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Accuracy of planar reaching movements

I. Independence of direction and extent variability

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Abstract This study examined the variability in movement end points in a task in which human subjects reached to targets in different locations on a horizontal surface. The primary purpose was to determine whether patterns in the variable errors would reveal the nature and origin of the coordinate system in which the movements were planned. Six subjects moved a hand-held cursor on a digitizing tablet. Target and cursor positions were displayed on a computer screen, and vision of the hand and arm was blocked. The screen cursor was blanked during movement to prevent visual corrections. The paths of the movements were straight and thus directions were largely specified at the onset of movement. The velocity profiles were bell-shaped, and peak velocities and accelerations were scaled to target distance, implying that movement extent was also programmed in advance of the movement. The spatial distributions of movement end points were elliptical in shape. The major axes of these ellipses were systematically oriented in the direction of hand movement with respect to its initial position. This was true for both fast and slow movements, as well as for pointing movements involving rotations of the wrist joint. Using principal components analysis to compute the axes of these ellipses, we found that the eccentricity of the elliptical dispersions was uniformly greater for small than for large movements: variability along the axis of movement, representing extent variability, increased markedly but nonlinearly with distance. Variability perpendicular to the direction of movement, which results from directional errors, was generally smaller than extent variability, but it increased in proportion to the extent of the movement. Therefore, directional variability, in angular terms, was constant and independent of distance. Because the patterns of variability were similar for both slow and fast movements, as well as for movements involving different joints, we conclude that they result largely from errors in the planning process. We also argue that they cannot be simply explained as consequences of the inertial properties of the limb. Rather they provide evidence for an organizing mechanism that moves the limb along a straight path. We further conclude that reaching movements are planned in a hand-centered coordinate system, with direction and extent of hand movement as the planned parameters. Since the factors which influence directional variability are independent of those that influence extent errors, we propose that these two variables can be separately specified by the brain.

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

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Introduction

An essential aspect of voluntary motor function is the ability to reach for targets in space. The highly developed manipulatory and prehensile abilities of the human hand are of little use if the hand cannot be moved quickly and accurately to the appropriate position for it to do its work. Until recently, behavioral and physiological investigations of targeted arm movements have largely focused on the production of movements and forces at single joints (Gottlieb et al. 1989). Although such studies neglect important features of natural reaching movements, they have highlighted certain key principles underlying movement control. First, accuracy is achieved largely by programming specific features of the response in advance of movement. Even though feedback can substantially improve accuracy, its effectiveness is limited in fast movements because of the relatively long loop delays (Woodworth 1899; Keele 1968). Second, the planning of reaching movements is simplified by the use of motor programs that incorporate general rules and require specification of a relatively small set of parameters (Bernstein 1967; Schmidt 1976). For example, movements to targets at different distances can be programmed by scaling a stereotyped trajectory profile in amplitude (height control), and/or in time (width control), depending on target and task variables (Gordon and Ghez 1987a; Gottlieb et al. 1989). Thus, a range of response amplitudes that are matched to stimulus values can be generated by a relatively simple transformational rule (Ghez et al. 1983).

In multijoint arm movements, such as those normally required for projecting the hand to different targets in space, the programming task is considerably more difficult because of kinematic and muscle redundancy and the complexity of the dynamics (Bernstein 1967; Soechting 1989; Hasan 1991). Therefore, the planning of multijoint reaching movements is also likely to necessitate simplifying strategies. One way to conceptualize such strategies for reaching movements is as coordinate transformations. As noted by several investigators, a fundamental aspect of the neural computations needed to aim and control such movements may be a transformation in the way in which intended hand position is represented by the brain (Saltzman 1979; Hollerbach 1982; Soechting and Terzuolo 1990; Kalaska and Crammond 1992). Information about target location, obtained through vision or other sensory modalities, is assumed to be initially encoded in a system of coordinates that specifies the desired end position (or the required hand path) in an external reference frame. This representation in extrinsic coordinates is thought to be transformed by the nervous system into an equivalent representation in intrinsic coordinates, which encodes the movements of the limb required to move the hand to that location. It may be noted that this framework is essentially equivalent to the notion of motor programs as transformational rules.

One approach to defining the nature of the coordinate systems and the control strategies used in the planning of arm movements has been to characterize the errors in the final hand positions (Soechting and Flanders 1989a,b). Such errors are of two types: variable errors, representing the dispersion of end points about the mean, and constant errors, representing the deviation of the mean end point from the target (Poulton 1981).

Variable errors can be considered to result from random variability in neural processing or mechanical events. By comparing this variability under different task conditions, it is possible to make inferences about the contributions of different mechanisms, such as visual or internally mediated corrections, to the control of movements (Gordon and Ghez 1987b). In addition, when movements are made in different parts of the workspace, characterizing the spatial patterns of variable errors can provide insights into the coordinate systems in which movements are planned. For example, when the shape or orientation of error distributions remains invariant in a particular coordinate system but not in others, then one can infer that the intended movement is represented in that coordinate system at some stage of the transformation.

Constant errors are generally defined with respect to a single target. However, when constant errors to a range of targets are governed by a general rule (e.g., tendencies of movement end points to cluster to one side of all the targets), they can be considered to be systematic. Systematic errors can reveal simplifications in the planning process, especially those arising because of a failure to fully compensate for the effect of a particular biomechanical or spatial variable. For example, Soechting and Flanders (1989a,b) have described characteristic systematic errors in positioning the hand at remembered locations that may arise from simplifications in the planning of joint angles.

This paper introduces a series of studies in which we analyze both the trajectories and the spatial errors of movements made by human subjects in a planar reaching task (see also Morasso 1981; Georgopoulos et al. 1982; Karst and Hasan 1991). Movements of the hand on a digitizing tablet were directed to visual targets displayed on a computer screen together with a cursor indicating hand position. The cursor was blanked during movement, and vision of the arm was blocked to preclude the visual detection of errors and feedback corrections. This allowed us to probe the processes involved in planning reaching movements, since otherwise it would be difficult to dissociate the effects of visually guided corrections from the effects of the initial plan. A crucial assumption in our approach is that analysis of invariant patterns in spatial errors will provide evidence about which coordinate systems are used to plan movements as well as which parameters of the movement trajectories are explicitly specified by the nervous system.

A primary goal of the experiments described in this paper was to investigate the origin of the coordinate system in which trajectories are planned. Flanders and colleagues (Flanders et al. 1992), on the basis of their analysis of errors made in reaching to remembered targets, have proposed that the direction and extent of hand movement is planned in a polar coordinate system with its origin at the shoulder and that a hand-centered system is used only for terminal corrections. In contrast, the finding by Georgopoulos and colleagues (Georgopoulos et al. 1982; Schwartz et al. 1988) that direction of hand movement is encoded in the firing of populations of cortical neurons is consistent with the idea that movements are represented in a coordinate system that has its origin at the starting position of the hand. In the experiments reported in this paper, we sought, by analysis of variable errors, to distinguish between these possibilities. In succeeding papers in this series, we will address the same general question by analysis of systematic errors.

A second goal was to determine whether the direction and extent of hand movement can be considered as distinct parameters whose values are specified by the motor programs governing reaching movements. In studies of single-joint isometric responses we have shown that direction and extent of force can be planned as separate and independent parameters of the motor program (Favilla et al. 1989, 1990b; Ghez et al. 1990b). In this study, by analysis of the determinants of variable errors, we sought to identify whether analogous parameters of a multijoint movement (e.g., direction and extent of hand movement) might also be separately specified. This question will be addressed further in succeeding papers.

Some of the present results have been published in preliminary form (Gordon and Ghez 1989; Ghez et al. 1990a; Gordon et al. 1992a,b).

Materials and methods

Subjects

Subjects were six neurologically normal adults, four men and two women, with ages ranging from 26 to 42 years. All subjects were right-handed, and, in the experiments described in this paper, they used their right hands. Two of the subjects were authors of this and related studies (J.G. and M.F.G.). The other subjects were recruited from among the personnel in this and other laboratories. All subjects signed an institutionally approved informed consent form. All findings were verified in subjects who were naive to the purpose of the experiments. Not all subjects participated in all experiments. The numbers of subjects participating in each of the different experiments are noted in the results.

Apparatus and general tasks

Subjects were seated facing the screen of a computer (17 cm by 12 cm, Macintosh SE, Apple Computer with a 16 MHz 68020 accelerator, Orion) and moved a hand-held cursor (12 cm long, 6 cm wide, 2 cm high, 70 g) on a digitizing tablet (size 42 cm by 30 cm, resolution 0.0025 cm, model 2200, Numonics). The position of the hand-held cursor on the tablet (x and y coordinates) was sampled by the computer at 200 Hz and displayed on the computer monitor as a screen cursor with the shape of a cross hair. The ratio of cursor movement on the tablet to cursor movement on the screen was approximately 2.4:1. In most of the experiments described in this paper (except for those involving finger-pointing, which are described below) the tablet was positioned at waist level, so that the upper arm was approximately vertical and the elbow was flexed at about 90°. The tablet was directly in front of the subject, so that its center was aligned with the midsagittal plane of the subject.

The subject moved the hand-held cursor on the surface of the tablet; the point on the cursor whose position was monitored corresponded to the tip of the subject's index or middle finger. Moving the cursor to the different targets primarily involved rotations of the shoulder and elbow joints. Wrist movement was not restricted in these experiments; however, subjects used relatively little wrist movement. Vision of the hand and arm was blocked by the combination of a drape attached around the neck and a two-way mirror covering the hand. Subjects moved the cursor to different targets by sliding it along the surface of the tablet. In order to minimize friction, the underside of the hand-held cursor was covered with Teflon and the tablet was covered with a sheet of Lucite. In addition, before each experiment, talcum powder was sprinkled on the surface of the tablet.

In the basic task used in these studies, subjects were required to move the cursor from one point to another on the tablet without visual feedback and without overt corrections. At the start of a trial, two small circles were displayed on the computer screen, a start circle and a target circle. During the initial alignment phase, subjects positioned the screen cursor in the center of the start circle. After a steady initial alignment was achieved, a "go" tone was presented; subjects were then to make a "single, quick, and uncorrected movement" to attempt to reach the target circle. Subjects were told to move "when ready" after the go tone; in other words, there was no requirement to minimize reaction time. The screen cursor was blanked at the time of presentation of the tone, so that visual information could not be used to correct the movement trajectory. At the end of the movement, the path taken by the cursor was displayed to the subject to provide knowledge of results; the path display consisted of a series of small circles every 20 ms. Subjects were encouraged to try to be as accurate as possible and were provided with a running score of their performance (points were awarded according to how close the movement end point was to the center of target). This score was used only to motivate subjects and was not analyzed.

Experimental designs

Targets were presented in a variety of locations on the screen, requiring movements of the hand on the tablet in different directions and of different extents. Directions of movement are described with reference to the starting cursor position (initial position of hand). Zero degrees refers to movements made to the right along a frontal plane (the three o'clock direction). Directions counter-clockwise to this reference direction are described with increasing positive angles. Two sets of targets were used in the experiments described in this paper. The first, referred to as the "8 × 2" target set," required hand movements from a central starting position in the midsagittal plane of the subject on the tablet to targets in eight different directions equally spaced around a circle and with two different extents (3.2 cm and 9.6 cm) for each direction. A second set of targets, the "2 × 5 target set," required hand movements in two directions (30° and 150°) and with five different extents (2.4, 4.8, 9.6, 19.2, and 33.6 cm) for each direction. The starting hand position was in the near right corner of the tablet for the 150° target and in the near left corner for the 30° target. This placement of the starting positions and targets maximized the range of target distances. The largest target distance was close to the maximum range of arm movement for our subjects.

Targets were round and their diameter increased as target distance increased. In early experiments we found that, with equal target diameters, targets requiring a large movement extent were too difficult to hit consistently. This discouraged some subjects. Therefore, an empirical formula was developed to approximately equalize the number of target hits [target radius = 0.64 cm + (target distance/15)]. Pilot experiments were run with two subjects using both constant and variable target diameters; trajectories and error distributions were essentially identical in the two cases.

The order of target presentation was varied in pseudorandom fashion, and no target was presented twice in succession, in order to prevent subjects from progressively refining a stereotyped movement strategy for a specific target. Twenty practice trials with visual feedback of the cursor on the screen during the movement were given at the beginning of each session. Test trials were then presented in blocks of 64 for the 8 × 2 target set and 40 for the 2 × 5 target set. Typically, about 5 s of rest were allowed between trials, and 2–4 min were allowed between blocks. A session with the 8 × 2 target set consisted of 192 test trials, and a session with the 2 × 5 target set consisted of 200 test trials.

Variants of the basic task

Slow movements

In some experiments, in order to assess the effect of movement velocity, subjects were asked to make slow movements. They were told to "move slowly and with a constant speed." In this condition, subjects were allowed to make corrections, and the trial was not terminated until they indicated verbally when they thought they had reached the target.

Finger pointing

In order to determine whether certain features of the results were restricted to multijoint movements involving the shoulder and elbow, several experiments were carried out with the subjects grasping a pen (17 cm long, 1.3 cm in diameter, 25 g) rather than a rectangular cursor. In these experiments, the tablet was oriented vertically rather than horizontally, and the subject used the pen, which was taped to the index finger, as a pointer. Motion of the forearm was mechanically restrained and pointing movements were accomplished entirely by rotations at the wrist joint. When using the pen as a pointer, the tip of the pen was close to, but not actually touching, the tablet. Therefore, in contrast to the experiments with the cursor, there was no external frictional resistance to movement.

In the experiments with the pen, the same set of targets was used as in the 8 x 2 target set, but, because the range of wrist and finger movement was less than for the whole arm, the required target distances were much smaller. This was achieved by changing the tablet-to-screen scaling factor to 0.3:1 instead of the normal 2.4:1 ratio. Thus, a given movement on the tablet appeared much larger on the screen, and the targets, which were displayed on the screen, required smaller distances (0.4 cm and 1.2 cm).

Data analysis

After completion of an experimental session, the x and y coordinates constituting the movement paths of each response were smoothed using a cubic spline (Press et al. 1986). Tangential velocity and acceleration were computed using standard digital differentiation techniques. Automatic routines were then used to mark movement onset, peak velocity, peak acceleration, and movement end point on each trial; the critical points were checked visually and re-marked manually if wrong. Movement onset was defined as the first bin in which tangential velocity exhibited a sustained deflection above zero. Movement end point was defined as the first bin in which zero velocity was achieved, even if only momentarily. Occasionally, a path exhibited a marked change in direction at the end of a movement without actually reaching zero velocity. In these cases the velocity always showed a clear minimum at the point of greatest curvature, and the end point of the movement was marked at that local minimum.

Two critical measures of the movement were computed from these points. Movement extent was defined as the straight-line distance between the starting point and the end point of the movement, irrespective of curves in the movement path. Similarly, movement direction was defined as the direction in degrees of the linear vector from the starting point to the end point.

To characterize the errors made by subjects in various conditions, we used standard measures of constant and variable error. To determine these errors, we first computed the mean end point ($\Sigma x/n$, $\Sigma y/n$) of a set of movements all aimed to the same target. *Constant error* was defined as the distance of the mean end point from the center of the target. *Variable error* was defined as the mean distance of the movement end points from the mean end point.

To further analyze variable error, we used two procedures: (1) principal components analysis (Sokal and Rohlf 1981), to characterize the shape of the distributions of end points for movements aimed to a specific target; and (2) decomposition of the variable errors into two separate errors representing the deviations of the end point from the mean direction and mean distance of the movement. The principal components procedure first determines the axis along which there is the greatest variability; this constitutes the principal or major axis of the distribution. The minor axis is then defined as orthogonal to the principal axis. The lengths of each of these axes were scaled to the respective eigenvalues of the variance-covariance matrix; these are equivalent to the variances along each axis. Then the two axes were used to construct an ellipse that characterized the shape of the distribution (Fig. 1A). We scaled the axes of the ellipses to construct an "equal frequency ellipse", within which, on average 95% of the population of end points should fall (Sokal and Rohlf 1981).

Because the principal components ellipses were not necessarily oriented in the direction of movement, we developed a second method of analyzing variable error to determine the degree to which the distributions were oriented in the direction of hand movement. This involved decomposing each error into two components: "off-axis error", the deviation of the end point from the mean direction of movement, and "on-axis error", the deviation from the mean extent of movement (Fig. 1B). To establish the mean direction of movement, a line was defined passing through

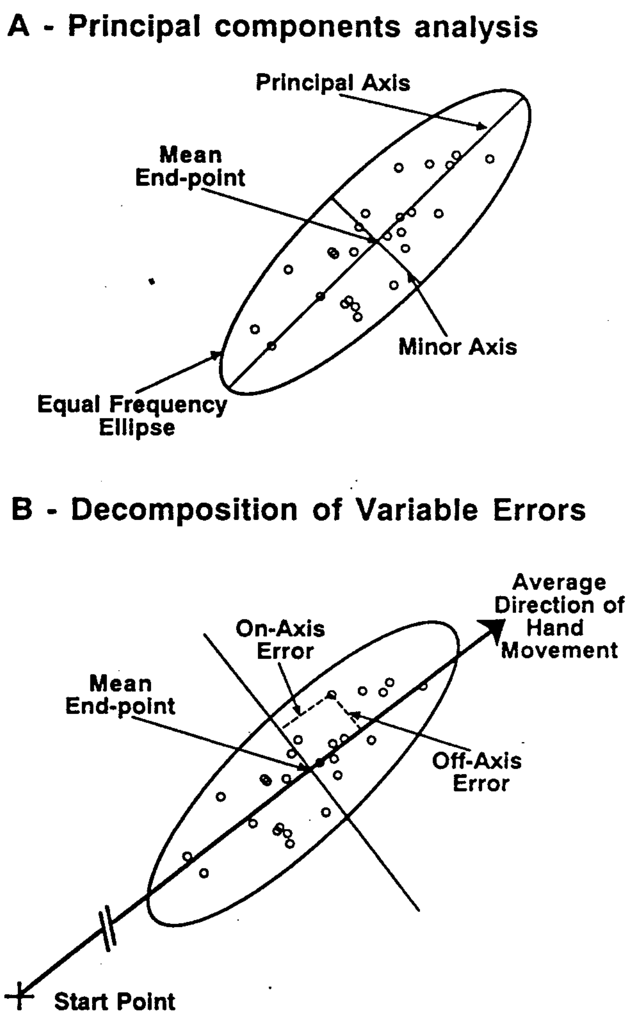


Fig. 1A, B Two methods used to characterize end-point distributions. **A** Principal components analysis is used to determine the axis along which there is maximum dispersion (principal axis). The orthogonal axis is the minor axis. The relative lengths of these two axes are equivalent to the variance along each axis. Here the lengths are scaled and an ellipse is drawn such that 95% of the population of end points should fall within the boundaries of the ellipse (see text). **B** Decomposition of variable errors is used to determine how much directional errors (off-axis errors) and extent errors (on-axis errors) contribute to the overall dispersion of end points the starting point and the mean end point. The perpendicular distance of each end point from this line was defined as its off-axis error. A line orthogonal to this axis passing through the mean end point defined the mean movement extent, and the perpendicular distance of each end point from this line was defined as its on-axis error.

In some cases, to increase the number of trials used to estimate the shape and orientation of end-point distributions, we created normalized end-point distributions, which included responses aimed from the same starting point to targets in different directions. First, an arbitrary direction was chosen, such as 45°. The mean direction for the responses aimed to a single target was then computed. All responses were then rotated by the same amount, using the starting position as the center of rotation, by the difference between the mean direction and the arbitrary direction. This procedure was repeated for responses in different directions, allowing us to then sum together a large set of movements.

Linearity of movement trajectories was computed using an index developed by Atkeson and Hollerbach (1985) and used by others (Georgopoulos and Massey 1988; Jakobson and Goodale 1989; Smit and Van Gisbergen 1990). For each movement, a straight line is drawn between start and end points, and the largest deviation of the trajectory from that line is determined. The linearity index is the ratio between that deviation and the length of the line connecting start and end points. Thus, a semicircular trajectory would have an index of 0.5.

Results

As detailed in Materials and methods, subjects were given two different sets of targets. The first, with targets in eight directions and at two distances (8 × 2) from a single initial position, was used to assess directional effects on error distributions. The other, with targets in two directions and five distances (2 × 5), was used to examine effects of movement extent. It should be emphasized that the overall findings were not essentially different between the two sets of targets.

Hand trajectories are planned in advance

Hand trajectories were similar in form to those described by other investigators (Morasso 1981; Abend et al. 1982; Atkeson and Hollerbach 1985; Georgopoulos and Massey 1988). Figure 2 shows representative hand paths to the 16 different targets, along with the tangential velocities associated with these individual move-

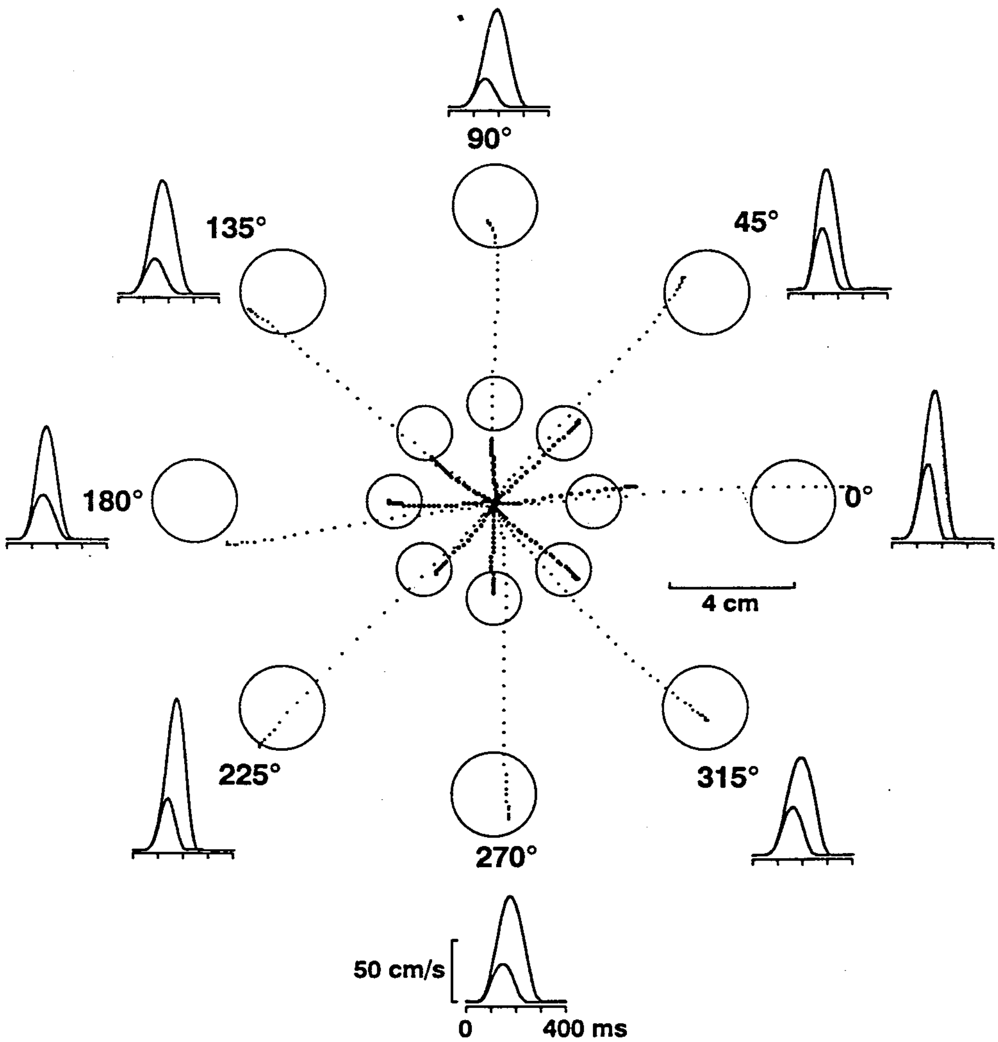
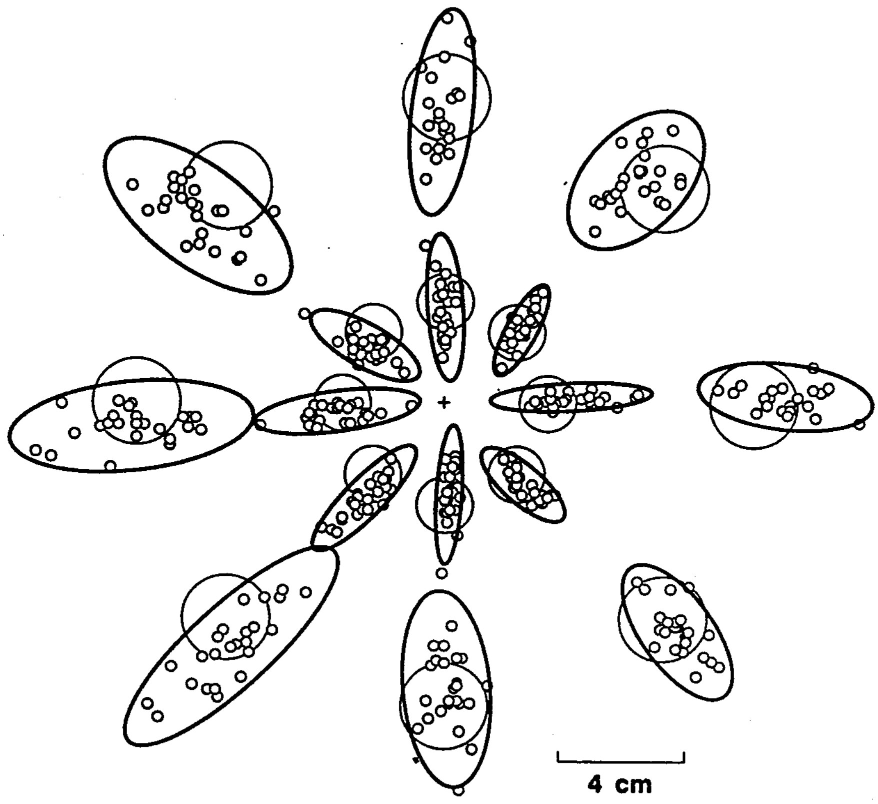


Fig. 2 Hand paths and trajectories for movements to targets in eight directions and two distances by one subject (J.G.). All movements begin from a central starting position. One response to each target was selected randomly. Each hand path is plotted as a *series of dots* representing the position of the hand at 20-ms intervals (every fourth data point). The individual tangential velocity profiles corresponding to the hand paths of the two movements made in the same target direction are displayed next to the far target in that direction. The higher peak velocities in all cases corresponded to movements to the far targets

Fig. 3 End-point distributions for movements to different targets in eight directions and two distances by one subject (J.G.). The subject made 24 movements aimed at each of the 16 targets presented in randomized order. All movements begin from a central starting position (designated by +). End points for individual movements are represented by *small circles*; *large circles* show target locations. The distributions of end points for movements to each target are fitted with surrounding ellipses whose dimensions were computed using principal components analysis



ments. This figure illustrates two important characteristics of movements made by all subjects. First, velocity profiles are single-peaked and bell-shaped, with a single acceleration phase and single deceleration phase. Moreover, peak velocity increases with increasing target distance. In the next paper of this series (Gordon et al. 1994), we will show that peak acceleration also increases with increasing distance. Since these early values of trajectory parameters are correlated with target distance, movement extent can be considered to be programmed in advance (Ghez 1979; Gordon and Ghez 1987a).

Second, movement paths are essentially straight, showing only small amounts of curvature. The mean linearity index (see Materials and methods) across subjects was 0.030 (range 0.025–0.036 in different subjects). These values are somewhat lower (indicating slightly straighter hand paths) than those reported by other investigators in two-dimensional arm movements. Georgopoulos and Massey (1988) reported a mean linearity index of 0.046 across subjects. In a study of vertical movements, Atkeson and Hollerbach (1985) reported a mean index of 0.053 in the direction with the least-curved movements. Most important, although hand paths were not perfectly straight, they were sufficiently so to justify concluding that the direction of movement was largely planned in advance and evident in the early part of the trajectory.

Characteristic shape of end-point distributions

All subjects showed a characteristic pattern of variability in their movement end points. For movements to a given target, end points were clustered in an elliptical pattern (Fig. 3). We quantified this dispersion in two dimensions by using principal components analysis to draw an elliptical contour around each set of end points. The ratio of the minor to the major axes of this ellipse indicates the shape of the end-point distribution. The size of each ellipse is scaled so that on average 95% of each population of end points will fall inside the contour (see Materials and methods). The elliptically shaped clusters of end points had a characteristic orientation: the major axis of the ellipse was oriented along the axis of the mean direction of movement. Thus, variability in movement extent was greater than variability in movement direction.

The elliptical shape and characteristic orientation of end-point dispersions was highly consistent across directions and extents in all subjects. We verified this finding by statistically testing two hypotheses (Sokal and Rohlf 1981): first, that the clusters significantly differed from being circular, and second, that the direction of the principal axis was closer to the mean direction of movement than to a direction perpendicular to it. Of the 64 individual end point clusters (eight directions × two distances × four subjects), 60 were significantly noncircular and of those 59 had principal axes closest to the movement direction ($P < 0.05$).

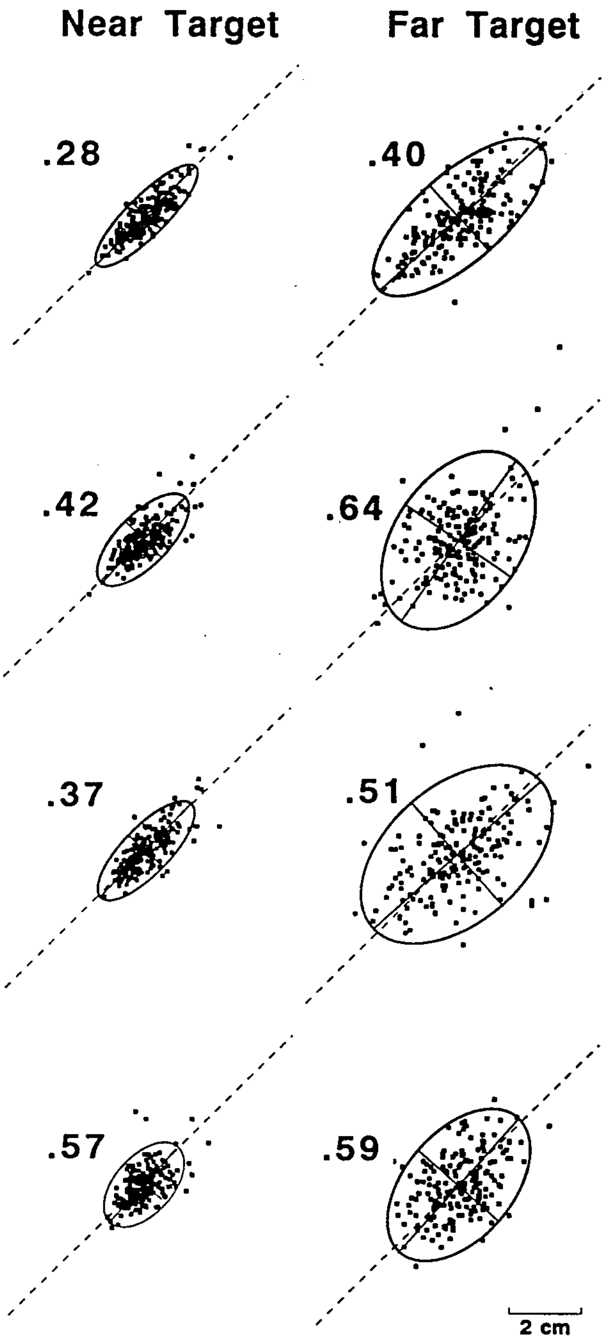


Fig. 4 Normalized end-point distributions for movements to near (*left*) and far (*right*) targets by four subjects (*from top to bottom:* J.G., M.G., C.C., M.F.G.). Normalized distributions are created by rotating the individual distributions to each target as if they had all been aimed in the 45° target direction (see Materials and methods), and then principal component ellipses were computed for the summed distributions. The *number* next to each distribution is the ratio of the major to the minor axis of the ellipse and is thus a measure of its shape; lower numbers indicate more eccentric ellipses. Each distribution consists of 192 end points (24 movements to each of eight targets). (*Dashes lines* mean directions of movements, *solid lines* major and minor axes)

In order to estimate the shape of end-point distributions independent of movement direction, we combined the responses to the different targets for each subject after rotating all responses as if they had been aimed to the same target (see Materials and methods). Figure 4 shows equal frequency ellipses for each of the four subjects tested with the eight-direction target array. In each distribution, a dashed line shows the mean direction of movement, while solid lines show the major and minor axes derived from the principal components analysis.

These normalized dispersions demonstrate that, for all subjects, the principal axis of the distribution is indeed quite close to the movement direction. The overall shape of each cluster is approximately elliptical, with greatest density at the center of the distribution. However, there were quantitative differences in the size and shape of the distributions for different subjects and targets. Some subjects made smaller directional errors than other subjects and therefore had ellipses that were more eccentric. To characterize the overall shape of each distribution, we computed the ratio of minor to major axes for each average ellipse (a circular distribution would have a ratio of 1.00). The mean ratio across all four subjects was 0.48 (range: 0.28–0.64). In order to test whether the size or shape of the error distributions were dependent on the direction of movement, we used ellipse shape (minor-major ratio) and size (area) as dependent variables in separate multifactorial repeated-measure

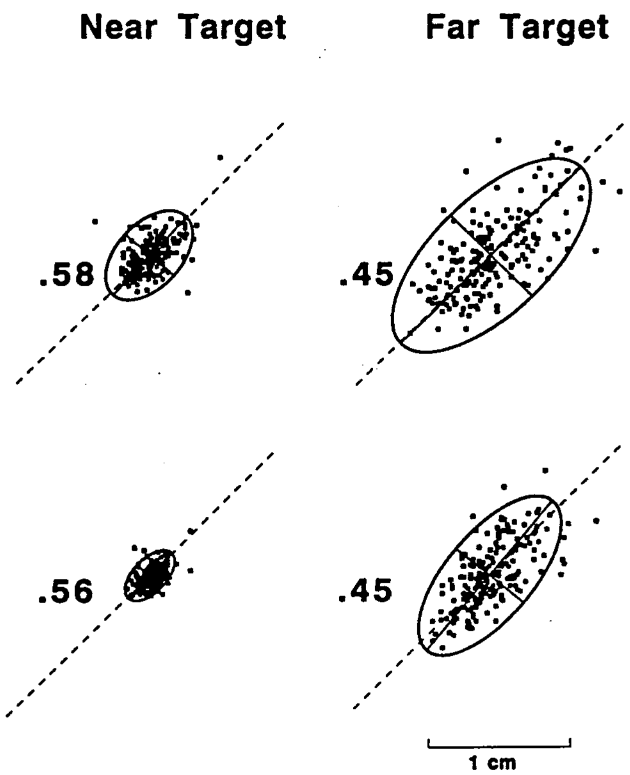


Fig. 5 Average end-point distributions for finger movements (toward near (*left*) and far (*right*) targets by two subjects (top M.F.G., bottom J.G.). Data presented as in Fig. 4

ANOVAs (eight directions × two distances). There were no consistent differences in ellipse shape or size as a function of target direction. There were, however, consistent changes in shape and size with different target distances. Larger target distances were associated with higher ellipse areas ($F_{1,3}=104.0$; $P=0.002$) and higher ratios ($F_{1,3}=157.0$; $P=0.001$). Thus, movements of larger extent involved greater variable errors, but distributions become less eccentric; this is apparent in the average distributions of all four subjects (Fig. 4). This dependence of distribution shape on target distance is analyzed further below using a paradigm with five target distances.

It is possible that the characteristic shape and orientation of end-point distributions is peculiar to the multijoint shoulder and elbow movement made in our standard task situation. Therefore, we also tested two subjects making movements at the wrist to point with a pen toward different targets on a vertically oriented tablet (see Materials and methods). Figure 5 shows the average end-point distributions of each subject. As in the shoulder-elbow configuration, the distributions were approximately elliptical in shape, with the major axis closely aligned with the mean direction of movement. The mean ratio of minor to major axis was 0.50 (range 0.45–0.58). Thus, elliptically shaped distributions with larger variability in extent than in direction appear to be a general feature of aimed two-dimensional movements rather than a specific characteristic only of hand movements produced by rotations at the shoulder and elbow.[1]

Effect of movement extent on the shape of end point-distributions

To analyze the effect of a larger range of target distances on distribution shape and size, we examined responses made by five subjects using the 2 × 5 target set. The end-point distributions of two subjects are shown in Fig. 6A. In these subjects, as in all others, end-point distributions were always elliptical, with the primary axis oriented in approximately the same direction as the mean movement direction. In this set of targets, in order to maximize the range of movement extents, the starting positions were different in the two directions.

In all subjects, the orientation of the end-point distributions to these two targets varied according to the direction of movement, as is shown for the two subjects in Fig. 6A. In contrast, neither the location of the target in the workspace nor its direction with respect to the shoulder was a substantial determinant of the orientation of end-point distributions. This is especially evident when the responses to the two targets in the middle of the workspace are compared (see solid arrows in Fig. 6A). Even though these two targets are close to each other in space, and have similar directions relative to the shoulder, the distributions are very differently oriented, depending on the starting position of the hand. These results confirm that the orientation of the end-point distribution is principally dependent on its location relative to the starting position of the hand.

Figure 6A shows that the end-point distributions increased in size with increasing target distance, but this increase in size was accompanied by a progressive change in shape. End-point distributions were relatively narrow (eccentric) for near targets and became proportionally wider as target distance increased. Thus the set of five distributions in each target direction form a roughly fan-shaped pattern.

Since the ellipses were always oriented with their principal axis aligned with the direction of movement, the length of the minor axis of each ellipse is determined by the size of the variable directional errors. The fan-shaped pattern of the combined set of distributions in each direction implies that the variable directional errors remained approximately constant and independent of movement extent. On the other hand, the length of the principal axis of each ellipse, which is primarily determined by variability in movement extent, increased as a function of target distance, but with a more complex relationship to target distance.

To analyze this effect quantitatively, we plotted the relative variable errors along the axis of movement (on-axis error) and orthogonal to it (off-axis error) as a function of the mean movement extent (Fig. 6B). The on-axis error represents the spatial variability caused by errors in movement extent; the off-axis error represents the spatial variability caused by variable directional errors. Each error is expressed as a percentage of the mean movement extent. Note that in these plots mean movement extent is plotted on a log scale. Relative off-axis error remained essentially constant with increases in movement extent (in some subjects, it decreased by a small amount). Thus, the widths of the different distributions were an approximately constant proportion of movement extent, confirming that directional variability in angular terms remained invariant and independent of movement extent.

Relative on-axis error, on the other hand, decreased linearly as a function of the log of movement extent. Thus, although extent variability increased with increasing movement extent, this increase was less than proportional. The logarithmic relationship between relative on-axis error and movement extent indicates that increasing movement extent leads to progressively less increase in extent variability. At the same time, off-axis variability increases in proportion to movement extent. This dual trend is clear in Fig. 6A, in which the distribu-

[1] It should be noted that the change in eccentricity with target distance was not present in the two subjects tested making finger movements. This difference between finger movements and arm movements may reflect biomechanical factors or differences in the way the movements are planned. Alternatively, there may indeed be systematic changes in shape that are not seen in these movements because the movements were rather small and there was a limited range of distances. In any case, because we have not systematically analyzed finger movements using a large range of target distances, we cannot offer an explanation for this difference

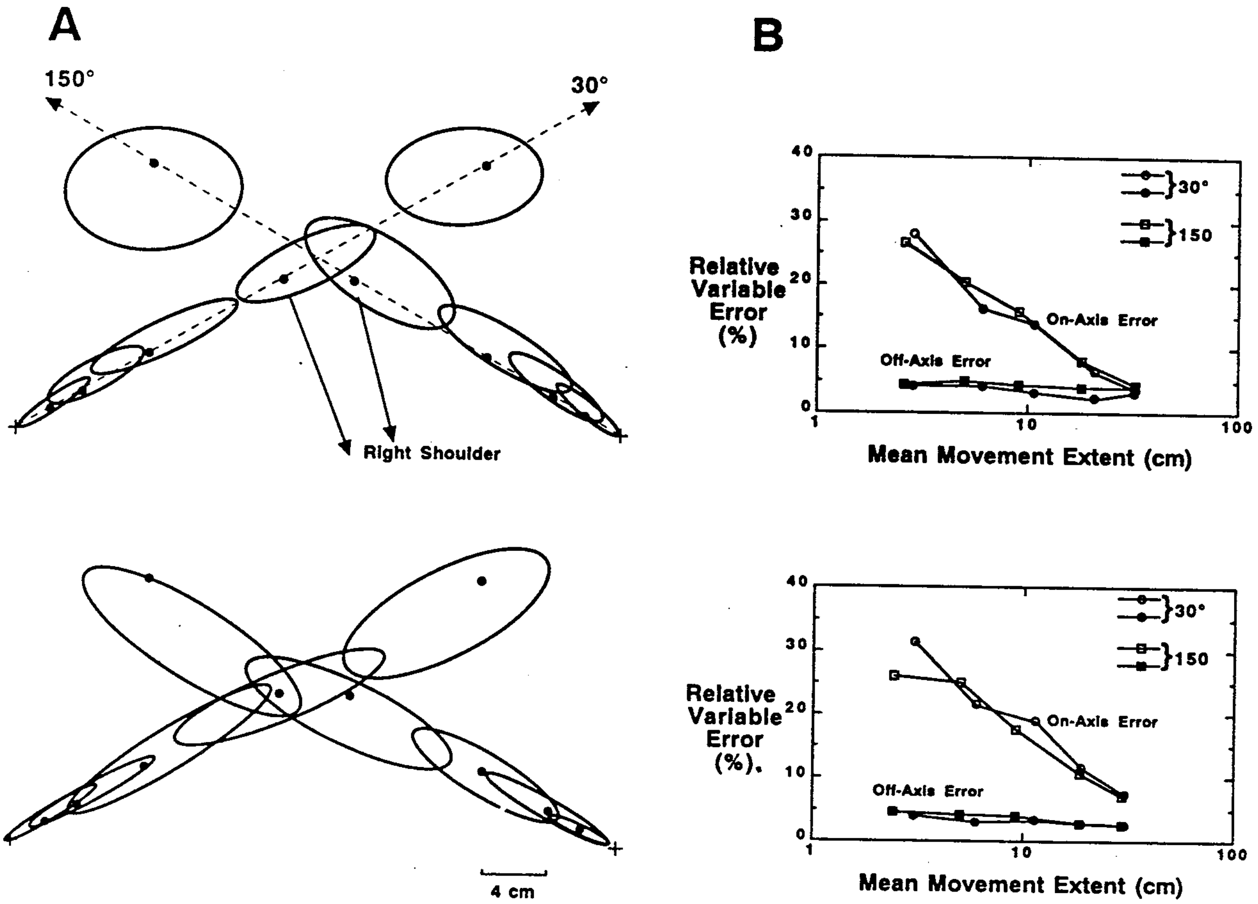


Fig. 6 End-point distributions (A) and relative variable errors (B) for movements to targets in two directions and five distances for each of two subjects (top M.F., bottom O.P.). Each subject made 20 movements to each target in randomized order. **A** End-point distributions are depicted by the principal components ellipses computed for each distribution. *Small filled circles* show target locations; *dashed arrows* show target directions (30° and 150°); *solid arrows* point toward location of subject's right shoulder. **B** Variable errors were decomposed into two components, on-axis error, or variability due to extent errors, and off-axis error, or variability due to directional errors. These errors were then divided by the mean movement extent to yield a relative variable error in each dimension. The means of these are plotted as a function of mean extent separately for movements to the 30° and 150° targets. Note that mean extent is plotted on the *horizontal axis* with a logarithmic scale

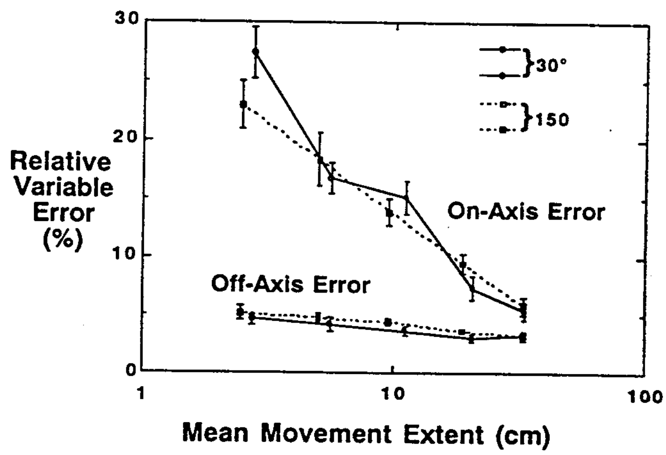


Fig. 7 Relative variable errors as a function of mean movement extent averaged across five subjects (J.G., M.F.G., M.F., C.C., O.P.). The plot has the same format as Fig. 6B. The *error bars* on each data point indicate standard errors of the means

tions become more circular in shape as extent increases. These relationships between relative variable errors and movement extent were highly consistent across subjects (Fig. 7).

In order to determine whether the characteristic elliptical shape of error distributions was dependent on subjects making relatively fast movements, we tested three subjects with the same set of targets, but asked them to make their movements "slowly and with a constant velocity" (see Materials and methods). The error distributions for one subject are shown in Fig. 8A; mean variable errors across all three subjects are plotted in Fig. 8B. The sizes and shapes of the distributions in the slow condition were almost identical to those in the fast condition, indicating that speed of movement does not play a major role in determining the variable error. The one minor difference between the two conditions was that, for small target distances, distributions were somewhat less eccentric in shape (compare Fig. 8A with Fig. 6A). Mean variable errors, however, did not differ

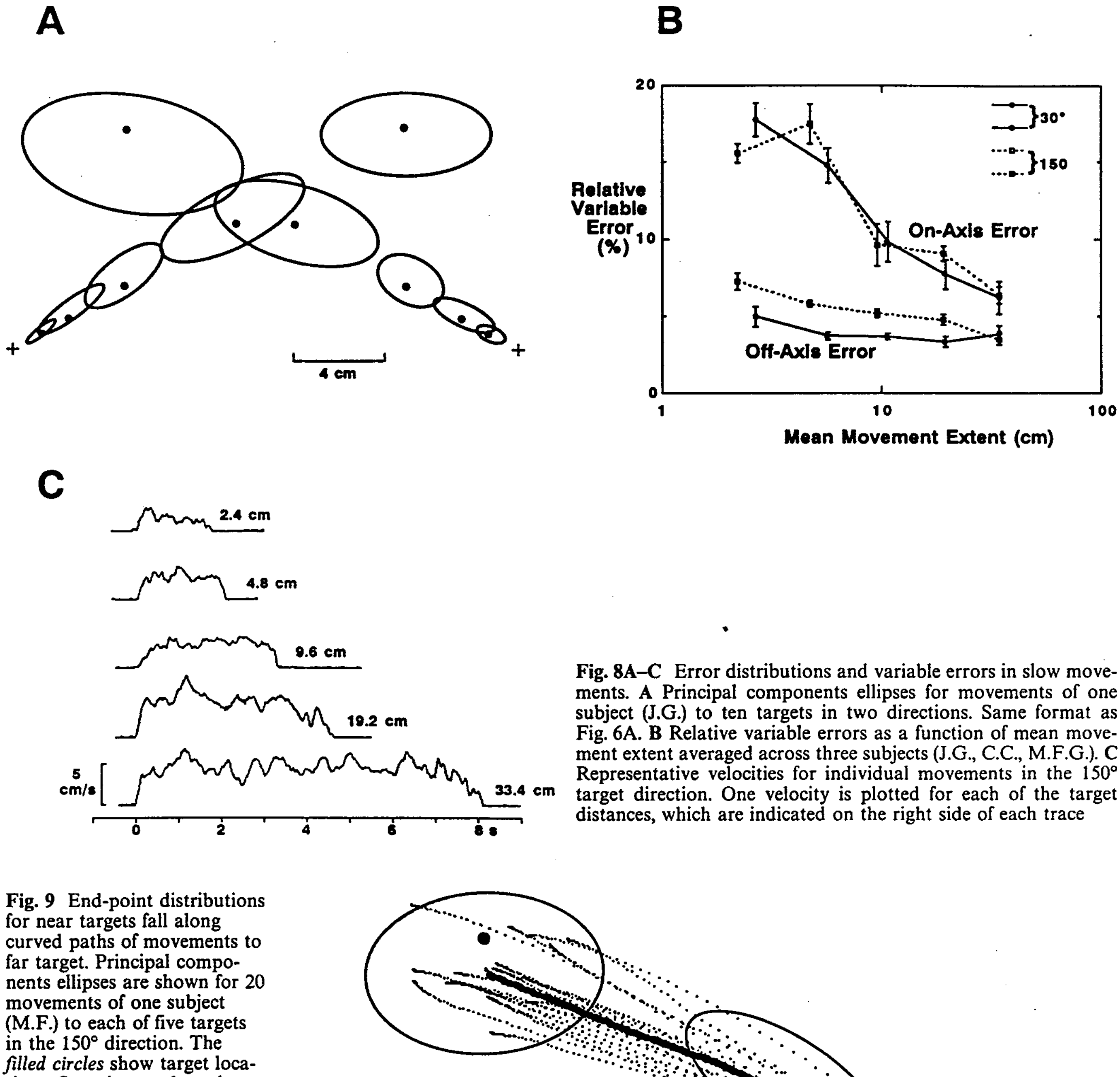


Fig. 8A–C Error distributions and variable errors in slow movements. **A** Principal components ellipses for movements of one subject (J.G.) to ten targets in two directions. Same format as Fig. 6A. **B** Relative variable errors as a function of mean movement extent averaged across three subjects (J.G., C.C., M.F.G.). **C** Representative velocities for individual movements in the 150° target direction. One velocity is plotted for each of the target distances, which are indicated on the right side of each trace

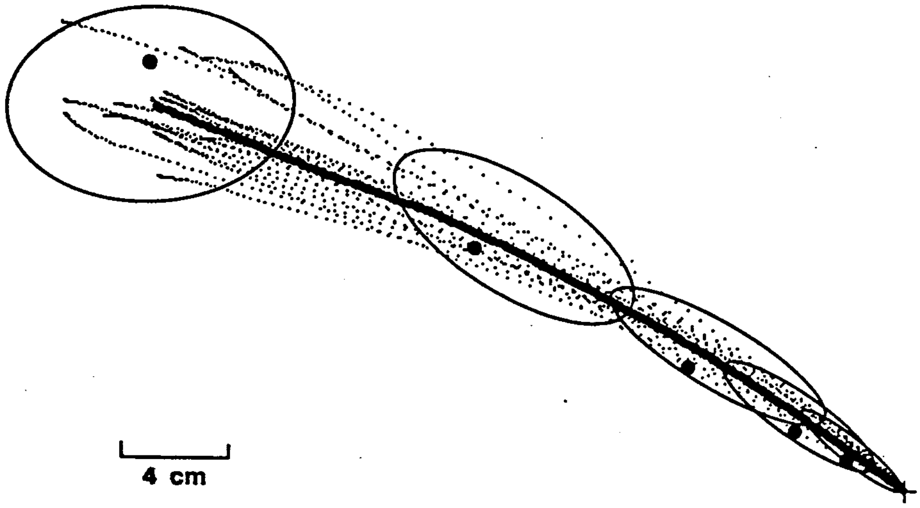


Fig. 9 End-point distributions for near targets fall along curved paths of movements to far target. Principal components ellipses are shown for 20 movements of one subject (M.F.) to each of five targets in the 150° direction. The *filled circles* show target locations. Superimposed on these ellipses are the movement paths to the farthest target (target distance 33.6 cm). Paths are plotted as described for Fig. 2. The *thick line* shows the average path, computed after normalizing all 20 paths in time

significantly between slow and fast conditions in the three subjects in whom we made this comparison.

There was considerable variability in movement times (MT) between subjects, but the following means give an idea of the difference between the slow and fast movements. For the smallest target distance, mean MT was 225 ms in the fast condition and 1073 ms in the slow condition. For the largest distance, mean MT was 483 ms in the fast condition and 7674 ms in the slow condition. Figure 8C shows typical velocity profiles for the slow movements (compare with Fig. 2). In contrast to the fast movements, the slow movements were controlled primarily by modulating MT, while peak velocity was kept relatively constant. Despite this difference in control strategies, the end-point distributions were remarkably similar between the two conditions.

A subtle but consistent trend emerged in the positions of the error distributions in the 2 × 5 target set. All subjects made, in varying degrees, systematic errors (deviations of the center of each ellipse from the center of the corresponding target) for the close targets that matched subtle curves in their responses to far targets. For example, Fig. 9 shows for one subject a set of error distributions in the 150° direction, along with the paths of movements to the farthest target. In this case, the centers of the distributions follow the same curved path as the average movement path (thick solid line). Not all subjects showed the same direction and degree of curvature for movements to the far target, but, in all subjects, the centers of the distributions of end points for nearer targets closely followed the curvature of the path to the farthest target. This finding suggests that subjects used a similar interjoint coordination pattern for movements of different distances, even though it led to consistent directional errors for movements to certain targets.

Discussion

There were two major findings in this study. First, the spatial distributions of movement end points in two-dimensional reaching movements were shaped approximately as ellipses whose orientations depended on the direction of movement: the major or principal axis of each distribution was aligned with the average direction of hand movement. As will be discussed below, this finding provides support for the idea that movements are planned in a coordinate system that has its origin at the initial position of the hand. Second, variable errors in extent of hand movement increased nonlinearly with target distance while variable errors in direction remained essentially constant. This finding suggests that direction and extent of hand movement are planned separately as independent parameters of the movement program. We will discuss each of these two major findings in turn. Then we will consider reasons why we believe that these findings provide evidence about the planning of movements and not merely about biomechanical factors that influence variability. Finally, we will present a working hypothesis regarding how direction and extent of hand movement may be planned.

Planning in a hand-centered coordinate system

Previous investigators (Georgopoulos et al. 1981; Morasso 1981; Abend et al. 1982) have argued that the straightness of the paths in most reaching movements could only occur if the trajectory of the hand were planned explicitly. This would not occur readily if planning were to take place in other coordinate systems (i.e., in joint space). Moreover, invariances in the velocity profiles of movement trajectories indicate that the tangential velocities of the hand path rather than of the joints are probably being optimized (Flash and Hogan 1985; Kaminski and Gentile 1989). Our finding that the direction of hand movement is the primary determinant of the orientation of elliptical error distributions provides further evidence that planning and execution of reaching movements involves specification of the hand trajectory.

In addition to providing evidence for planning in hand space, the characteristic shape and orientation of end-point distributions suggest that reaching movements are planned in a hand-centered coordinate system, that is, with its origin at the initial position of the hand.[2] We envisage this to apply to an early phase of planning in which the intended hand movement is still represented in an external reference system and not yet in an intrinsic space whose dimensions are related to joint angles or muscles. Soechting and colleagues, in studies of three-dimensional movements to remembered targets, found evidence for invariances in the distributions of systematic errors when these were plotted in a shoulder-centered coordinate system (Soechting and Flanders 1989a,b; Soechting et al. 1989; Flanders and Soechting 1990; Tillery et al. 1991). They proposed that the coordinates of the desired end point of the hand are converted to coordinates that specify its distance and direction from the shoulder. However, in succeeding papers we will show that, in our task, systematic errors are also best described in a hand-centered coordinate system (Gordon et al. 1992a). The reason for the differences between our results and those of Soechting and colleagues is not yet clear, but there were important differences between our task conditions and theirs. Different classes of errors may in fact exist, and different task conditions may simply make one class more prominent than another.

The idea that reaching movements are represented in hand-centered coordinates is consistent with the growing body of evidence that neurons in motor cortex encode reaching movements in a coordinate system that is hand-centered. In particular, single-unit recordings in primate motor cortex indicate a close correspondence between the direction of the neuronal population vectors and the direction of the actual movement, with both determined from the starting position of the hand

[2] When we use the term "hand-centered" coordinate system and contrast it to a "shoulder-centered" coordinate system, we are comparing two possible vectorial representations of an intended movement in *extrinsic space*. In both systems, the hand or target position is represented as a direction and distance in one or another of two alternative egocentric reference systems. One has its origin at the hand, the other at the shoulder. The term "shoulder-centered" might also be used to refer to a joint-based coordinate system, that is, a representation of the movement in *intrinsic space*. In this paper, the term does not imply an intrinsic coordinate system

(Georgopoulos et al. 1982; Schwartz et al. 1988). It is unlikely that a similar correspondence would be found if the population vectors and hand directions were computed in shoulder-centered coordinates. This is because the transformation between two polar coordinate systems with different origins is complex and not linear (Soechting and Flanders 1989b). Thus, these studies suggest that the direction of hand movement is a fundamental variable for the neural control of reaching movements.

Caminiti and colleagues (Caminiti et al. 1990; 1991) have shown that the preferred directions of individual neurons in premotor and motor cortex rotate as the initial shoulder angle rotates. Population vectors, on the other hand, are invariant with respect to target direction in external space. Nevertheless, the preferred directions of cortical neurons as well as the directions of the population vectors make sense only if they are plotted with respect to the direction of hand movement in a coordinate system that has its origin at the initial position of the hand, not at the shoulder. If the cells' firing frequencies were plotted in a shoulder-centered coordinate system, that is, where direction of movement is plotted as a vector with its origin at the shoulder (Soechting and Flanders 1989a), some cells would show both maximal and minimal firing frequencies for movements in the same direction. The results of these studies therefore suggest that the firing of individual neurons depends in part on the angle of the shoulder, and presumably on other aspects of the current configuration of the arm (Burnod et al. 1992). However, the results do not indicate that the firing of cortical cells encodes movement in a shoulder-centered coordinate system.

Separate planning of hand direction and extent

The finding of elliptical end-point distributions oriented in the direction of movement might suggest that specification of the extent of hand movement is subject to greater error than specification of direction. This conclusion should, however, be qualified, since the eccentricity of end-point distributions is not invariant. For targets requiring relatively large movements, the distributions approach a circular shape. Moreover, as we will show in later papers in this series, subjects do make significant errors in direction that are often quite large, but these errors are systematic (see for example Fig. 9) and depend on the initial position of the hand in the workspace (Ghilardi et al. 1991; Gordon et al. 1992a).

The more significant observation appears to be that variable errors in direction and extent of hand movement are differentially affected by target distance. When subjects were presented with a large range of target distances, the variability arising from directional errors (off-axis errors) increased in proportion to movement extent. This is equivalent to stating that the variable angular error in movement direction was relatively constant and independent of movement extent. In our experiments, the variability arising from extent errors (on-axis errors) increased with increasing movement extent, but less than proportionally. Similar relationships of extent variability to target distance have been described by other investigators (Schmidt et al. 1979; Newell et al. 1982; Gordon and Ghez 1987a; Meyer et al. 1990).

The differential dependence of direction and extent variability on target distance implies that direction and extent of hand movement are planned separately by the nervous system. Separate planning of direction and extent is consistent with our previous findings that, in single-joint isometric responses, the specification of movement direction and movement extent can occur concurrently in time and relatively independently of each other (Favilla et al. 1989, 1990b; Ghez et al. 1990b). Similar data were later obtained in a task involving control of two-dimensional force at the wrist where direction was a continuous rather than a discrete variable (Bermejo et al. 1989) and in a reaching task analogous to the one used here (Favilla et al. 1990a). These studies, along with those of others (Rosenbaum 1980; Bonnet et al. 1982; Bock and Arnold 1992), provide converging evidence for parametric specification of direction and extent in both single-joint and multijoint movements.

Variable errors – planning or biomechanics?

In the current study, we have shown that the two-dimensional spatial variability of end points shows an invariant pattern only if it is decomposed into separate coordinates reflecting the direction and distance of movement with respect to the initial hand position. Thus far, we have argued that the observed patterns reflect an independence in the planning of movement direction and extent. It is also possible, however, that the patterns of variable errors result primarily from biomechanical factors that differentially affect movement direction and extent. If so, then our results do not provide evidence about the planning process but merely about factors that affect the execution of the movements. For example, an intuitive explanation for these findings might be that, if the muscle contractions that brake the movement were incorrectly timed or scaled, this would produce errors in movement extent but not in direction. This explanation, however, is based on the fallacy that there is an inherent tendency for the hand to move in a straight line, as if it were a point mass. In fact, as Hogan (1985) has shown, because the hand moves as part of a multi-segmented limb, the inertia at the hand is anisotropic, a property whose implications will be explored in the next paper of this series. This means that, in general, if the muscular contractions controlling the movement of the hand through space were to cease suddenly, the hand would not continue to move in the same direction, but would veer to one direction or the other. Furthermore, the muscular contractions that brake the hand do not act at the hand but at the various joints. Therefore, unless the errors in the contractions of different muscles maintain the same ratio to each other as in correctly applied braking contractions, improper timing or scaling of the contractions would also produce curvature in the movement. Thus, biomechanical factors alone cannot explain the tendency for variable error distributions to be aligned with the direction of movement. Indeed, the very fact that the hand moves *as if* it were an inertial point mass provides evidence for the action of neural mechanisms that explicitly control the trajectory of the hand.

In addition to this logical argument, three aspects of our results suggest that the characteristic shape and orientation of end-point distributions reflect trajectory planning and not simply biomechanical factors. First, elliptically shaped distributions oriented in the direction of movement were not only present in arm movements but also in pointing movements made with the finger. Thus, the finding appears to be general and may be characteristic of all movements in which a distal point on the limb is aimed to a target.

Second, the orientation of a specific end-point distribution was not dependent on its location in the workspace, since two distributions in the same area of the workspace could have very different orientations (Fig. 6A), depending on the starting position of the hand. Soechting and Flanders (1989b) have suggested the desired hand path is transformed into a hand path in a shoulder-centered coordinate system. If the hand path is specified in this different coordinate system, errors should then have a different distribution. For example, movements made toward the shoulder might have decreased variability, while those away from the shoulder would have increased variability. There is no unique dependence of end-point error on shoulder position in our data, indicating that if such a transformation does take place it has a negligible effect on the variable errors. A dependence of variability on absolute hand location might also be expected if movements were planned as shifts in equilibrium points, since the static stiffness of the hand is anisotropic and generally oriented toward the shoulder. One would expect therefore, to see greater variability in directions in which stiffness was least (Shadmehr et al. 1993). It is unlikely, however, that static stiffness fields can account for the observed elliptical end-point distributions in a simple way, since the shapes of such fields are workspace dependent (Mussa-Ivaldi et al. 1985; Flash and Mussa-Ivaldi 1990) while the orientations of the error distributions are not.

Third, and perhaps most important, the shape and orientation of end-point distributions did not vary with instruction-dependent changes in movement speed. This indicates that the patterns of variable spatial errors do not simply reflect biomechanical factors, but are primarily dependent on processes responsible for planning the direction and extent of the movement. Furthermore, changes in movement speed had little effect on the size of the distributions (see also Schmidt et al. 1979). This suggests that caution should be exercised before assuming that slower movements are necessarily more accurate. The most likely explanation for the similarity in the errors of slow and fast movements is that, because visually based corrections were impossible, errors depended in both cases primarily on the accuracy of the specification process itself.

These features of our results suggest that the characteristic alignment of end-point distributions results from the independence of hand direction and extent in planning the movements. If the patterns of variable errors demonstrated in this study were the only factor pointing to independent planning of direction and extent, we might be more cautious about this conclusion. However, there is considerable evidence from behavioral studies that direction and extent represent separate variables in the planning process (Rosenbaum 1980; Bonnet et al. 1982; Favilla et al. 1989; Bock and Arnold 1992). Moreover, in the following paper (Gordon et al. 1994) and succeeding papers of this series we will present additional evidence from analysis of systematic errors that direction and extent of hand movement are planned independently.

Our results do not rule out the possibility that the hand path is initially planned in hand-centered coordinates but that this representation of the movement is transformed into another coordinate system. They simply suggest that the independent processes involved in planning direction and extent of hand movement are the principal sources of variable error. We take this to indicate that planning in a hand-centered coordinate system is not simply a very early stage of planning, but that some degree of separation of these parameters is present through much of the overall process of planning and control. Nevertheless, the degree to which these parameters remain separately controlled during the unfolding of the movement plan is very much an open issue.

Planning movement direction and extent – implications

Our working hypothesis is that the nervous system plans reaching movements by separately specifying the direction and extent of the hand path. Direction of hand movement might be represented as a specific kinematic plan for varying the angles of the joints of the arm relative to each other; for small movements such a strategy produces relatively straight paths (Mel 1991). Alternatively, direction might be planned by transforming a desired direction of movement directly into a specific pattern of coordination, or synergy, among different muscles (Burnod et al. 1992). In this case, a specific synergy would establish the relative intensities in different muscles appropriate for moving the hand in a given direction. Extent of movement could then be varied by applying a general scaling factor to all muscles. There is some evidence from neurophysiological studies that the overall level of activation of a population of cortical neurons is related to the planned force or extent of movement, although the findings here are not as clear as they are for the representation of movement direction (see Georgopoulos 1991 for a review).

This hypothesis also implies that a common strategy for planning direction is used for all target distances, both small and large. Our finding that systematic endpoint errors reflect curves in the trajectories of movements to distant targets (Fig. 9) provides evidence for such a strategy. Instead of taking the curvature into account for each target distance, the nervous system uses a single synergy, or coordination pattern, for all movements in a given direction, even though this entails significant systematic biases for some target distances.

This example of a systematic error in direction raises an important issue. Independent specification of hand direction and extent must lead to some degree of error, because direction and extent of hand movement are not mechanically independent of each other. Therefore, if our hypothesis is correct, we should see specific errors that vary systematically with direction. In succeeding papers of this series we will provide evidence that such systematic errors do indeed occur.

The design of the experiments presented here does not allow us to analyze why extent variability should generally be greater than directional variability. One possibility could be that this reflects the specific ranges of targets that we examined. Thus, directional variability might be increased relative to extent variability if there were many different target directions and only one distance. Another possibility is that accuracy in extent is, to a greater degree than direction, dependent on the precise time course with which agonist and antagonist motor neurons are activated. In contrast, accurate directional specification reflects primarily a spatial pattern of muscle activation over the entire duration of the movement.

Finally, stimulus-response "mappings" for direction may be represented in a more stable fashion than those for extent. Indeed, we have repeatedly found that subjects adapt within a very few trials to changes in display gain, which affect the scaling of movement extent to displayed target distance (unpublished observations). It is always much more difficult for subjects to adapt to changes in the directional relation between hand movement and displayed movement on the screen. An inherently greater plasticity of extent control may be an advantage in daily life, since we must often adapt central commands to variations in contractile force of muscles (e.g., with fatigue) or in the relation between force and movement (e.g., with variant loads). It is likely that such rescaling of motor commands depends on processing of various sensory inputs as well as models derived from previous experience. Therefore, the underlying mechanisms may be distributed among multiple neural systems, and the relationship of neural firing in any one system to movement distance might be variable from trial to trial. Thus, specification of extent might depend on an intrinsically more variable process than specification of direction. This might also explain why the neural correlates of movement extent have been more elusive than the neural correlates of direction (e.g., Riehle and Requin 1989).

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