directed along the axis of the forearm. In all subjects, the directional variation in peak acceleration was similar to that predicted by the model and shifted in the same way when the initial position of the hand was displaced. The pattern of direction-dependent variations in initial acceleration did not depend on the speed of movement. It was also unchanged when subjects aimed their movements toward targets presented within the workspace on the tablet instead of on the computer monitor. These findings indicate that, in programming the magnitude of the initial force that will accelerate the hand, subjects do not fully compensate for direction-dependent differences in inertial resistance. The direction-dependent differences in peak acceleration were associated with systematic variations in movement extent in all subjects, but the variations in extent were proportionately smaller than those in acceleration. This compensation for inertial anisotropy, which differed in degree among subjects, was associated with changes in movement duration. The possible contributions of elastic properties of the musculoskeletal system and proprioceptive feedback to the compensatory variations in movement time are discussed. The finding that the magnitude of the initial force that accelerates the hand is planned without regard to movement direction adds support for the hypothesis that extent and direction of an intended movement are planned independently. Furthermore, the lack of compensation for inertia in the acceleration of the simple reaching movements studied here suggests that they are planned by the central nervous system without explicit inverse kinematic and dynamic computations.

Key words Multijoint arm movements · Reaching Accuracy · Coordinate transformations · Human

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Introduction

In the preceding paper, we presented an analysis of the spatial variability of movement end points in a planar reaching task performed without visual feedback. We reported that, for movements in a given direction, variable errors in direction are constant and independent of target distance, while variable errors in extent increase with increasing target distance. This difference in the determinants of the two types of variable errors led us to suggest that direction and extent represent distinct features of reaching movements that are planned independently of each other by the brain. We hypothesized that planning the direction of a hand movement might correspond to the selection of a particular spatiotemporal pattern of muscle activation, or synergy. This would specify the relative amounts by which different muscles must be activated in order to project the hand in a given direction. Planning the extent of hand movement was proposed to involve the specification of a scaling parameter: the degree of activation applied in common to the muscles in the synergy.

The idea that movements are planned as trajectories at the hand with independently specified extents and directions relative to an initial hand position encounters certain difficulties. In general, at the level of joint angles or torques, direction and extent of hand movement are not mechanically independent. A specific problem that arises, and one that will be considered in detail in this paper, is that the inertial resistance to movement of the hand is not uniform but varies according to the direction of hand movement (Hogan 1985). Thus, to produce straight and accurate trajectories to targets in different directions the brain would seem to have to precompute precisely the joint angles and torques appropriate for the intended direction, taking into account the differences in inertial load. One suggestion has been that this computation is the outcome of a series of coordinate transformations (Saltzman 1979; Hollerbach and Flash 1982; Soechting 1989). In a first stage, the intended trajectory of the hand is planned in an extrinsic system of coordinates that correspond to the desired positions of the hand in external space. Second, this representation of the hand trajectory is transformed into a set of joint angle changes appropriate to move the hand along the planned path; the computation required for this transformation is referred to as the inverse kinematic transform. Third, given the planned joint angle changes, the joint torques necessary to achieve them are computed (inverse dynamic transform). At this stage the inertial resistance and other forces opposing movement would be taken into account. Finally, the computed joint torques would be used to specify the appropriate muscle contractions at each joint.

This framework presupposes a serial process; for example, the joint torques are computed from the desired joint trajectories and therefore can only be computed after the inverse kinematic transformation has been accomplished (Gordon et al. 1992a). This "inverse kinematics/dynamics hypothesis," in the form described here, is clearly incompatible with our proposal that direction and extent of hand movement are planned independently: the inverse kinematic and the inverse dynamic computations each require information about both the direction and the extent of the planned hand trajectory.

A critical prediction of a serial inverse kinematics/dynamics model for the planning of hand movement is that, despite the fact that the inertial resistance to movement varies in different directions, the acceleration and velocity of the hand should be invariant or at least independent of direction. This is because, under this hypothesis, the hand trajectory is planned first, then the associated joint movements, and finally the torques necessary to achieve the planned trajectory. It is only in this latter stage that the differential inertial torques are taken into account. Therefore, if the brain plans reaching movements in this way, joint torques should be planned to compensate for the direction-dependent variations in inertia.

If, instead, the brain planned the direction and extent of hand movement independently, information about the direction of movement will not be available to specify correctly the extent. Since the inertial resistance at the hand varies with the direction of movement, accelerations should show corresponding variations and systematic direction-dependent errors would be expected to occur. For example, in directions in which overall inertia is relatively low, initial accelerations should be excessive and subjects should, on average, overshoot the target.

In the previous paper (Gordon et al. 1994), we pointed out that there do occur systematic errors that depend on the direction of movement. In this paper, we further analyze the systematic errors in movement extent. In the next paper in this series (in preparation), we will examine systematic directional errors. The purpose of the experiments reported in this paper was to determine whether the pattern of systematic extent errors support the evidence presented in the preceding paper in this series, that reaching movements are planned in a hand-centered coordinate system, and to determine whether extent of movement is planned independently of direction. Our findings indicate that the systematic errors in extent occur because trajectory planning does not take into account direction-dependent changes in inertial load. Preliminary accounts of this work have been presented elsewhere (Gordon and Ghez 1989; Ghez et al. 1990a; Gordon et al. 1990, 1992b).

Materials and methods

Subjects

Subjects were nine neurologically normal adults, six men and three women, with ages ranging from 26 to 42 years. Eight subjects were right-handed and used their right hand in the experiments described. The ninth subject (F.F.) was left-handed; he used his left hand in these experiments. Two of the subjects were authors of this and related studies (J.G. and M.F.G.). The other subjects were volunteers from among the personnel in this and other laboratories. All subjects signed an institutionally approved informed consent form. All findings were verified in two or more subjects who were naive to the purpose of the experiments. Not all subjects participated in all experiments in this series. The numbers of subjects participating in each of the different experiments are noted in the results.

Apparatus and tasks

The experimental apparatus and movement tasks are described in detail in the previous paper of this series (Gordon et al. 1994). Briefly, subjects viewed a computer screen and moved a hand-held cursor on a digitizing tablet. The position of the cursor on the tablet was displayed on the computer screen together with two circles representing a starting and a target location. At the start of a trial, subjects were to position the cursor in the start circle. Then a "go" tone was presented and they were to make a "single, quick, and uncorrected movement" to the target circle. Subjects were told to move "when ready" after the go tone; there was no requirement to minimize reaction time. The screen cursor was blanked when the tone was presented to prevent feedback corrections. Knowledge of results (KR) was provided by displaying the movement path on the screen after the movement. In some experiments KR was withheld. Targets in different directions and at different distances from the starting position were presented in a pseudorandom order. The hand and arm were hidden from view by a drape.

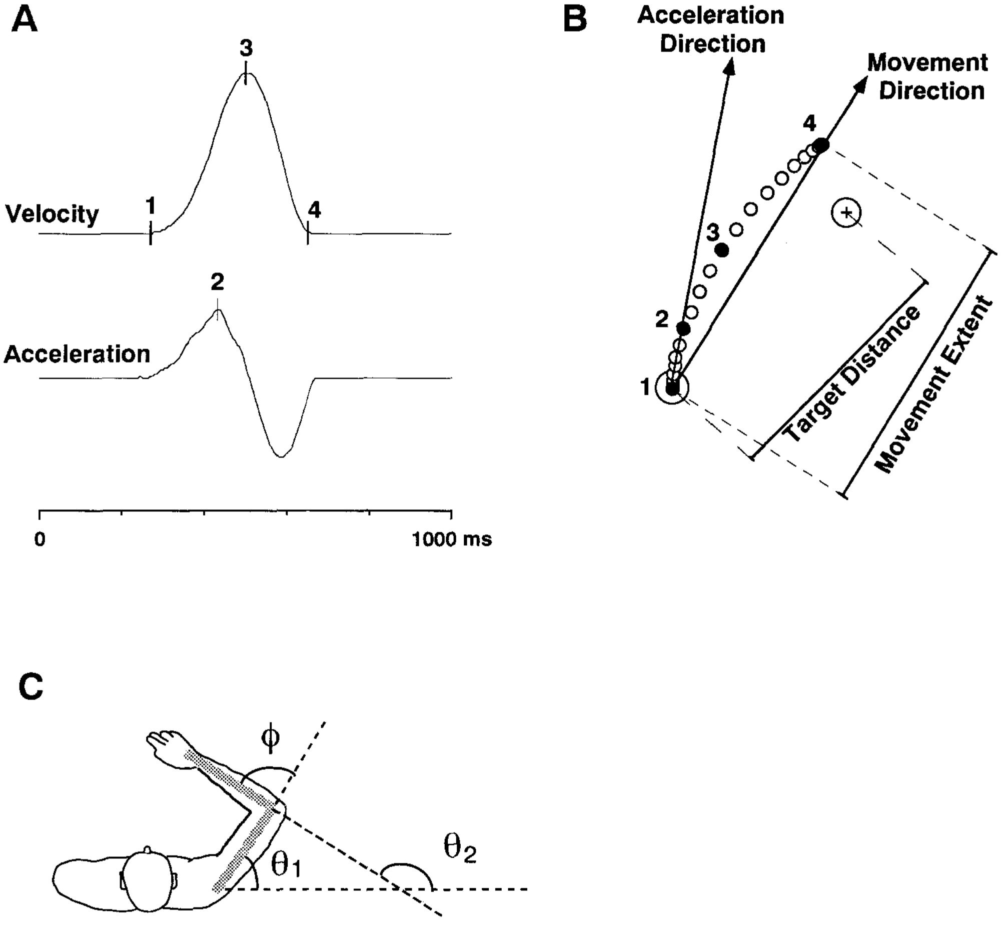
In this paper, data were collected using two positions of the tablet relative to the subject. In the first set of experiments, the tablet was at waist level directly in front of the subject. In the second set, the tablet was approximately at shoulder level. With one exception, noted in the results, the tablet was again directly in front of the subject. In the experiments with the tablet at waist level, targets were presented requiring movements in two directions, with five extents in each direction. These experiments are described in detail in the previous paper in this series, and the results presented here represent additional analyses of these data. In the experiments with the tablet at shoulder level, targets were presented in 24 equally spaced directions around a circle from a central starting position. The distances from the initial position to the target were equal in each direction.

For the experiments with the tablet at shoulder level, the upper arm was supported by a sling suspended by a cable 2.7 m long connected to the ceiling. This was done to eliminate the need for shoulder muscles to act continuously against gravity. During the experiment the subject was positioned with the sternum against a rigid brace and instructed to maintain steady pressure against the brace. This prevented shifts in body position relative to the tablet during the course of the experiment. Finally, each subject wore a lightweight cast, custom molded from plastic casting material, that immobilized the wrist and held the cursor in a constant position relative to the forearm. Thus, the movements were carried out almost entirely by rotating the shoulder and elbow joints. However, the scapula was not immobilized, and therefore small translations of the shoulder contributed to the movement of the hand. These scapular movements were, however, not measured and were neglected in the mathematical modeling.

Data analysis

Many of the details of the data analysis are described in the previous paper. The data collected consisted of x and y coordinates

Fig. 1 **A** Tangential velocity and acceleration of the hand path in a single trial. *Numbers* indicate critical points marked on each trial: 1 movement onset, 2 peak acceleration, 3 peak velocity, 4 movement termination. **B** Hand path of a single trial with *numbers* showing where points indicated in **A** occur on path. *Large circles* indicate locations of start position and target. Computed directions and extents are shown (see text for details). Note that this path is considerably more curved than is typical; it was chosen in order to make the differences between directions more easily seen. **C** Definitions of segment angles (see text for details). (ϕ elbow angle, θ_1 upper arm angle, θ_2 forearm angle)



constituting the movement paths of each trial, sampled at 200 Hz. Each path was smoothed using a cubic spline, the tangential velocity and acceleration were computed, and automatic routines were then used to mark movement onset, peak velocity, peak acceleration, and movement end point on each trial (Fig. 1A). The movement extent was then computed as the length of a straight line from the starting point to the end point of the movement (Fig. 1B). Movement direction was computed as the orientation of this vector. Zero degrees was defined as the horizontal direction from left to right (three o'clock); angles increased in a counterclockwise direction. We also computed the direction of the peak acceleration and peak velocity. These were defined as the orientations of the vectors from the starting point of the movements through the location of the hand at the time that each of these peaks occurred (Fig. 1B). The orientations of these vectors therefore do not indicate the instantaneous direction at the time of the peak acceleration or velocity; rather they correspond to the mean directions of the path from movement onset until the time of the peak acceleration and peak velocity.

For each subject, the lengths of the upper arm and forearm-hand segments were measured. The length of the upper arm was defined as the distance from the tip of the acromion process to the lateral condyle of the humerus. The distal segment was measured from the lateral condyle to the tip of the index finger (the cursor was aligned with this point). The shoulder and elbow angles were then measured with the hand in the starting position on the tablet. The elbow angle was measured using a goniometer. Because it was difficult to measure shoulder angle with a goniometer, we instead measured the orientation of the forearm-hand segment relative to the tablet. We did this by positioning the hand and cursor over the starting position. Then, maintaining the upper arm segment immobile, we flexed and extended the elbow joint passively, at the same time collecting the $x$and y coordinates of the arc described by the change in cursor position. We then computed the tangent to this arc at the starting position of the hand. The orientation of the forearm was assumed to be perpendicular to this tangent. Using the measured elbow angle, ϕ , and the orientation of the forearm segment, θ_2, we then computed the orientation of the upper arm segment according to the formula: $\theta_1 = \theta_2 - \phi$ (Fig. 1C). The segment lengths and angles were used to compute the inertia of the arm according to procedures outlined in Appendix A.

In order to characterize the relationship between movement direction and various trajectory parameters, we used a nonparametric, curve-fitting procedure, called LOWESS, or locally weighted scatterplot smoother (Cleveland 1979). This procedure is a locally weighted moving average with an iterative robustness procedure that reduces the influence of outliers. LOWESS provides for a user-supplied width parameter that defines the number of points around each value on the abscissa to be used in the moving average. We adjusted the value of this parameter so that it was the same in all plots and corresponded to a width of ±20°.

Results

Direction-dependent extent errors are associated with differences in the scaling of peak acceleration to target distance

The starting point for this study was the finding, mentioned briefly in the preceding paper, that when subjects made movements of varying extents in two directions, the mean errors in extent differed systematically for sets of targets in the two directions (Fig. 2). For targets in the 150° direction, mean movement extents were close to those required by each target; movements directed to targets in the 30° direction, however, were generally overshot. This dependence of extent error on target direction was statistically significant across the five subjects tested (repeated measures ANOVA, $F_{1,4} = 8.89$, $P < 0.05$) and in separate analyses of each subject's means ($P < 0.01$ for all subjects). In all subjects, movement extents were systematically greater in the 30° direction for all target distances except the largest (33.6 cm). At this distance, some of the subjects exhibited a tendency to consistently undershoot in both directions, and this apparently offset the systematic dependence of extent on direction. The tendency to undershoot the far targets was part of an overall range effect (Poulton 1981; Hening et al. 1988); movements to the near targets were generally hypermetric (Fig. 2). Nevertheless, in the middle of the target range (requiring movements of 9.6 cm), mean movement extents in the 30° direction were approximately 2 cm greater than those in the 150° direction. Thus, in this case the systematic dependence of error on direction produced differences that were more than 20% of the target distance.

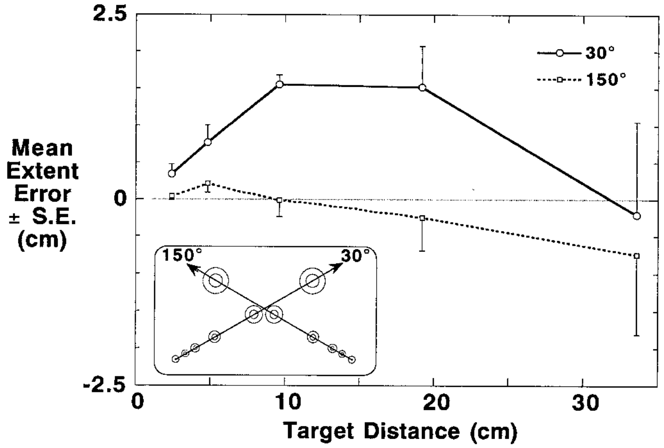


Fig. 2 Mean extent errors of five subjects (J.G., M.F.G., O.P., M.F., M.G.) as a function of target distance and direction. Data from an experiment in which subjects made movements to five targets in each of two directions (see *inset*). *Error bars* show standard errors of the means

To determine the source of the directional dependence of extent errors, we compared the trajectories of the hand in the two directions. For all subjects, peak hand velocity and hand acceleration were higher when the target direction was 30° than when it was 150°. Figure 3 shows ensemble averages of tangential velocities and accelerations and illustrates this effect for one of the subjects. For movements in each direction, peak velocity and acceleration increase with increasing target distance and are larger for the movements at 30°. However, when comparing trajectories between the two directions, higher peak accelerations and velocities were associated with shorter movement times. Thus, in order to move the same distance, in the 30° direction subjects produced higher initial accelerations and reached higher peak velocities than in the 150° direction, but they compensated by decreasing movement time.

Hand trajectories to targets at different distances were scalar multiples of a common waveform. As can be

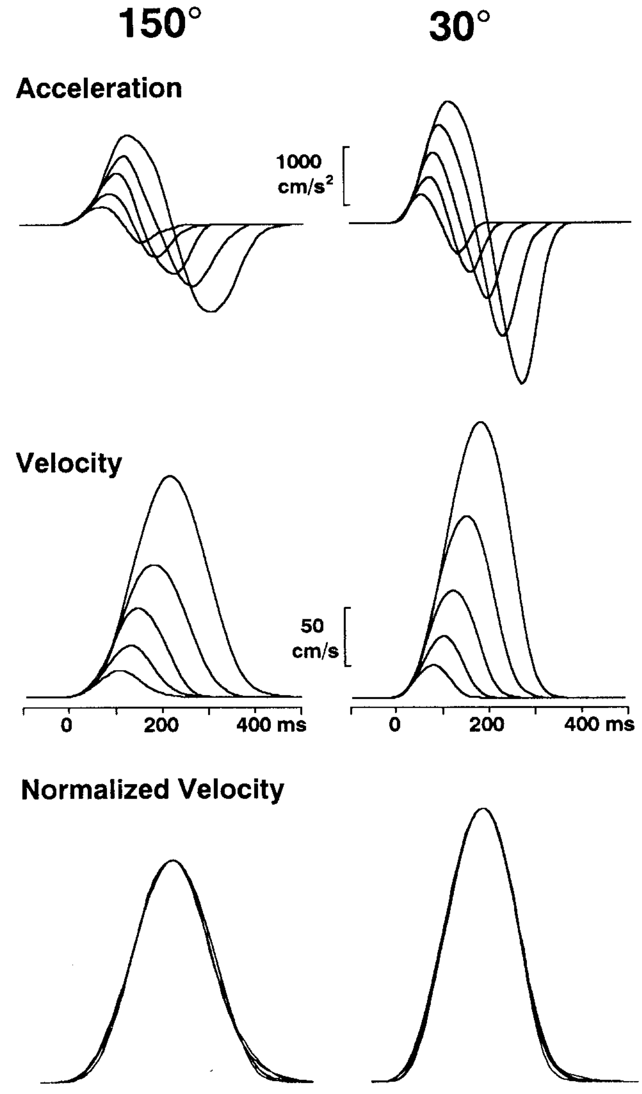


Fig. 3 Average accelerations and velocities of the hand for movements in two directions and with five distances. Each trace is the average of 20 movements by one subject (M.F.G.) aligned on movement onset. Hand acceleration is shown at the *top*, velocity in the *middle*, and velocity normalized by time and amplitude at the *bottom*. The velocity traces were normalized using procedures described in Atkeson & Hollerbach (1985). Averages of movements to targets in the 150° direction are on the left; those to 30° targets are on the *right*. Averages for movements to the five target distances are superimposed; the target distances were 2.4, 4.8, 9.6, 19.2, and 33.6 cm

seen in Fig. 3, when the tangential velocities were normalized in both magnitude and time, they had an identical shape. This invariance of shape means that peak acceleration and peak velocity occurred at the same relative time within the trajectory, regardless of target distance. This feature of trajectory formation is important because it implies that the nervous system can use a simple scaling rule to plan movements of different extents (Ghez and Vicario 1978; Ghez 1979; Atkeson and Hollerbach 1985; Gordon and Ghez 1987).

To quantify the differences between hand trajectories in the two directions, mean trajectory parameters were

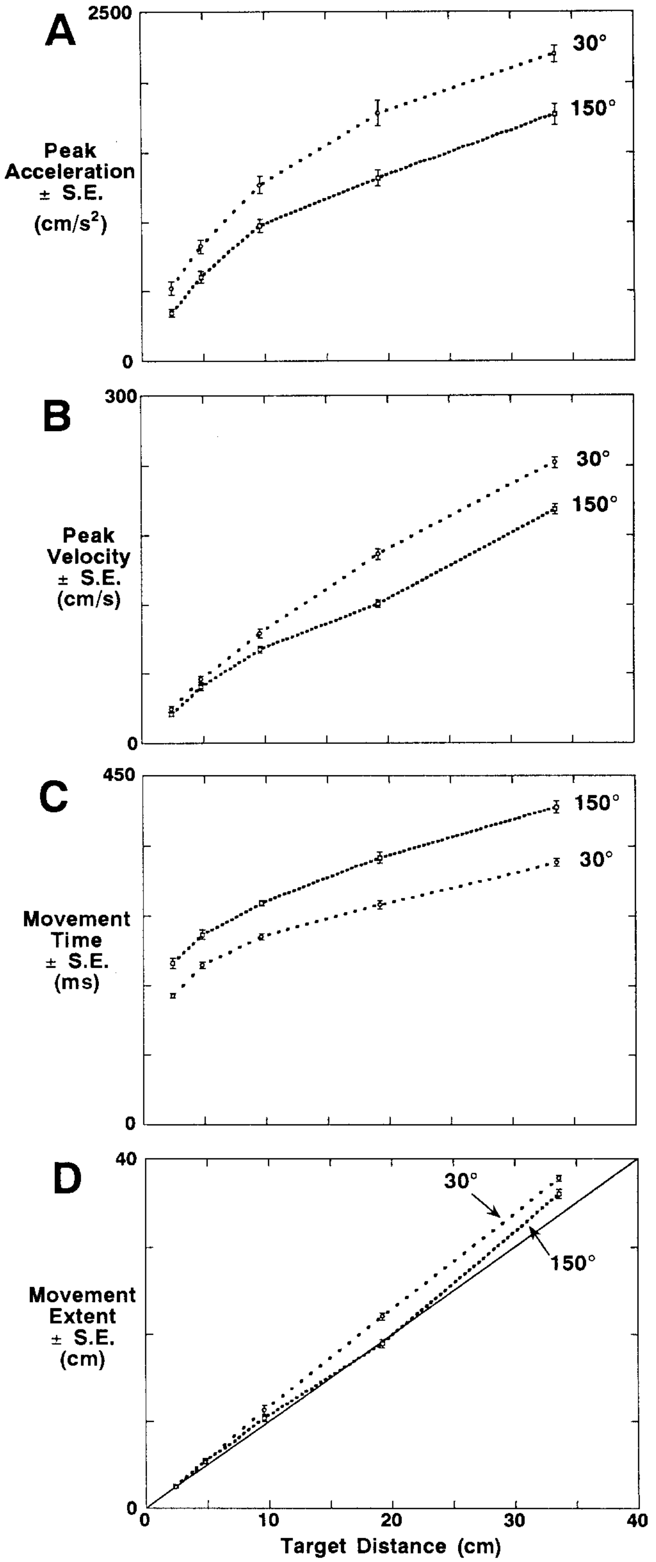


Fig. 4 Mean peak acceleration (**A**), peak velocity (**B**), movement time (**C**), and movement extent (**D**) plotted as a function of target distance for each target for one subject (M.F.G.). In each plot, *circles connected by widely spaced dashes* indicate means for 30° targets, *squares connected by narrowly spaced dashes* indicate means for 150° targets. The *solid diagonal line* in **D** shows where means would fall if the movements were perfectly accurate; means that fall above this line represent average overshoots. *Error bars* show standard errors of each mean

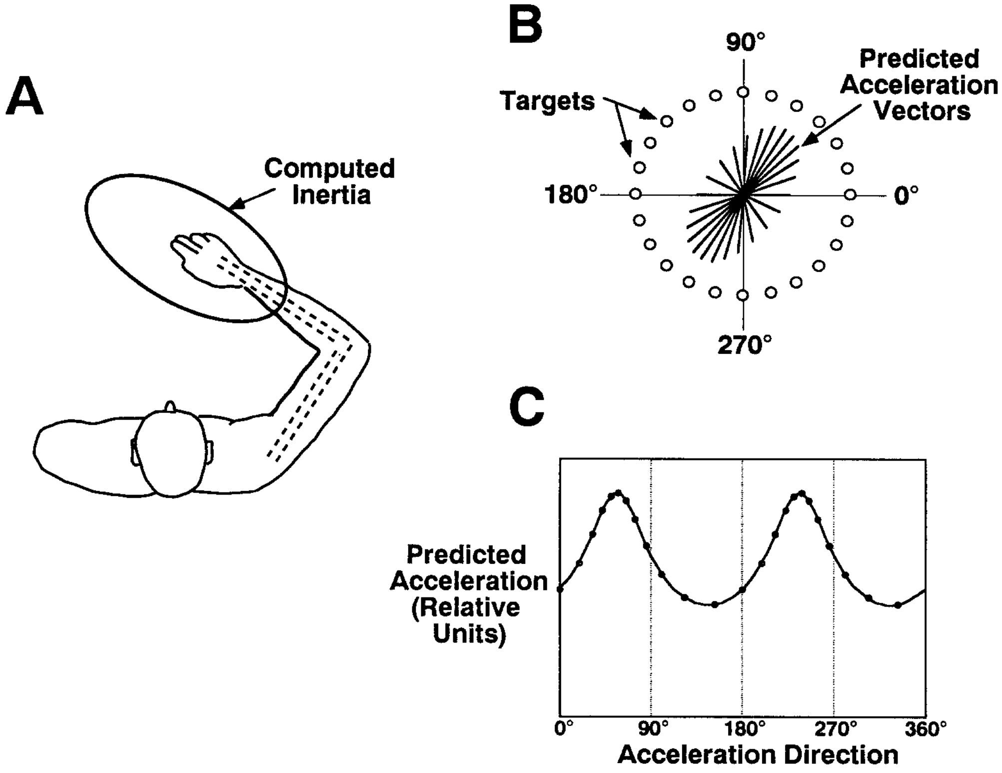


Fig. 5A–C Estimated inertia and "mobility" of the upper limb. **A** Apparent inertia acting at the tip of the hand. The relative differences in inertia for displacements of the hand in different directions form an ellipse whose major axis is close to the long axis of the arm's distal segment. **B** Acceleration vectors for movements aimed in 24 equally spaced directions around a circle. This computation assumed that the initial forces acting to displace the hand were directed toward each target and were of equal magnitude in all directions. The resulting initial accelerations have unequal magnitudes, which form a "mobility ellipse" that is oriented orthogonally to the inertial ellipse. Note that the forces were directed to the targets, but the resulting accelerations are not necessarily oriented in the same directions as the forces. **C** The relative magnitudes of the acceleration vectors plotted on a linear axis as a function of actual acceleration direction. The magnitudes are scaled arbitrarily, but the relative differences are preserved

plotted as a function of target distance separately for each direction. Figure 4A,B shows, for the same subject as in Fig. 3, that both peak acceleration and peak velocity of the hand scale with target distance. The deviation from linearity that is evident in Fig. 4 was typical for all subjects and sessions. For all subjects the form of the relationship between peak acceleration and target distance was fit well by a power function, in which the squared value of the peak acceleration was proportional to target distance. The relationships between peak acceleration and target distance, as well as between peak velocity and target distance, were similar in form across the two directions, but the slopes were always greater for movements in the 30° direction.

Figure 4C shows that movement time also increased with increasing target distance, but the slope of this relationship was higher for movements in the 150° direction. Thus, shorter movement times compensated for the higher peak accelerations and velocities in the 30° direction. This compensation was not, however, complete. The final movement extent achieved was systematically greater in this direction (Fig. 4D), and, as shown for all subjects in Fig. 2, movements in the 30° direction were systematically overshot relative to those in the 150° direction. All five subjects tested with this array of targets showed the same qualitative relationships between trajectory parameters, but, because they moved the hand at different average speeds, the magnitudes of the peak accelerations and movement times varied among the subjects.

Differences in limb inertia produce systematic differences in hand acceleration

Why does the hand move with higher peak accelerations and velocities in the 30° direction than in the 150° direction? One answer might be that the inertial load to be moved was different in the two directions. In the experiments described thus far, the tablet was at waist level and the upper arm was nearly vertical. When the hand moved in the 30° direction, the movement was accomplished almost entirely by rotation of the upper arm around its long axis. Thus, the mass of the upper arm contributed little to the total inertia. When the hand moved in the 150° direction, on the other hand, the subject had to push the hand across the body. This meant that the total mass being accelerated included both the upper arm and the forearm and hand. We therefore hypothesized that the accelerations differed in the two directions because the subjects did not take into account the differences in amount of force needed to move the arm.

In order to test this hypothesis, we used a two-segment model derived from that of Hogan (1985) to compute the effective inertial load at the hand for movements in different directions by each subject (see Appendix A). We then calculated the accelerations that should result from the same initial forces (Fig. 5). In order to simplify the computations and to eliminate the influences of gravitational torques, we carried out these experiments with the arm in the horizontal plane at shoulder level. With the arm at shoulder level, only one degree of freedom at the shoulder and one at the elbow contribute to hand motion (the wrist was splinted and movement of the scapula was neglected).

Figure 5A shows for one subject the computed inertia of the hand for movements in different directions starting from an initial position at the midline. As Hogan (1985) showed, initial inertial resistance to movement of the hand varies around the initial hand position as an ellipse whose long axis has the same orientation as the distal segment. Thus, the resistance to acceleration of the hand is greatest when it moves along this axis and least when it moves in directions perpendicular to the orientation of the distal segment. For directions between these two axes, the inertia assumes intermediate values that match the shape of an ellipse.

We next computed the accelerations of the hand in different directions if the same force were applied in 24 directions (Fig. 5B). Since for a constant force the acceleration is inversely related to the inertia, the result of this computation yields an ellipse of the same shape but whose long axis is now orthogonal to the axis of the distal segment; this is referred to as the mobility ellipse (Hogan 1985). Thus, for constant initial forces there is a predicted anisotropy in initial acceleration of the hand. For movements that are directed to targets close to the axis of the forearm, initial acceleration will be less than for movements directed 90° away of this axis.

The force applied in this model is arbitrary; the size of the mobility ellipse scales linearly to changes in magnitude of force but the shape (the ratio of the major and minor axes of the ellipse) remains the same. For the limb characteristics that we have used (see Appendix A), the ratio of the major axis to the minor axis for both the inertia and the mobility ellipses was approximately 2:1. For a given elbow angle, this ratio depends on how the mass is distributed between the two segments. We have assumed values for the distribution of mass in the different segments based on average anthropometric measurements (Winter 1990), so for a given initial hand position the shapes of the modeled inertial and mobility ellipses do not vary between subjects. Because the shape (i.e., the ratio of minor to major axes) of the predicted mobility ellipse is quite sensitive to the anthropometric parameters, we have chosen not to make quantitative comparisons between the predicted and observed ratios. It is worth noting, however, that in all subjects the fit improved as more detailed descriptions of mass distribution were incorporated into the model: using empirically determined values of r (see Appendix A) gave a better fit than assuming that the center of mass was midway along the segment, and using empirical values of I (see Appendix A) gave a better fit than treating the segments as homogeneous cylinders. In the model shown in Fig. 5, we have also assumed that the elbow angle is 90°. In this case, the long axis of the inertial ellipse exactly coincides with the long axis of the forearm-hand segment. Deviations from 90° lead to small shifts (of a few degrees) in the elliptical axis from the angle of the forearm orientation. In our experiments, the angle of the elbow at the starting position was always close to 90°.

It should be noted that, although the directions of the forces in Fig. 5B are equally spaced (15° apart), the predicted directions of the hand accelerations are not. Rather, the computed initial directions are biased toward the axis of least inertia. In the following papers in this series (in preparation) we will show that there are also systematic errors in direction in these movements. We find that directional errors are influenced by multiple factors; however, the inertial anisotropy of the limb can explain some of the errors.

A simple static model of the limb's inertia (Appendix A) would predict, as shown in Fig. 5, that if a subject were to produce the same magnitude of force at the hand in different directions, the magnitude of the initial acceleration would vary as described by the elliptical function shown. To test whether the inertia of the limb is an important determinant of hand trajectories, we presented five subjects with targets in 24 different directions, all requiring that the hand move the same distance (Fig. 5B). Subjects were now tested with their arms in the horizontal plane at shoulder level. An assumption we made was that the pattern of variation in the first *peak* of the acceleration of the hand (a value that can be reliably measured) would provide a good estimate of the variation in the *initial* acceleration of the hand (the true initial acceleration is vanishingly small and cannot be measured).

The results of this experiment are illustrated in detail for one subject in Fig. 6. In this figure the same data is plotted in a linear format on the left side and in a polar format on the right side. In each plot, the scatter of points of each variable is fitted with a LOWESS line to show the overall shape of its relationship to movement direction. Figure 6A shows that the magnitudes of the peak hand accelerations varied systematically as a function of the initial direction of the movement. In polar coordinates, this variation had an elliptical shape. On this plot, the mobility ellipse is superimposed on the data points and the LOWESS fit. This shows the shape and orientation of the distribution of peak accelerations expected simply from differences in inertia. However, since we do not know the actual force at the hand, the size of the ellipse is scaled to approximate the average magnitude of the LOWESS fit. The shape of the relationship of the observed peak accelerations to the initial movement direction closely matches the shape of the mobility ellipse.

Figure 6B,C shows that the initial difference in acceleration in the different directions is compensated as the trajectory unfolds. The magnitude of the peak velocity shows substantial direction-dependence (Fig. 6B), but

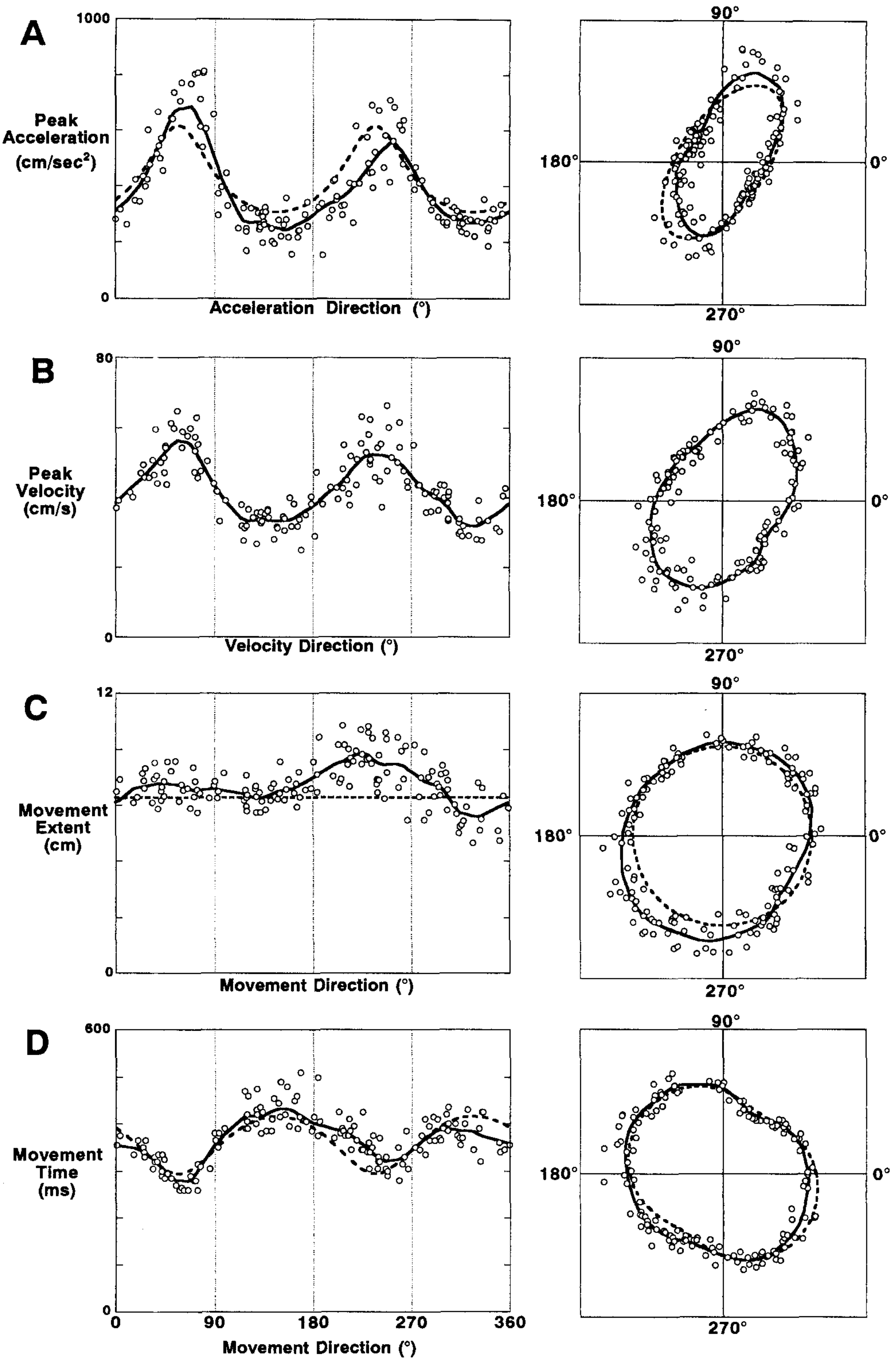


Fig. 6 Variation in peak acceleration (**A**), peak velocity (**B**), movement extent (**C**), and movement time (**D**) for 144 movements in 24 different directions by one subject (C.A.). The *horizontal axis* represents acceleration direction in **A**, velocity direction in **B**, and movement direction in **C** and **D**. On the *left* side, the data are plotted on a horizontal axis; on the *right* side, the same data are plotted in a polar format. In each plot, the *solid line* through the data points represents a best-fitting line computed using LOWESS (see Materials and methods). In **A**, the *dashed line* corresponds to the mobility ellipse (see Fig. 5 and Appendix A) plotted with an arbitrary scaling factor (chosen so that the mean of the real data would approximate the mean of the predicted values). In **D**, the *dashed line* shows movement times that are proportional to the square root of the inverse of the mobility ellipse (see Appendix B). The *dashed line* in **C** represents the target distance

movement extent shows only a modest residual effect of inertial anisotropy (Fig. 6C). Nevertheless, the differences in mean errors between high and low inertia directions in this subject averaged about 1.5 cm, about 20% of the target distance (compare with Fig. 2). Finally, Fig. 6D shows that, as in the previous experiment, the large differences in initial acceleration are compensated by substantial changes in the movement time (in this subject the difference in mean movement times between high and low inertia directions was approximately 110 ms, or 30% of the overall average movement time of 368 ms). The *dashed line* represents an estimate of the movement time to be expected if inertial anisotropy were to be perfectly compensated by a process that would simply scale response profiles to the required target distances (see Appendix B). The predicted shape and orientation of the relationship of movement time to movement direction is very close to what was observed.

A similar correspondence between directional variations in peak acceleration and mobility ellipses (computed on the basis of anthropometric data) to that illustrated in Fig. 6 was present in all subjects. It was present in all sessions and was independent of the degree of the subject's practice. Similarly, all subjects showed large direction-dependent variations in movement time that mirrored this anisotropy in peak acceleration. What varied among subjects was the degree to which they compensated for inertial anisotropy. We estimated the magnitude of this compensation by computing the correlation between peak acceleration and extent in movements made with a constant target distance. A high positive correlation indicates that the anisotropy in peak acceleration was associated with a corresponding anisotropy in movement extent. In four of seven subjects, the correlation coefficient (Pearson's *r*) was significantly positive, but the strength of this relationship was generally modest (median 0.29, range 0.03–0.34), indicating only a small residual extent error. The data illustrated in Fig. 6 had a correlation coefficient of 0.29.

To quantify the extent to which actual variations in movement time compensated for the anisotropy in peak acceleration, we computed, for each session by each subject, the correlation coefficient between peak acceleration and movement time. A high negative correlation indicates that the larger peak accelerations were compensated by shorter movement times. In six of seven subjects, the correlation coefficient was significantly negative (median −0.54, range −0.18 to −0.59). The data illustrated in Fig. 6 had a correlation coefficient of −0.54. Thus, the small size of the residual extent error in the movements of our subjects can be explained, at least in part, by a substantial compensatory modulation of movement time.

It might be expected that the ability to compensate for differences in inertial resistance by modulating movement time might represent a learned strategy or an effect of practice. For example, subjects might use information about their errors to make compensatory adjustments to the time course of the trajectories on succeeding trials. This, however, was not the case. Movement time compensation for variations in acceleration was present to the same degree in sessions in which subjects received no KR, that is, in which they were not shown the errors they were making. (Results of experiments with no KR will be presented in detail in a future paper concerning directional errors.) To determine whether movement-time compensation required specific practice in our task, we tested one subject with no KR in his first two sessions, one with the hand in the standard initial position, and another with the hand displaced to the right, as in Fig. 7B. Because he had no experience at all with the task, his extent errors were large and quite variable. Nevertheless, the movement times compensated for the acceleration anisotropy to approximately the same degree as those of more experienced subjects. The correlation coefficient between peak

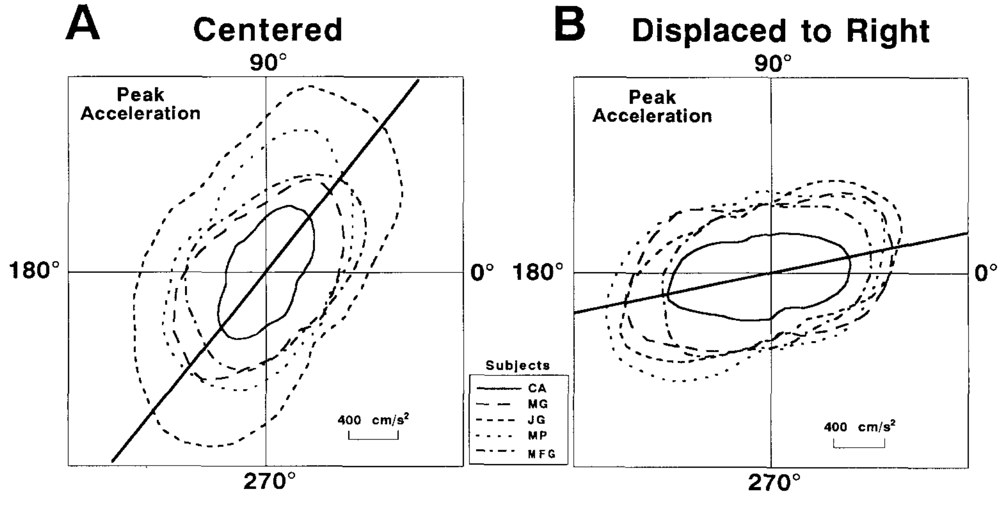


Fig. 7 Variations in peak acceleration with changes in movement direction for five subjects (J.G., M.F.G., C.A., M.G., C.C.) with the initial position centered in the midsagittal plane (**A**) and displaced to the right (**B**). The format of this figure is similar to that of the right side of Fig. 6A, except that individual data points are not shown. Each figure shows best-fitting LOWESS lines for the acceleration data of individual subjects making 144 movements to 24 targets in the two positions. The *solid straight line* in each plot shows the predicted direction of greatest peak acceleration based on the computed mobility ellipse. This direction is a line perpendicular to the forearm orientation. There were slight differences in forearm orientation across the five subjects in each position. Therefore, we rotated each subject's distribution by the difference between that subject's forearm orientation and the mean orientation. In the centered initial position, mean forearm orientation was 102° (range 88–119°). In the displaced initial position, mean forearm orientation was 142° (range 134–154°)

acceleration and movement time was −0.78 in the standard position and −0.57 in the displaced position. Thus, the movement time compensation did not require specific practice in our task, although of course it may depend on practice of reaching movements in daily life. On the other hand, practice in our task over many sessions did typically result in increased compensation for acceleration anisotropy (and increased accuracy) through directional modulation of movement time. The effects of practice will be analyzed in a future paper in this series.

Effects of initial hand position on peak acceleration anisotropy

If the anisotropy in peak acceleration that we have described is related to the inertia of the limb, it should shift as the orientation of the forearm changes. In the experiments described thus far, the starting position of the hand was always directly in front of the subject. We therefore tested five subjects with a different placement of the tablet, that is, with the starting position of the hand displaced to the side. In these experiments, the initial orientation of the forearm was rotated about 40° from its orientation in the standard position. In this new position elbow angle was the same but the upper arm was more extended than in the standard position. Figure 7 demonstrates that the orientation of the distribution of peak accelerations in the different directions rotated in the predicted way, while the overall shape remained the same. In this figure, the LOWESS lines describing the distributions are superimposed in each position for all five subjects.

Figure 7 illustrates three important results, each of which is consistent with the idea that peak acceleration was primarily determined by inertial anisotropy. First, the orientations of the peak acceleration distributions rotate as the initial forearm orientation rotates. Second, the shapes of the peak acceleration distributions are approximately the same in the two positions; peak acceleration is approximately twice as large in the low inertia directions as in the high inertia directions. Third, the shapes of the acceleration distributions are very similar across subjects, even though they moved at different speeds (i.e., the average magnitude of the peak acceleration varies by a factor of 2–3 across subjects).

Effects of changes in movement speed on peak acceleration anisotropy

The similarity in the shapes and orientations of these acceleration distributions in subjects who moved at dif-

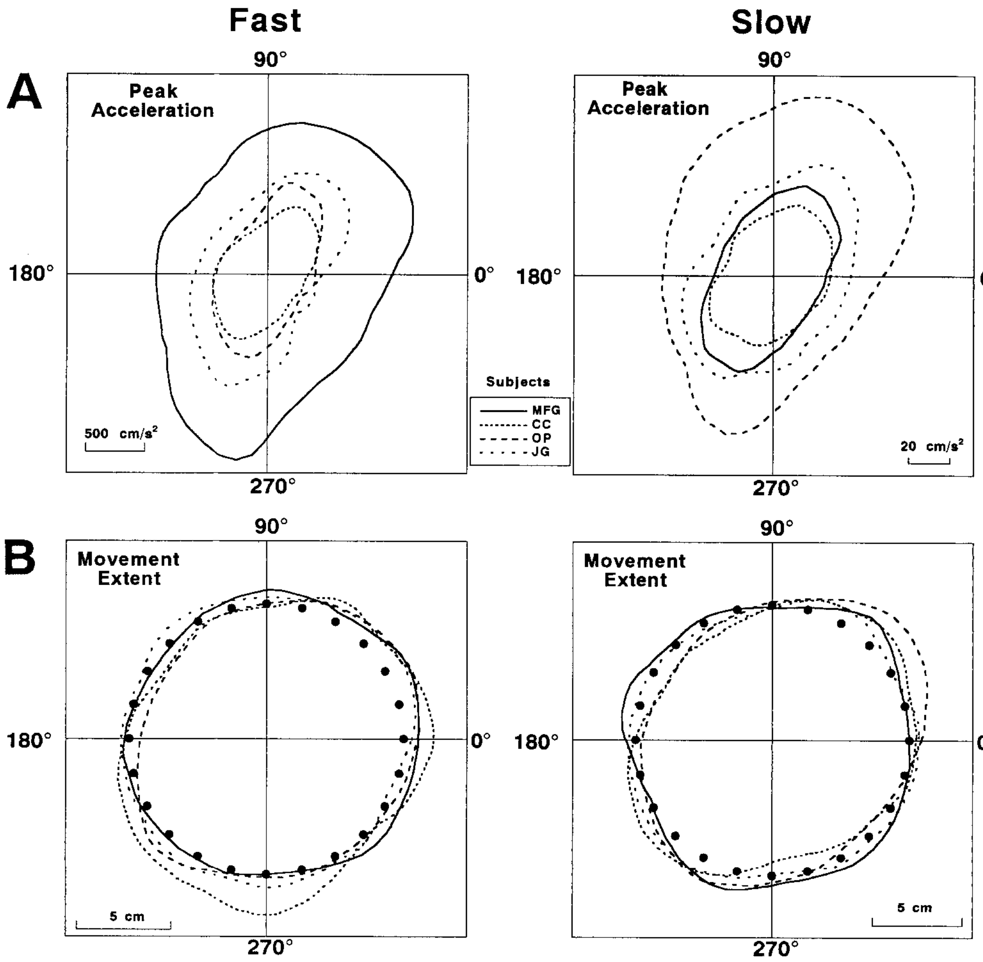


Fig. 8 Variations in peak acceleration (**A**) and movement extent (**B**) with changes in movement direction for four subjects (J.G., M.F.G., C.C., O.P.) in fast (*left side*) and slow (*right side*) movements. Each figure shows best-fitting LOWESS lines for the data of individual subjects making 144 movements to 24 targets in the two positions. Peak acceleration is plotted as a function of acceleration direction, movement extent as a function of movement direction. The *small black circles* in **B** show the target locations (target distance was constant in all directions)

ferent speeds led us to question whether a similar invariance would be seen for much slower movements. In the experiments described thus far, the subjects were told to "make a quick movement" (but not necessarily "as fast as possible"). We then tested four subjects with the instruction to "move very slowly." Here the range of movement times varied considerably across subjects (slow: mean movement time 1722 ms, range 987–2698; fast: mean movement time 291 ms, range 211–333). As shown in Fig. 8A,B, an anisotropy in peak acceleration was also evident in the slow movements and had a shape and orientation that were similar to those seen in the fast movements. Thus, the shape and orientation of the acceleration anisotropy is independent of movement speed, at least over the range we have examined. Figure 8C,D shows that systematic extent errors were also similar in both fast and slow movements. Thus, the tendency to overshoot in directions in which inertia is low is independent of the speed of movement.[1]

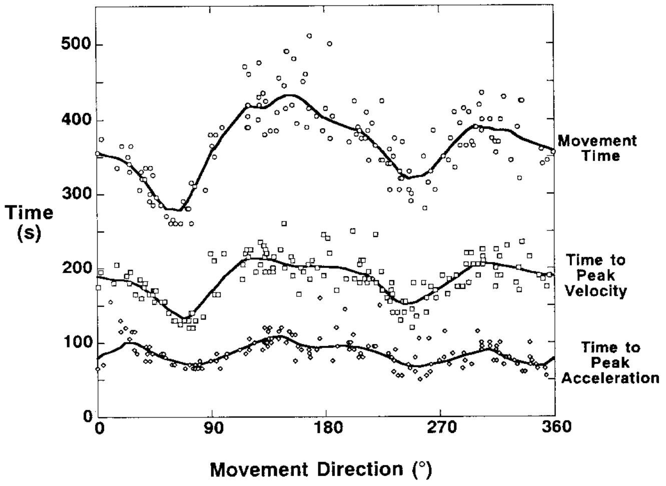
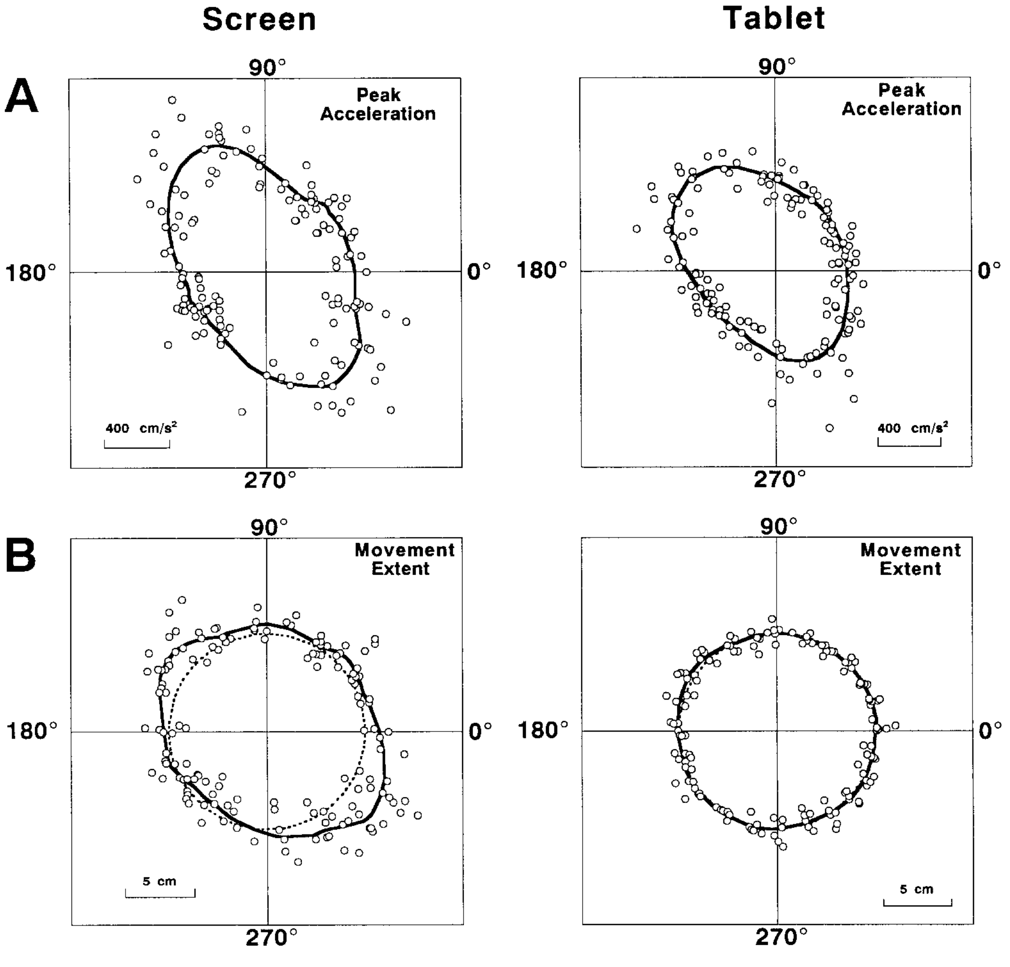


Fig. 9 Variations in movement time (*circles*), time to peak velocity (*squares*) and time to peak acceleration (*diamonds*) with changes in movement direction for one subject (A.C.) making 144 movements in 24 directions. Movement time is plotted as function of movement direction, time to peak velocity is plotted as a function velocity direction, and time to peak acceleration is plotted as a function of acceleration direction. The *solid lines* superimposed on the individual data points represent the best-fitting LOWESS lines

Fig. 10 Variations in peak acceleration (**A**) and movement extent (**B**) with changes in movement direction for one subject (F.F.) viewing targets on the computer screen (*left side*) and directly on the tablet (*right side*). Note that this subject was left-handed. Each figure shows best-fitting LOWESS lines superimposed on the data for 144 movements to 24 targets in each condition. Peak acceleration is plotted as a function of acceleration direction, movement extent as a function of movement direction. The *dashed line* in **B** shows the target distance (constant in all directions)



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[1] As noted in the first paper in this series (Gordon et al. 1994), the trajectories of these slow movements were quite different from those of the more rapid movements that formed the bulk of our data. In the slow movements, movement extent was controlled by varying the duration of movement (width control strategy). As a result, the inertial effects on initial accelerations did not account for a significant amount of movement-time variability

Direction-dependent variations in movement time

We have already shown that the directional differences in peak acceleration are compensated by corresponding directional variations in movement time. This raises the question of whether adjustments in movement duration reflect the operation of feedback mechanisms. In other words, are adjustments in movement time made during the terminal phase of the movement based on information obtained during the early phase of the trajectory, or is the entire trajectory (i.e., during both early and late phases) prolonged or shortened according to the direction? To distinguish between these alternatives, we compared the directional variations in the time to peak acceleration and time to peak velocity in each movement with the variations in movement time. Figure 9 shows that the direction-dependent modulation of the time course of the trajectories was not limited to the latter part. Both time to peak acceleration and time to peak velocity were proportionally shorter in those directions in which movement time was short. The same was true in all subjects: the time to peak acceleration was significantly modulated such that high peak accelerations occurred earlier. Thus, trajectories were modified as a whole, either prolonged or shortened in time according to the direction of movement. This is similar to what we saw for different movement extents: the shapes of the trajectories remain invariant. Peak acceleration and peak velocity occur at the same relative time within the trajectory regardless of direction.

Effect of viewing targets directly in workspace

In the task examined thus far, subjects viewed the target and a cursor representing the initial hand position on a computer monitor. It might therefore be thought that our findings are specific to tasks requiring this type of transformation. To determine whether this was the case, we tested two subjects in a reaching task where the targets were presented on the tablet itself. Here the subject was able to see both the hand and the target before, during, and after the movement. Results from one subject are shown in Fig. 10. This subject was left-handed and used his left hand to move the cursor, so the acceleration anisotropy has a different orientation from other subjects. The direction-dependent variations in acceleration were essentially identical with targets presented on the screen (left) and with the targets presented on the tablet (right). On the other hand, presumably because the subject could see his hand and make corrections based on visual feedback, the end-point errors were reduced when targets were presented directly on the tablet (Fig. 10B). The other subject we tested in these two conditions showed similar results.

Discussion

There were two major findings in this study of two-dimensional reaching movements. *First*, the acceleration and velocity of the hand varied systematically with the direction of movement. This variation could largely be explained by the influence of biomechanical factors, specifically the differences in inertial resistance of the limb to movement of the hand in different directions (Hogan 1985). *Second*, subjects made systematic errors in movement extent that paralleled the directional variations in acceleration; movements in the high inertia direction were generally overshot and were often more than 20% greater in extent than those in the low inertia direction. However, directional variations in movement duration substantially compensated for the differences in acceleration so that directional differences in movement extent were proportionally smaller than those in acceleration.

Our findings lead us to three general conclusions about the planning of planar reaching movements. *First*, they argue against the notion that reaching movements are planned by a serial computation of required joint angles (inverse kinematics) and joint torques (inverse dynamics). *Second*, they support the hypothesis advanced in the preceding paper that planning of movement is carried out in hand-centered coordinates with extent and direction representing independently specified dimensions. *Third*, they also support the view that the nervous system does not fully preplan the actual kinematic changes and the time course of the movement. Rather it plans an equilibrium trajectory (Bizzi et al. 1984) that leads the actual trajectory in time. We will discuss each of these conclusions after considering certain potential limitations of our experimental design and of our computational model.

Limitations of the experimental design

First, in our task, motion of the hand is not unconstrained. Because the hand-held cursor remains in contact with a horizontal surface, movements are subject to frictional forces. It is possible that such movements are controlled with a different strategy to those in which the hand moves freely in space (Brady et al. 1982; Atkeson and Hollerbach 1985). Furthermore, the hand-held cursor, although relatively light, did represent a mass to be moved in different directions. Subjects might use a different strategy when the hand is holding an object. In addition, gravitational forces, not present in our task, further complicate the control of unconstrained reaching movements. Nevertheless, the finding that velocity of movement varies systematically with direction of hand movement has also been reported by Karst (1991) for unconstrained vertical movements, and as early as 1893 by Alfred Binet, for movements made with a pen on a horizontal surface (Worringham 1992). Thus, the principles outlined here are likely to apply to different types of movements, including unconstrained three-dimensional movements.

Second, a significant feature of our paradigm is that the locations of targets and initial hand positions are displayed on a vertical computer screen; subjects must transform this visual representation into actual workspace coordinates. Thus, the generality of our conclusions might be limited by this extra transformational requirement. Nevertheless, the trajectories and the dependence of accelerations on movement direction were similar when subjects viewed the targets directly on the tablet (Fig. 10).

Limitations of the computational model

It should be emphasized that the model we used to explain the directional variations in initial acceleration was purely static and relied only on estimates of limb inertia to predict initial accelerations. Its ability to explain errors in movement trajectories and end points is limited because it neglects the effects of acceleration- and velocity-dependent torques that arise during the course of movement itself. These "interaction" or movement-dependent torques can significantly influence trajectories (Hollerbach and Flash 1982; Smith and Zernicke 1987) and produce errors (Sainburg et al. 1992). We are currently studying how neglecting these torques in programming movements can give rise to spatial errors in reaching and other types of movements (Sainburg et al. 1993), and we will describe these effects in later reports. A second limitation of our model is that it assumes a two-segment limb and neglects translational movements of the shoulder. However, because the hand movements were relatively small (typically about 8 cm), the contributions of such shoulder movements are also likely to have been small.

Despite these limitations, directional variations in peak acceleration closely matched the variations in initial acceleration predicted by a static model of the limb, regardless of movement speed and with different initial positions of the hand (Figs. 7–10). It is likely therefore that they were, in fact, due to directional differences in inertial resistance.

Evidence against the serial inverse kinematics/dynamics hypothesis

Our findings provide evidence that the nervous system does not plan reaching movements through sequential inverse kinematic and dynamic computations. There are two main reasons for rejecting this serial model. *First*, if the nervous system explicitly planned the kinematics of the movement before the dynamics, one would expect that the kinematic parameters of the trajectory, notably the peak acceleration and movement time, would be kept invariant for movements of the same extent but different directions. Indeed, we find that, for movements in a single direction, the peak acceleration, peak velocity, and movement time are scaled to target distance. However, we also find that these parameters do not maintain an invariant relationship to movement distance for movements in different directions, but instead they vary systematically according to the changing inertial load. It is possible that the nervous system might plan different trajectory kinematics for movements in different directions. However, because in the serial model the specification of kinematics necessarily precedes that of dynamics it could not plan these in such a way that they would vary systematically according to the varying inertial load. Thus, our findings strongly suggest that, for movements in different directions, significant details of the movement kinematics are emergent, determined largely by biomechanical conditions, rather than being explicitly planned (see also Flash 1987).

Second, if the nervous system explicitly computed the joint torques required for moving the hand in different directions, one would expect that it would program the torques to take into account the varying inertial load, as this is an essential aspect of the inverse dynamics computation. This clearly did not occur; thus, we conclude that, for the movements we have examined, an inverse dynamics model does not provide an adequate description of the planning process (Flash 1987; Hasan 1991; Shadmehr et al. 1993). Nevertheless, it is possible that the nervous system attempts to take varying inertial loads into account but does so imperfectly.

Independence of direction and extent planning

The systematic errors in movement extent described here, like the variable errors analyzed in the preceding paper, show a consistent and invariant pattern when plotted by direction of hand movement. The findings are therefore consistent with the conclusion that the planning of reaching movements is carried out in a hand-centered coordinate system. The results of the preceding study (Gordon et al. 1994) showed that variable errors in extent and direction are influenced differently by target distance, suggesting that direction and extent of hand movement are planned by distinct processes. The current study shows that systematic errors in extent reflect direction-dependent variations in inertia that are not taken into account in the planning of the initial impulse that moves the hand to the target. The effect of these variations in initial acceleration on the final errors in extent is partially compensated by variations in the time course of trajectories; the possible mechanisms underlying this compensation will be discussed below. Thus, the planning of movement extent appears to be carried out, at least in part, independently of the direction of movement.

Similarly, in studies of an isometric force task requiring critically timed responses, we found that subjects plan direction and extent relatively independently and in parallel (Favilla et al. 1989, 1990; Ghez et al. 1990b). Presumably, this allows subjects to respond more rapidly to stimuli because planning of the direction and extent of movement can occur concurrently rather than as a serial process.

In addition to its advantage for rapid responding, this parallel processing strategy may simplify certain aspects of the planning of reaching movements. First, a possible advantage of planning reaching movements by specifying the magnitude of force at the hand may be that it allows for relatively simple scaling of the dynamics for changes in load at the hand. Because the brain is already scaling muscle forces with respect to the hand, additional scaling to take into account the mass of a hand-held object would be a relatively simple process, requiring only addition of the force required to move the object.[2] Atkeson and Hollerbach (1985) made a similar point with respect to the advantage of keeping the shape of hand trajectory profiles invariant. Second, there are advantages to keeping as much as possible of the planning of movement in hand-centered coordinates, since errors will be perceived in this coordinate system. For example, if the hand overshoots or undershoots the target, simple adjustments can be made to the scaling factor that determines movement extent to make the next attempt more accurate.

These simplifications should, however, be expected to be at the cost of accuracy since, at the level of joint angles and torques, direction and extent of hand movement are not independent of each other. Because of varying inertial loads and interaction torques produced when the hand is moved in different directions, a strategy that treats direction and extent independently must lead to errors. Moreover, these errors should vary systematically with the direction. In this paper, we have shown that subjects do indeed make such errors in the extent of movement. It should be emphasized, however, that the movements we have examined were carried out without visual feedback. When visual feedback is available, as in most normal movements, subjects can make corrective adjustments to eliminate these systematic errors (Fig. 10, right side).

Factors determining the time course of the trajectory

Our results indicate that the kinematic features of the hand trajectory are not invariant for movements to targets of equal distance made in different directions. The peak acceleration, peak velocity, and movement time all vary substantially. The variations in the time course of the trajectory are strongly related to movement direction and appear to compensate, at least in part, for the direction-dependent differences in initial acceleration. The differences in movement times between high and low inertia directions were surprisingly large, typically about 30% of the average movement time (see Figs. 4C, 6D). The question arises, therefore, whether these systematic changes in the time course of the movement are explicitly planned in advance, by computations of kinematics and dynamics, to provide such compensation.

Although we cannot rule out this possibility, we feel that it is implausible. The computations required for such a form of trajectory control would be quite complex and roundabout. If the planned initial force at the hand were not adapted to the inertial resistance in different directions, the nervous system would have to compute an anticipated hand trajectory. It would then have to compute modifications to the time course of the hand trajectory appropriate to compensate for the actual initial acceleration. If the nervous system has the capacity to do this sort of computation (which in effect represents an implementation of the forward kinematics and dynamics transforms), it should also be able to program the initial force at the hand to compensate for the variations in inertial load in the first place.

Two alternative, but not mutually exclusive, explanations for the compensatory changes in movement time appear more plausible. First, they may depend on sensory inputs arising from muscle receptors, and, second, they might occur because of the spring-like properties of muscle. We will discuss each of these in turn.

First, the nervous system might plan a given initial force at the hand for a particular target distance and rely on proprioceptive feedback to compensate for differences in inertial load in different directions. Given appropriate gamma drive, the primary endings of muscle spindles may have the dynamic sensitivity needed to signal mismatches between intended and actual accelerations (Merton 1953; Vallbo 1970; Gordon and Ghez 1991). The well-known reciprocal connections to agonist and antagonist motor neurons could then provide the circuit for trajectory control through negative feedback. Insufficient gain of the stretch reflex pathway might, given this framework, account for the observed systematic extent errors (Houk and Rymer 1981).

Consistent with the view that directional differences in limb inertia are compensated through proprioceptive feedback, patients with large-fiber sensory neuropathy show much larger direction-dependent extent errors than normal subjects, and these errors can largely be attributed to failure to compensate for inertial anisotropy (Ghez et al. 1990a). However, the errors are substantially attenuated when deafferented patients are allowed to briefly view their limb shortly before movement, indicating that the nervous system can use feed-

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[2] If the nervous system controlled joint torques directly, compensating for a load at the hand would require a nonlinear transformation of its resistive force into joint-torque coordinates followed by vector addition of the limb and load resistances to determine the required motor output. Inertial (and frictional) loads at the hand are, however, frequently isotropic in tip but not joint coordinates. If the limb inertia were already treated as isotropic in tip coordinates, compensation for a load at the hand, assuming that its inertia is reasonably isotropic, would be accomplished by simple scalar addition. The more variable and unpredictable component of the inertial, that is, the external load, would be handled in the coordinate system where it had the simplest description

forward mechanisms to compensate for directional differences in limb inertia. Whether intact subjects use proprioceptive cues for feedforward control in this way is, however, not yet known.

A second and complementary possibility is that the nervous system does not directly plan the actual kinematic trajectory of the hand, but rather a time-varying equilibrium position (Bizzi et al. 1984; Feldman 1986; Flash 1987; Hogan 1988). This hypothesis envisages that reaching movements are generated simply by gradual shifts in the equilibrium position of the hand toward the target at a rate that is independent of direction. The driving force at the hand is determined by the stiffness of the limb and the disparity between actual and equilibrium positions. For movements in directions of high limb inertia, this force would be acting against greater resistance, and acceleration would be lower, as observed in the present experiment. However, because the driving force arises from the disparity between actual and equilibrium positions, the force would persist longer in exact proportion to the greater length of time required to reach the target, and the movement duration would be prolonged in a compensatory fashion. This effect would be spread out over the entire movement, rather than appearing only at the end, in agreement with our observations. Thus, our findings of direction-dependent variations in acceleration and of reciprocal variations in movement time provide substantial support for the idea that, at some level of planning, movements are specified as equilibrium trajectories.

By itself, however, the equilibrium trajectory hypothesis does not predict the occurrence of direction-dependent errors in movement extent that parallel the inertial effects on initial acceleration. A possible explanation for the systematic errors could be that stiffness during movement is inadequate to overcome the inertial effects. This, implies that, in addition to specifying an equilibrium trajectory, neural controllers would have to explicitly control limb deceleration, for example by reciprocal commands to antagonist muscles or by increasing joint stiffness at the movement end point. In future experiments, which will involve recording joint motions and muscle activation patterns, we intend to examine these possibilities.

Is movement extent planned as a force exerted at the hand?

Our results suggest that the force exerted at the hand is controlled more explicitly by neural processes than are kinematic variables. This conclusion is based on the finding that, for targets at a constant distance, acceleration varied with movement direction like the simulated accelerations generated by a constant force at the hand. Moreover, the orientation of the distribution of peak accelerations rotated as predicted when the position of the hand was changed (Fig. 7). This might therefore imply that, as in our static model, subjects produced equal initial forces in all directions.

We could have computed the initial forces from the initial accelerations and the limb inertia (see Appendix A). However, we have chosen not to do so, because, as noted in the results, there is uncertainty associated with both quantities. First, we could only estimate initial acceleration based on peak acceleration. Second, the estimate of limb inertia is sensitive to anthropometric parameters and we used average values for those parameters. Therefore, we would only be able to *estimate* the patterns of variation in the initial force at the hand. Thus, while it may have been the case that the magnitudes of the forces were equal in all directions, our data only permit us to state that they were not adapted to the variations in limb inertia.

Indeed, anisotropies in static stiffness measured at the hand (Mussa-Ivaldi et al. 1985) should also contribute to directional differences in initial acceleration, and variations in stiffness are likely to significantly affect the trajectory itself. Since we did not measure stiffness and we did not take account of stiffness fields in our model, we are unable to estimate this contribution. Nevertheless, qualitative considerations suggest that limb inertia was the dominant factor. Stiffness fields, measured under static conditions, are elliptical and oriented with their major axis close to a line between the shoulder and hand (Mussa-Ivaldi et al. 1985; Flash and Mussa-Ivaldi 1990). In the standard position in our experiments, this line would always point in a direction substantially greater than 90° (see Fig. 5). If the stiffness of the limb were a major determinant of the initial force, and therefore of the acceleration, the acceleration should be higher along this axis. In all our subjects, however, accelerations were lower than average along this axis. Flash (1987) suggested that very fast movements would be more influenced by the inertia of the limb than by its stiffness. In our experiments, the anisotropies in acceleration and errors of slow movements did not differ appreciably in form from those of fast movements.

However, Shadmehr and colleagues (Shadmehr et al. 1993) have recently shown, in experiments requiring subjects to move a manipulandum that could be braked unexpectedly, that the magnitudes of initial forces produced by subjects were not equal in all directions, and that the directions of the initial forces were, in general, not aligned with the direction of the targets. Based on measurements of the static stiffness fields of the same subjects, these authors concluded that the observed initial forces were consistent with a control strategy that involved shifting the equilibrium point of the hand toward the target. They did not analyze movement accelerations, however, and because we were not able to measure forces directly, it is difficult to compare our findings with theirs. Nevertheless, their finding that force magnitude varied significantly with direction is difficult to reconcile with our finding that the acceleration varied in a way that suggests relatively little direction-dependent variation in force. It is possible that these differences result from differences in the task, such as the presence of visual feedback, or perhaps the anisotropic properties of the manipulandum they used.

It should also be noted that, because of the limb's inertial anisotropy, the direction of initial hand acceleration differs from the initial direction of the force applied at the hand. We have not presented analyses of directional errors here, as they are the subject of succeeding papers in preparation. In general, however, we find multiple sources of directional errors, including both biomechanical and cognitive factors (Ghilardi et al. 1991, 1993). Although some of the initial deviations in direction can be explained by inertial anisotropy, the idea that movements are planned by producing a force at the hand in the direction of the target does not provide a complete explanation of the systematic directional errors that we observe. This is in agreement, therefore, with the findings of Shadmehr et al. (1993), as well as those of Karst and Hasan (1991a,b), that the initial direction of the force at the hand is not necessarily in the same direction as the target. We would emphasize, however, that the initial direction of force cannot be assumed to be accurate and therefore to reflect the nature of the control strategy, since it is also subject to systematic errors.

Because of the above considerations, we have always plotted the magnitudes of the initial accelerations not as a function of target direction, but rather as a function of the initial direction of movement ("acceleration direction"). The close match of the peak accelerations to those predicted by a constant initial force therefore indicate that the principal determinant of the *magnitude* of the initial acceleration is the anisotropic inertial behavior of the limb. This in turn suggests that the magnitude of the initial impulse of force is scaled, without regard to direction, according to the required distance to be moved. The direction of the initial force applied at the hand is another matter, and one that will be analyzed in future papers.

Conclusions

The striking finding in this study is that trajectory kinematics are not invariant with respect to direction. The variation in kinematics is systematic and related to limb inertia. It could be explained in either of two ways. First, the particular pattern of variation may be deliberately planned by the nervous system. Second, the pattern may be emergent, *resulting from* the limb's inertia. The second explanation is more parsimonious because it explains the observation with a phenomenon that is already known to exist, namely, limb inertia. The first explanation postulates a new entity: an additional set of computations that the nervous system would be required to perform.

We conclude that the brain does not plan the type of movements examined in this study by an explicit computation of inverse kinematics and dynamics. Clearly, however, there must be some mapping of intended hand movements into the muscle activations necessary to achieve those movements. In the preceding paper of this series we suggested that movement distance might be specified as a scaling factor, a general level of activation of the muscles involved in a synergy, and that it might be computed independently of direction. The results of this study support that hypothesis in that the magnitude of the initial force does not take into account direction-dependent differences in inertia. This overall idea is consistent with neurophysiological data suggesting that ensemble firing of populations of neurons in several regions of the cerebral cortex encode the direction of intended hand movement and that the overall magnitude of firing is related to distance and the direction of force change (Kalaska et al. 1989; Georgopoulos 1991; Georgopoulos et al. 1992). Burnod and colleagues (Burnod et al. 1992) have presented a plausible model, based on the neurophysiological data, of how intended movement directions might be transformed by populations of cortical neurons into signals that activate appropriate muscle synergies for moving the hand in the intended direction. In the broadest sense, such a mapping might be considered an implementation of an inverse transform. Nevertheless, it is important to note that this model deals only with how hand movements in different directions might be initiated. Implicit in the model is the notion that direction can be planned independently of the extent of movement.

Although our findings argue against an explicit inverse kinematics computation, they do not imply the absence of a kinematic plan. Rather, a general plan that specifies the overall speed or tempo of movement is likely to determine the shape of the trajectory profile. However, our data indicate that the details of the movement kinematics emerge only at the moment of movement execution, are strongly influenced by inertial factors, and are therefore not invariant across movement directions.

As a final point we should note that control of reaching movements might consist of several processes with different time courses. Indeed, for aimed single-joint movements and forces, we have previously proposed that the nervous system plans a command with two distinct phases (Ghez 1979). Initially a dynamic or phasic component, represented as a pulse, would determine the magnitude of initial muscle activity and therefore the overall speed of the movement. A second more slowly varying or tonic component, represented as a step, would function to maintain the limb in the intended final position and could have a more gradual build-up. A similar strategy with two independently planned phases could operate in multijoint movements. The initial acceleration pulse in the movements we have studied here would reflect the operation of a predictive mechanism that depends on an estimate of the distance to be moved, without regard to direction. The direction of initial hand movement might be also specified by using rough approximations or simple rules, such as those proposed by Karst and Hasan (1991a,b) or Flanders and colleagues (Flanders et al. 1992). The specification of the step, or final position, might exert its effect on the trajectory more gradually and might reflect processes that specify an equilibrium trajectory or some computation of inverse dynamics.

Thus, we believe that it is likely that movements are planned with contributions from different processes whose relative importance varies with task context. Nevertheless, planning the magnitude of the initial impulse of force applied at the hand, in hand-centered coordinates, does appear to represent a significant part of the planning process for the class of movements we have studied. This mode of control may be supplemented, in different task conditions, by independent processes that specify such things as a gradual shift in equilibrium position (Bizzi et al. 1984; Feldman 1986; Flash 1987; Hogan 1988) and precise joint angles and torques (Hollerbach 1982; Soechting 1989). If that is so, then a critical research problem in motor control is to identify what modes of control are possible and how they interact in different task contexts.

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Appendix A

The method we used for computing the inertia and predicted acceleration at the hand assumed a horizontal, two-segment arm with two degrees of freedom, one each at the shoulder and elbow. Segment 1 was the upper arm, and segment 2 was the forearm and hand considered as a single segment.

The direction-dependent inertia of the two-segment arm was computed in the following way. First, a 2 × 2 inertia matrix, **I**, was computed with the following form:

$$\mathbf{I}=\begin{bmatrix}\mathbf{I}_{11} & \mathbf{I}_{12}\\ \mathbf{I}_{21} & \mathbf{I}_{22}\end{bmatrix} \tag{A1}$$

$$\mathbf{I}_{11}=(\mathrm{I}_1+\mathrm{m}_1\mathrm{r}_1^2)+(\mathrm{I}_2+\mathrm{m}_2\mathrm{r}_2^2)+2(\mathrm{m}_2\mathrm{r}_2\mathrm{l}_1\cos\phi)+\mathrm{m}_2\mathrm{l}_1^2 \tag{A2}$$

$$\mathbf{I}_{12}=(\mathrm{I}_2\ \mathrm{m}_2\mathrm{r}_2^2)+2(\mathrm{m}_2\mathrm{r}_2\mathrm{l}_1\cos\phi) \tag{A3}$$

$$\mathbf{I}_{21}=(\mathrm{I}_2+\mathrm{m}_2\mathrm{r}_2^2)+2(\mathrm{m}_2\mathrm{r}_2\mathrm{l}_1\cos\phi) \tag{A4}$$

$$\mathbf{I}_{22}=(\mathrm{I}_2+\mathrm{m}_2\mathrm{r}_2^2) \tag{A5}$$

where I_1 and I_2 are the moments of inertia about the centers of mass of the arm and forearm-hand segments respectively; r_1 is the distance from the shoulder to the center of mass of the upper arm segment, r_2 is the distance from the elbow joint to the center of mass of the forearm-hand segment, m_1, m_2, l_1, and l_2 are the masses and lengths of these segments, and ϕ is the elbow angle (Fig. 1C). The lengths of the segments and the angles between them were measured for each subject individually (see Materials and methods). The masses, centers of mass, and moments of inertia of each segment were derived from tables of average anthropometric data (Winter 1990).

The inertia matrix **I** expresses the inertias of the segments in joint coordinates (Hollerbach and Flash 1982; Mussa-Ivaldi et al. 1985). In order to express the inertia in tip coordinates, it is necessary to transform it using the Jacobian matrix of the inverse kinematic transform, **J** (Hogan 1985; Mussa-Ivaldi et al. 1985). **J** has the following form:

$$\mathbf{J}=\begin{bmatrix}\mathbf{J}_{11} & \mathbf{J}_{12}\\ \mathbf{J}_{21} & \mathbf{J}_{22}\end{bmatrix} \tag{A6}$$

$$\mathbf{J}_{11}=-l_1\sin\theta_1-l_2\sin\theta_2 \tag{A7}$$

$$\mathbf{J}_{12}=-l_2\sin\theta_2 \tag{A8}$$

$$\mathbf{J}_{11}=\mathrm{l}_1\cos\theta_1+l_2\cos\theta_2 \tag{A9}$$

$$\mathbf{J}_{11}=l_2\cos\theta_2 \tag{A10}$$

where θ_1 and θ_2 are segment angles. θ_1 is the angle of the upper arm segment (Fig. 1) and θ_2, the angle of the forearm-hand segment, is equal to $\theta_1 + \phi$.

Using the inverse of the Jacobian matrix, $\mathbf{J}^{-1}$, and its transpose, $(\mathbf{J}^{-1})^t$, the inertial matrix, **I**, was transformed with the formula:

$$\mathbf{M}=(\mathbf{J}^{-1})^t\cdot\mathbf{I}\cdot\mathbf{J}^{-1} \tag{A11}$$

The matrix **M** expresses the total inertia of the arm as an apparent inertia at the hand. The inverse of this matrix, $\mathbf{M}^{-1}$, is the mobility tensor (Hogan 1985), since it expresses the tendency of the hand to accelerate in different directions when a unit force is applied to it. We now used this matrix to compute the initial acceleration vector, **a**, that would result from a unit force vector, **f**, applied to the hand, according to the formula:

$$\mathbf{a}=\mathbf{M}^{-1}\cdot\mathbf{f} \tag{A12}$$

For a given direction of force, φ, the unit force vector, **f**, has x and y components,

$$f_x=\cos\varphi \tag{A13}$$

$$f_y=\sin\varphi \tag{A14}$$

For each direction of force applied to the hand, premultiplying the **f** vector by the inverse of **M** yields an acceleration vector, **a**, which also has x and y components, $a_x$and a_y. The actual direction of acceleration, a_φ (not necessarily the same as the force direction), and its relative magnitude, a_m, are then computed:

$$a_\varphi=C+\tan^{-1}(a_y/a_x) \tag{A15}$$

$$\text{where}\quad C=0^\circ \quad \text{if } a_x\geq 0$$

$$C=180^\circ \quad \text{if } a_x<0$$

$$a_m=(a_x^2+a_y^2) \tag{A16}$$

Appendix B

If the tangential velocity profile has an invariant shape with a single peak acceleration and a single peak velocity then, for a constant movement distance, peak velocity, $v_{\max}$, will be inversely related to movement time, T,

$$v_{\max} = k_1/T \qquad \text{(B1)}$$

Again assuming an invariant trajectory shape, the peak acceleration, $a_{\max}$, will be proportional to peak velocity and inversely proportional to movement time,

$$a_{\max} = k_2(v_{\max}/T) \qquad \text{(B2)}$$

The values of the constants k_1 and k_2 depend on the shape of the trajectory.

Substituting Eq. B1 in Eq. B2 yields

$$a_{\max} = k_1 k_2/T^2 \qquad \text{(B3)}$$

Rearranging Eq. B3 and defining $K = \sqrt{k_1 k_2}$, yields

$$T = K/\sqrt{a_{\max}} \qquad \text{(B4)}$$

Thus, if the trajectory has an invariant shape then, for a constant distance moved, movement time should be inversely proportional to the square root of peak acceleration.

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