Sensorimotor Representations for Pointing to Targets in Three-Dimensional Space

JOHN F. SOECHTING AND MARTHA FLANDERS Department of Physiology, University of Minnesota, Minneapolis, Minnesota 55455

SUMMARY AND CONCLUSIONS

1. The accuracy with which subjects pointed to targets in extrapersonal space was assessed under a variety of experimental conditions.

2. When subjects pointed in the dark to remembered target locations, they made substantial errors. Errors in distance, measured from the shoulder to the target, were sometimes as much as 15 cm. Errors in direction, also measured from the shoulder, were smaller.

3. An analysis of the information transmitted by the location of the subject's finger about the location of the target showed that the information about the target's distance was consistently lower than the information about its direction.

4. The errors in distance persisted when subjects had their arm in view and pointed in the light to remembered target locations.

5. The errors were much smaller when subjects used a pointer to point to the target or when they were asked to reproduce the position of their finger after it had been passively moved to the target.

6. From these findings we conclude that subjects have a reasonably accurate visual representation of target location and are able to effectively use kinesthetically derived information about target location. We therefore suggest that errors in pointing result from errors in the sensorimotor transformation from the visual representation of the target location to the kinematic representation of the arm movement.

INTRODUCTION

Errors in the execution of a motor task can lend insight into the principles according to which movement is organized and controlled. This idea has been common since the work of Woodworth (1899). For example, Fitts (1947) used this approach when he analyzed the relationships between errors in movements and the speed and distance of these movements. From this analysis he determined that the speed of a movement affects its accuracy, and he derived an hypothesis regarding the maximum rate at which information can be transmitted in a sensorimotor system (Meyer et al. 1982; Schmidt et al. 1979).

Movement errors can also be used to reveal the steps in the process of transforming sensory information into motor commands. For an arm movement directed to a target in extrapersonal space, the information about target location is normally provided by visual input, whereas information about the initial position of the arm and about deviations from the intended trajectory can be provided by kinesthetic input. In some cases, information about target location may also be kinesthetically derived (Flanders and Cordo 1989). To combine information from different sensory modalities, the information must be related to a common frame of reference (Knudsen et al. 1987; Konishi 1986; Simpson and Graf 1985; Soechting 1989). The transformation into a common frame of reference may be one step in the process which ultimately produces the patterns of muscle activation that are appropriate for attaining the target.

In this series of papers, we use the errors in the end-point of targeted arm movements to try to understand the nature of the sensorimotor transformations that are involved in this task. In this paper we will show that human subjects produce large errors when pointing to remembered target locations. By studying the errors in pointing under various experimental conditions, we will try to determine where in the sensorimotor process these errors occurred. In the paper which follows (Soechting and Flanders 1989), we will examine the hypothesis that these errors occurred because the nervous system implements an approximation in the transformation of visual information about target location to a frame of reference in common with that used to represent the location of the hand in space.

Some preliminary results of this work have been published (Soechting and Terzuolo 1989).

METHODS

Motor tasks

Errors in pointing movements to a target were assessed in five different experimental conditions. In each condition we were concerned only with the error in the final position, and we did not record the movement of the arm toward the target. Each of the experimental conditions was designed to provide the subject with different kinds and amounts of sensory information or to require the subject to produce a different type of movement to attain the target. Before describing each of the experimental conditions in detail, we will describe those aspects which were common to all experiments.

Subjects stood erect and were presented with targets which encompassed most of the possible range of arm motions: from $\sim 45^{\circ}$ medially to 45° laterally to the subject's sagittal plane, as well as from 45° above or below the shoulder and at distances ranging from ~ 20 to 70 cm from the shoulder. The subjects were asked to maintain a stable posture of the trunk and to restrict their movements to the right arm. Therefore, we did not study movements which normally involve rotation of the trunk (for example movements to targets located at the side or to the back of the subject). No restrictions were imposed on head or eye move-

ments. We were interested in studying movements to targets located in extrapersonal space rather than those which could be referred to a point on the body. Therefore, all targets were located at least 10 cm away from the body surface. Target location was varied at random throughout the region described above; each experiment consisted of at least 60 and more usually 100 different target locations. For purpose of reference, we provided an indication of the anterior direction by means of three LEDs which were spaced vertically and located 3 m in front of the subject. Interviews at the end of each experiment indicated that none of the subjects made conscious use of this landmark.

There were five experimental conditions.

VIRTUAL TARGET (DARK). Subjects were presented with a target which was the tip (~ 1 cm) of a pencil-sized stylus held by the experimenter. They were asked to remember the location of this target. The target was removed, the room lights were turned off and the subjects then pointed to the remembered location of the target. Movements were initiated from a common starting position (the hand waist-high at the subject's side), the subject holding a stylus similar to the one used to indicate target location. The location of the tip of the subject's stylus was recorded after he or she had verbally signaled the end of the movement. The interval between the target presentation and the termination of the movement was typically 3–5 s.

In this first experimental condition, subjects had no visual information about target or hand location during the movement, but could potentially avail themselves of kinesthetic information about arm position.

VIRTUAL TARGET (LIGHT). This second experimental condition was similar to the preceding one except that the room lights were not extinguished. Thus visual information as well as kinesthetic information about the location of the hand was available to the subjects at all times.

VIRTUAL TARGET (POINTER). In this third series of experiments, subjects were again presented with targets as in the first and second experimental conditions. However, in this condition they were given a pointer ~ 1 m in length and asked to point to the remembered target location with the tip of the pointer. The room lights remained on during these experiments. This experimental condition was designed to change the characteristics of the goal-directed arm movements. In the first and second condition, these movements involved primarily the shoulder and elbow, whereas in this third condition, the motion involved primarily the wrist.

REPRODUCE PASSIVE MOVEMENT. The subject's arm was moved passively to the target location and was held there momentarily. The arm was then returned passively to the original position. We asked the subject to point to the remembered position of the target (i.e., to reproduce the position of his or her hand) after the room lights had been extinguished. Thus, in contrast to the first three experimental conditions, subjects had available kinesthetic as well as visual information about target location.

REPRODUCE ACTIVE MOVEMENT. In this final series of experiments, subjects were asked to point to a target which remained in place. After they had moved their arm back to the side, the target was removed, the room lights were turned off, and they pointed again to the remembered target location. The information available to the subjects in this experimental condition was similar to that in the fourth condition with one addition: in principle this task could be accomplished in the absence of any sensory information simply by reproducing the motor commands used to effect the original, accurate movement.

Four different subjects participated in each of the five series of experiments.

Recording system

The location of the target and of the "finger" (the stylus grasped by the subject) was measured ultrasonically (GP8-3D, Science Accessories). The source for the ultrasound was provided by a spark gap at the tip of each stylus. Other styli were attached to the limb at the shoulder, elbow, and wrist joints. Thus the location of the target and the finger and the orientation of the limb segments (arm and forearm) could be measured with a resolution of 0.1 mm anywhere within a volume which was a cube 1.5 m to a side. Microphones located at the four corners of one side of the cube picked up the ultrasonic signal and the location of the tips of each of the styli was calculated trigonometrically after conversion of signal transmission time to distance.

Coordinate systems

Three parameters are required to define the location of a point in space and a variety of coordinate systems could be used. We used several different coordinate systems to characterize the error in pointing.

CARTESIAN. The location of the target is given by its mediolateral (x), anteroposterior (y), and vertical (z) extent. We have taken the lateral, anterior, and upward directions to be positive.

CYLINDRICAL. The relevant parameters here are horizontal radial distance (r), azimuth (x), and vertical (z). The conversion from Cartesian to cylindrical coordinates is given by

$$r = \sqrt{(x^2 + y^2)}$$

$$\chi = \tan^{-1} x/y \qquad (1)$$

SPHERICAL. The parameters in this coordinate system are radial distance (*R*), azimuth (χ), and elevation (ψ).

$$R^{2} = x^{2} + y^{2} + z^{2}$$

$$\psi = \tan^{-1} z / \sqrt{(x^{2} + y^{2})}$$
(2)

and azimuth is defined as in Eq. 1.

In a Cartesian coordinate system, a change in the origin involves only a translation: x, y, and z will differ by constant amounts in two coordinate systems which differ by a translation. In cylindrical or spherical coordinates, two frames of reference whose origin differs will be related in a nonlinear manner. Therefore we defined errors in pointing in cylindrical and spherical coordinates using both the shoulder and the head (location halfway between the two eyes) as the origin.

Multivariate linear regression analysis

The error in pointing will have two components: a constant error and a variable error.¹ An estimate of the constant error and its dependence on target location was obtained by means of multivariate linear regression analysis. Each of the three parameters defining the location of the finger was fitted to linear, quadratic, and cubic polynomial functions of the three parameters describing the location of the target. For example if, in the spherical coordinate system, R_f , x_f , and ψ_f define the position of the finger, and R, x, and ψ are the corresponding parameters for the target, then

$$R_{\rm f} = a_0 + a_1 R + a_2 \chi + a_3 \psi + \epsilon_{1j} \tag{3}$$

for the linear model and

 $R_{\rm f} = a_0 + a_1 R + a_2 \chi + a_3 \psi + a_4 R^2 + a_5 R \chi + a_6 R \psi$ $+ a_7 \chi^2 + a_8 \chi \psi + a_9 \psi^2 + \epsilon_{2i} \quad (4)$

¹ Constant error is the distance between the finger and the target. Variable error is the variability of the constant error.

for the quadratic model, and similarly for the cubic model (which contains 20 terms). In these equations, ϵ_{1j} or ϵ_{2j} is the remainder for the *j*th trial, that is, the part which is not accounted for by the model. If the model is an adequate representation of the constant error, then the variance of ϵ provides an estimate of the variable error. An analogous regression analysis was also performed on the other two parameters, azimuth (χ) and elevation (ψ).

In general not all of the coefficients a_i will contribute significantly to reducing the variance of ϵ . Therefore, we also computed the model with the minimum number of parameters a_i which could account for the data by following procedures described by Johnson and Wichern (1982). We first found the coefficients in the linear, quadratic, and cubic polynomials whose 95% confidence limits (Eq. 7–14 of Johnson and Wichern 1982) did not bracket the value zero. We then used an iterative procedure, adding or deleting terms one at a time until all terms included in the model and no others were significant.

Information transmitted

The information transmitted by the final position of the finger about target location, in the sense first defined by Shannon (1948), was used to provide a quantitative measure of the variable error. We assumed that there are three separate channels for the transmission of information, for example, one each for R, χ , and ψ if a spherical coordinate system is used. The information transmitted by the subject in the channel for R is

$$T(R_{\rm f}, R) = H(R) + H(R_{\rm f}) - H(R, R_{\rm f})$$
(5)

where H(R) is the information about the distance of the target, $H(R_f)$ is the information about distance in the subject's response, and $H(R, R_f)$ is the mutual information. Similar expressions hold for χ and ψ .

In the case where R and R_f take on distinct values, the average information about the distance of the target is given by

$$H(R) = -\Sigma p_i \log_2 p_i \tag{6}$$

where p_i is the probability that *R* takes on the *i*th value. In our experiments, both the target location as well as the position of the finger were distributed over a continuum. Therefore we adopted the modification of Shannon's formulation introduced by Sakitt (1980) for the continuous case and elaborated by Sakitt et al. (1983) and Georgopoulos and Massey (1988). We divided the range of target parameters into 16 equally spaced bins (e.g., if x

ranged from -40 to 56°, each bin would span 6° and the first bin would range from -40 to -35°). We computed the corresponding bins for finger position from the regression of χ_f on χ (e.g., if $\chi_f = -10^{\circ} + 0.8\chi + 0.005\chi^2$, the first bin would range from -34 to -21.875°).

Because we used 16 bins, the maximum amount of information which could be transmitted is 4 bits ($\log_2 16$). There is some arbitrariness in this definition. Had we used a larger or smaller number of bins, we would have obtained a different estimate for the amount of information transmitted in each channel. To minimize this effect of bin size we computed the sensorimotor efficiency (SME) of information transmission in each channel, defined by Sakitt (1980) as the ratio of the information transmitted divided by the maximum information transfer possible

$$SME = T(R_f, R)/H(R)$$
⁽⁷⁾

RESULTS

Pointing to a virtual target in the dark

When subjects could see neither the target nor their arm, there were consistent errors in the final position of the finger. These errors were primarily in the radial distance (R) from the shoulder; errors in direction as measured by the azimuth (χ) and elevation (ψ) were much smaller. For targets ≥ 50 cm distal to the shoulder, the final position of the finger could be as much as 15 cm short of the target while there was a small tendency to overshoot targets which were close to the shoulder.

These findings are illustrated in Figs. 1–4. Figures 1 and 2 present results from one subject, whereas pooled data from all four subjects who participated in this experiment are shown in Figs. 3 and 4. In these figures we have used a spherical coordinate system with its origin at the right shoulder.

Figure 1 shows the measured position of the finger plotted against the target location for all trials from one subject. The radial distance of the finger from the shoulder is plotted against the radial distance of the target, and similarly for azimuth and elevation. For the latter two parameters, which define the direction of the target, the measured direction of the finger corresponds closely to the target direc-



FIG. 1. Errors in pointing to a virtual target in the dark. The measured position of the finger is plotted against the position of the target. These positions are represented in terms of the radial distance from the shoulder and the azimuth and elevation relative to the shoulder (see insert in Fig. 2A). Each data point represents the results from 1 trial. The data are from 1 subject.



FIG. 2. Analysis of errors in pointing to a virtual target in the dark. The horizontal axis of each panel represents the radial distance of the target from the shoulder (R), the direction of the target from the shoulder in terms of azimuth (x), and elevation, respectively. Inset in A depicts how these angles are defined. A: top row shows (on the vertical axis) the location of the finger predicted by fitting a 20-term polynomial to the data (see METHODS). Each point represents the predicted value from 1 trial. Below each plot in A, we show the difference between predicted finger location and the measured finger location. B: values predicted by the polynomial after all the terms that were not statistically significant were set to 0. Data are the same as those shown in Fig. 1.



FIG. 3. Errors in pointing to a virtual target in the dark. Results from 4 subjects have been combined. Data are plotted in the same format as in Fig. 2B. Note that the error in the radial distance of the finger location is larger than the errors in azimuth and elevation.



FIG. 4. Distortion of extra-personal space for pointing movements to a virtual target in the dark. Top left: perspective view (from the subject's right shoulder) of the portion of space within which targets were presented. This space is represented in spherical coordinates of radial distance (R), azimuth (X), and elevation (ψ), with the origin at the shoulder. R ranged from 30 to 70 cm, X and ψ from -45 to 45°. Heavy solid lines denote the edges of the surfaces which bound this region. Lighter solid lines denote lines of constant radius, azimuth, or elevation on the surfaces in view; those which are dashed are hidden from view. Top right: perspective view of the finger locations (predicted by the polynomial model) which correspond to the target locations shown on the left. Bottom: comparison between the target location; —, finger location; ----, projection of the finger location on to the plane of constant azimuth. The difference between the solid and dashed lines gives an indication of the error in azimuth.

tion. But there are appreciable differences between the measured distance of the finger and the target's distance: in general, subjects did not point far enough.

The scatter in these plots can be due to two factors. For repeated trials with the same target location, there can be variability in the position of the finger. For trials where the target is located at the same distance but in different directions (for example), the finger's distance could consistently depend on target azimuth and/or elevation.

To separate these two sources of variability, we performed a multiple regression analysis (see METHODS). The results of this analysis for the data in Fig. 1 are shown in Fig. 2. In Fig. 2A (bottom), we show the variable error, i.e., the error due to randomness in performance. In Fig. 2A (top), 2B, and in subsequent figures, we show the error due to a consistent dependence of one target parameter on other target parameters. To identify these errors, we used a model which could encompass either a cubic (20 term) polynomial or only those terms which were statistically significant. In Fig. 2A (top), we have plotted the parameters describing finger position (R_f, χ_f, ψ_f) that were predicted by fitting a cubic polynomial in the parameters denoting target position $(R, \chi, \text{ and } \psi)$. Each data point represents the prediction for one trial. If the data points all fell on a single line, one would conclude that radial distance of the finger depended only on radial distance of the target, and likewise for azimuth and elevation. Since they do not, one must conclude that each of the parameters for finger position depends on two or more parameters of target position, the scatter of the data points being related to the amount by which each of the parameters for finger position depends on the other parameters for target location.

In Fig. 2A (top), the data points for azimuth lie close to a line with a slope of 1.0, which represents a perfect correspondence between the finger azimuth predicted by the model and the target azimuth. The same is true for elevation. The data points for radial distance lie below this line, indicating that the subject tended to undershoot the radial distance from the shoulder.



FIG. 5. Errors in radial distance under 4 other experimental conditions. Each panel shows the combined results from 4 subjects. Results are plotted in the same format as in Fig. 3. The experimental conditions are described in METHODS. Note that pointing to a virtual target in the light (*upper left*) leads to appreciable errors, whereas pointing under the other 3 conditions does not.

In Fig. 2A (bottom), we show the difference for each trial between the value predicted by the model and the experimentally measured value for the subject's finger position, i.e., the variability in finger position which could not be accounted for by the cubic polynomial. In this experiment the root mean square (RMS) values of this error were 2.15 cm (R), 2.93° (x), and 4.25° (ψ).

The total RMS error in the distance from the finger to the target (which depends on R, χ , and ψ) was 11.66 cm. Total RMS error is composed of both variable error (which was 4.15 cm) and constant error (which was 10.90 cm). Thus, in this experiment, the constant error was much larger than the variable error.

Finally, Fig. 2B shows the data from the same experiment, this time including only those polynomial coefficients whose 95% confidence intervals did not bracket zero. (In this experiment 4 coefficients were required for R, 3 for χ , and 5 for ψ .) Because we only omitted coefficients that were insignificant, the amount of scatter in the plots in Fig. 2, A and B, is nearly the same.

Figure 3 shows the pooled data for all four subjects, i.e., those errors in the performance common to all. As in Fig. 2B, the data points are derived using a polynomial fit including only those coefficients which are statistically significant. Once again, the undershoot in the radial distance (R) of the finger for distal targets is readily apparent. There is no scatter in this plot for radial distance since only terms in

R and R^2 were found to be statistically significant.² When the data for individual subjects were analyzed, finger radial distance did depend significantly on target direction (see Fig. 2), but this dependence was different from subject to subject. Errors in direction are much smaller, although there is a slight bias to position the finger medially (smaller values of azimuth) and at a higher elevation than the target, especially for targets located below shoulder level (negative values of ψ).

This spatial distortion in pointing can be appreciated in the perspective plots in Fig. 4. On the left we show the portion of the sphere throughout which target positions were distributed, as viewed from the perspective of the subject's shoulder. In this plot, R ranges from 30 to 70 cm, whereas azimuth and elevation both range from -45 to

² For this experimental condition, the best fit to the data was given by:

$$R_{\rm f} = 1.22R - 0.56R^2$$
(0.05) (0.08)

$$x_{\rm f} = 0.36 - 0.12R + (0.84 + 0.22R)x$$
(0.16) (0.06) (0.09) (0.18)

$$\psi_{\rm f} = -0.05 + (1.01 - 3.50x - 13.16x^2 + 6.33Rx)\psi - 11.16\psi^3$$
(0.01) (0.05) (2.60) (10.11) (4.74) (9.82)

where the numbers in parentheses denote the 95% confidence intervals and the units of R are meters and elevation and azimuth are expressed in radians.



FIG. 6. Slopes of the linear regressions of finger location on target location for the 5 experimental conditions. Lightly stippled bars indicate the 95% confidence limits of the values for each subject; heavier stippled bars are the 95% confidence limits of the estimate obtained by combining the data from 4 subjects. The horizontal lines delimit the 95% confidence interval of the combined data obtained when subjects pointed to a virtual target in the dark. For R, we also indicate the 95% confidence interval for when subjects reproduced an active movement. If the subjects made no errors, the slopes of the linear regressions would be 1.0.

45°. On the right we show for comparison the corresponding positions of the finger predicted by the polynomial fit (Fig. 3).²

Below, we show vertical planar sections through this space at values of azimuth ranging from -45 to 45° . The solid heavy lines indicate the predicted finger position while the heavy dashed lines are its projection on to the particular planar section. The distance between the solid and dashed lines represents the error in azimuth. Once again the compression in the radial distance of the finger position is apparent, whereas errors in elevation are largest for targets located at the medial (-45°) and lateral (45°) extremes.

To permit a direct comparison among the results obtained under different experimental conditions, we also computed the slopes of the linear regressions (for example, a_1 in Eq. 3). They are shown in the leftmost part of Fig. 6. In all four subjects the slope of the linear regression for R was substantially smaller than 1.0, ranging from 0.50 to 0.69, with the pooled data yielding an estimate of 0.65 \pm 0.04, as indicated by the bar with heavier stippling. The estimates for azimuth and elevation were much closer to 1.0, the pooled data giving values of 0.98 \pm 0.02 and 0.95 \pm 0.02 for the two angles.

Errors in pointing under other experimental conditions

The substantial undershoot in the radial distance from the shoulder (Figs. 1-3) persisted when subjects had their arm in view (i.e., when they pointed to a virtual target with the room lights on). This can be appreciated in the plot in Fig. 5 (*upper left*), which shows pooled results from four other subjects obtained under this experimental condition. The values of the slope of the linear regression coefficients on *R* ranged from 0.60 to 0.82 (Fig. 6). They were significantly different from unity in all four subjects, and in three of the four the value fell within the 95% confidence limits of the value obtained when subjects pointed to a virtual target in the dark (horizontal lines).

When subjects had their arms in view, errors in direction (azimuth and elevation) were quite small but comparable to those in the dark, values for the slopes of the linear regression coefficients averaging 1.01 ± 0.02 and 1.01 ± 0.01 , respectively (Fig. 6).

From this experiment it can be concluded that subjects must be able to see the target as well as the hand during the movement if movement distance is to be accurate. If view of the target is occluded prior to movement onset, the



FIG. 7. Sensorimotor efficiency of the transmission of information. Information transmitted by the subject's finger about the target's radial distance, azimuth, and elevation is shown as a fraction of the information provided by the target. The horizontal lines indicate the range of values obtained in the first experimental condition (Virtual Target, Dark). Note that the information provided by the subject about target distance is consistently less than the information about direction (azimuth and elevation).



FIG. 8. Distortion of extrapersonal space in pointing movements to a virtual target in the dark in a head-centered frame of reference. Data are the same as those shown in Fig. 3. This time they are represented in a spherical coordinate system with origin at the head. Plots show the distortion in 4 vertical planes of constant azimuth ranging from -20° to 40° .

errors are substantially the same as when neither the target nor the hand are seen. This finding points to two possible interpretations: 1) the subjects misperceive the location of the target in terms of its radial distance from the shoulder or 2) target location is perceived accurately but the amplitude of the arm movement is scaled inappropriately.

The next series of experiments was designed to distinguish between these two interpretations. The results obtained when subjects were given a pointer and asked to use it to point to a virtual target with the lights on show that subjects do not misperceive the target location. The data points in Fig. 5 (*upper right*) cluster close to a line with unity slope; on average the slope of the linear regression on R was 0.91 \pm 0.03 (Fig. 6). The main difference between this experiment and the preceding one was in the movement required to attain the target: with the pointer, the task





FIG. 10. Distortion of space in Cartesian coordinates. Perspective plot (*top left*) shows a representation of target space (x ranging from 40 cm medial to 40 cm lateral, y from 20 to 70 cm anterior, and z from 40 cm below to 40 cm above the shoulder). *Bottom left*: perspective view of the corresponding location of the finger. *Right*: comparison of target and finger location at 5 different planes of constant height. Plots were generated using polynomial fits to the data obtained when subjects pointed to a virtual target in the dark.

involved primarily motion at the wrist; without it, movement was confined mostly to the shoulder and elbow joints (Lacquaniti et al. 1987). Since the visual information about target location was the same in both instances, one can conclude that the error in pointing in the latter case is due to an inappropriate scaling of motion at the proximal joints. [The observations depicted in the Fig. 5 (*top*) also lead to a curious conclusion: subjects can be more accurate when manipulating a tool than when they are moving their own limb!]

Finally Fig. 5 (*bottom*) shows that subjects can effectively utilize kinesthetic information to point to a target. Both when they were asked to reproduce a passive or an actively generated movement to a target position, the error in radial distance was quite small. However, it is noteworthy that when subjects attempted to reproduce passive movements, in three of the four subjects the slope of the linear regression coefficient for elevation differed significantly from those found under other experimental conditions (Fig. 6). Furthermore, the variability of the data was larger for botl.

elevation as well as for R, as evidenced by the larger 95% confidence limits in Fig. 6.

The gravitational torque about the shoulder and elbow exerted by the weight of the arm depends on R and on elevation, but not on the azimuth. When the arm is supported (as during the passive movement), information about gravitational torques is lacking. Therefore the results suggest that sensory information about torque is utilized in positioning the arm, in agreement with observations of Worringham and Stelmach (1985).

Information transmitted

One way of providing a quantitative measure of movement variability is to compute the information transmitted by the final finger position about the location of the target. We assumed that there are three distinct channels of information transmission $(R, \chi, \text{ and } \psi)$ and computed the sensorimotor efficiency (SME) in each channel as the ratio of the transmitted information to that provided by the target



FIG. 11. Distortion of space in cylindrical coordinates when subjects pointed to a virtual target in the dark.

(see METHODS). If subjects made the same error on repeated movements to the same target, this measure would be 1.0, whereas if the movements were perfectly random it would be 0.

The results of this analysis are shown in Fig. 7. Although the number of subjects for each experimental condition is too small to permit statistical comparisons among the different experimental conditions, some clear trends do emerge. First, SME for radial distance (R) is consistently smaller than the efficiency for the two angles defining direction. Second, movement variability was smallest (and SME was largest) when subjects reproduced an actively generated movement (as might be expected) and when they pointed to the virtual target with a pointer. One possible interpretation of this latter finding is that wrist movements are performed with less variability, i.e., with finer control of position, than is motion at the more proximal joints.

The values of sensorimotor efficiency for azimuth and elevation obtained in these experiments are comparable to those obtained by other investigators; e.g., Sakitt et al. (1983) reported a value of ~ 0.72 for uniarticular arm movements to 16 different targets, whereas Georgopoulos

and Massey (1988) reported a similar value for the direction of planar limb movement.

Alternative coordinate reference frames

In the presentation of the data so far we have used a spherical coordinate system whose origin was located at the shoulder joint. Other reference frames also merit consideration.

For example, it would be equally plausible to utilize a spherical coordinate system which is head-centered since information about target location is visually derived. In Fig. 8, the data from the same experiments shown in Figs. 3 and 4 have been replotted in this frame of reference. We show the finger position predicted by the polynomial fitting of the data in four vertical planar sections (values of constant azimuth), ranging from 20° medial to 40° lateral to the head. There is a substantial distortion of finger position in this representation. The radial distance from the head to the finger depends considerably on target elevation and the lines predicted for finger position at a constant radius of target distance are skewed about an origin lower than the

head, i.e., an origin closer to shoulder level. Thus errors in radial distance of pointing are proportional to the radial distance of the target from the shoulder (Fig. 4) but not to the radial distance of the target from the head.

Figures 9-11 show the data from this same series of experiments (pointing to a virtual target in the dark) when they are represented in Cartesian coordinates (x, y, and z, z)Figs. 9 and 10) or in cylindrical coordinates (r, x, and z, z)Figs. 9 and 11). The conclusions to be drawn from the representation of the data in these two other coordinate systems are the same as those which have already been reached: there was an undershoot of the movement in the anterior (Y) or the horizontal radial (r) direction, analogous to that shown for radial distance (R) in Fig. 3. For targets that are far above the shoulder (z = 40 cm), the finger position was too low, whereas for targets far below the shoulder it was too high. Thus there are errors in height as well. Nevertheless this observation is consistent with the conclusion stated previously: pointing in the right direction but not far enough will lead to the errors in height just described.

Since all three of the coordinate representations lead to the same conclusion, it is appropriate to ask: is any one of them preferable to the other two? To answer this question, one could choose the system in which the data are described most parsimoniously, that is to say the one which requires the least number of polynomial terms to represent the data. According to this criterion one would pick a spherical coordinate system centered at the shoulder. In this coordinate system, 13 parameters are required to fit the data (2 for R, 5 for x, and 6 for ψ , see footnote 2). Cylindrical coordinates require a total of 15 (3 for r, 7 for x, and 5 for z), whereas 18 are required for Cartesian coordinates (6 each for x, y, and z).

Another possible criterion would be to pick the coordinate system which minimized the amount of cross-talk between the three channels of information. To state this more precisely, one might prefer a coordinate system in which the scatter of the data points in the regression plots (Figs. 3 and 9) were minimal. According to this criterion, in the preferred coordinate system, there should be minimal error in the regression plots in which the first coordinate of finger position depended only on the first coordinate of the target, and similarly for the second and third. On that basis, once again, one would choose spherical coordinates.

Finally, as we shall show in the next paper, representing target location in spherical coordinates provides a simple explanation for why subjects make the errors they do when they point to targets which are not visible (Soechting and Flanders 1989).

DISCUSSION

As we mentioned in the INTRODUCTION, we propose that pointing to targets is accomplished by a process of sensorimotor transformations. The general scheme of such a process is shown in Fig. 12. When a subject points to the remembered location of a visually presented target, he or she uses a visually derived representation of the target location (Fig. 12A). This representation must ultimately be transformed into a pattern of muscle activity that produces



FIG. 12. Hypothetical scheme for the sensorimotor transformation involved in pointing to a target. Target location is given by a visual representation (A) and is transformed ultimately into a pattern of muscle activity to produce arm movement (B). The transformation may be direct (solid arrow) or it may proceed through an intermediate step in which target position and arm position are represented in a common frame of reference.

the arm movement (Fig. 12B). A kinesthetically derived representation of arm position (Fig. 12C) may also be useful in this process. In our first and second experiments, the transformation from a visual representation to arm movement resulted in large and consistent errors (Figs. 1-4). Subsequent experiments were designed to identify the stage or stages in the sensorimotor process at which the error occurred.

Site of the errors

The third series of experiments was designed to test whether there was an error in the visual representation of target location (Fig. 12.4). We reasoned that if this were the site of the error, all movements that were guided by this representation would be in error equally. Our observation that the use of a pointer reduced errors indicated that the visual representation was not a substantial source of error.

The fourth series of experiments was designed to determine whether subjects could use kinesthetically derived information about target location (Fig. 12C) to produce accurate arm movements (Fig. 12B). Errors in radial distance from the shoulder were substantially reduced when subjects used a kinesthetically derived representation of target location instead of a visually derived one. In this series of experiments, the accuracy of radial distance was comparable to the accuracy of radial distance when subjects used a pointer or reproduced an active movement (Figs. 5 and 6).

Thus the error occurs in the transformation from the visual representation of target location (Fig. 12*A*) to the arm movement (Fig. 12*B*). This transformation could be direct (horizontal arrow in Fig. 12) or alternatively an intermediate step (dashed arrow) could be involved. That is to say, visually and kinesthetically derived information may both be represented in a common kinematic frame of reference to guide the movement. The results and analysis presented in this paper do not permit us to differentiate between these two possibilities and we will take up this question in the paper which follows (Soechting and Flanders 1989).

Nature of the errors

The errors in pointing were substantial, subjects missing the target by ≥ 15 cm, and they depend on the spatial locus of the target but not on the amplitude of the movement. This conclusion is based on the following reasoning. For the most part, the error was related to the radial distance of the target from the shoulder; errors in direction as measured from the shoulder were much smaller (Fig. 3) except at the mediolateral extremes (Fig. 4). Since all movements began with the hand at the waist level, it is evident that some small amplitude movements led to rather large errors (e.g., those to targets at waist level in front of the subject). In other instances, large amplitude movements were associated with small errors (targets close to the shoulder). Had the error been related to the required movement distance, one would expect the results to have been skewed about an origin \sim 30 cm below the shoulder (i.e., an origin at the waist) when they were represented in a shoulder-centered coordinate system. A comparison of Fig. 4 with Fig. 8, where we represented the data in head-centered coordinates, shows that our method of analysis is sensitive to the origin of the coordinate system.

At first glance, this conclusion appears to contradict a number of studies which point to movement error being related to the required movement amplitude. For example, Brown et al. (1948) found that subjects tended to overshoot the target when the distance to be moved was short (<5 cm) and to undershoot it when the distance to be moved was long (40 cm). However, these errors were generally very small (~ 1 cm) and movement direction was constrained since the subjects moved a slider along a response panel in the dark. More recently, Bock and Eckmiller (1986) found small errors related to movement amplitude when subjects were asked to point to targets spaced along a horizontal arc. These movements were also constrained since subjects grasped a lever which pivoted about an axis close to the shoulder, vision of the arm being occluded. Thus in both these experiments, motion was constrained to one degree of freedom. Slightly larger errors were found by Prablanc et al. (1979) when subjects pointed to targets located on a horizontal plane at different distances along the mediolateral (x) axis. In their experiments, hand motion was not physically constrained except by the planar surface.

All of these studies do point to an effect of movement distance on the error in pointing. They also indicate that this error is much smaller (by an order of magnitude) than the spatially dependent error we have described in this paper, where errors in both distance and direction were potentially possible. Our findings are in accord with the results presented by Fitts (1954), whose study is most comparable to ours. He presented subjects with a number of targets spaced along a spherical surface 30 in (75 cm) from the shoulder. His subjects were asked to point to one of the targets while fixating on lights directly in front of the subject, i.e., in the absence of direct vision of the target or the hand. The largest errors were in elevation, subjects pointing to a spot somewhat above the target when it was below shoulder level, and vice versa (see Fig. 4). Errors in azimuth appeared to be much less. Errors in radial distance were not examined by Fitts.

Error correction

The magnitude of the movement errors we have described may appear to be surprising since such errors do not manifest themselves under more typical conditions when both target and the hand are in view. Our results indicate vision of both target and hand are required for error correction. There is ample evidence that subjects are able to make quick and effective use of visual information to correct movement errors. When target location is changed, the latency to effect a change in trajectory is short, \sim 90-100 ms (Georgopoulos et al. 1981; Soechting and Lacquaniti 1983). A number of studies have also indicated that, when target location does not change, visual information is used primarily in the terminal stages of the movement when the limb is in the vicinity of the target (Carlton 1981; Hay 1979; Paillard 1982; Soechting 1984).

We have already pointed out that subjects have a good sense of where the target is located in space and that they can utilize strictly kinesthetic information to move accurately to the target (reproducing a passively generated movement). We have also suggested that they do not correct for the error unless this error is sensed visually. The question now is: Why does the error occur? This question will be taken up in the next paper (Soechting and Flanders 1989).

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Address for reprint requests: J. F. Soechting, Dept. of Physiology, Medical School, 6-255 Millard Hall, 435 Delaware St. S.E., Minneapolis, MN 55455.

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REFERENCES

- BOCK, O. AND ECKMILLER, R. Goal-directed arm movements in absence of visual guidance: evidence for amplitude rather than position control. *Exp. Brain Res.* 62: 451–458, 1986.
- BROWN, J. S., KNAUFT, E. B., AND ROSENBAUM, G. The accuracy of positioning reactions as a function of their direction and extent. Am. J. Psychol. 61: 167–182, 1948.
- CARLTON, L. G. Processing visual information for movement control. J. Exp. Psychol. Hum. Percept. Perform. 7: 1019–1030, 1981.
- FITTS, P. M. A study of location discrimination ability. In: Psychological Research on Equipment Design. Army Air Force Psychol. Prog. Res. Rep. 19: 207–217, 1947.
- FITTS, P. M. The information capacity of the human motor system in controlling the amplitude of the movement. J. Exp. Psychol. 47: 381-391, 1954.
- FLANDERS, M. AND CORDO, P. J. Kinesthetic and visual control of a bimanual task: specification of direction and amplitude. J. Neurosci. 9: 447-453, 1989.
- GEORGOPOULOS, A. P. On reaching. Annu. Rev. Neurosci. 9: 147-170, 1986.
- GEORGOPOULOS, A. P., KALASKA, J. F., AND MASSEY, J. T. Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty and change in target location. *J. Neurophysiol.* 46: 725-743, 1981.
- GEORGOPOULOS, A. P. AND MASSEY, J. T. Cognitive spatial-motor processes. 2. Information transmitted by the direction of two dimensional arm movements and by neuronal populations in primate motor cortex and area 5. *Exp. Brain Res.* 69: 315-326, 1988.
- HAY, L. Spatial-temporal analysis of movements in children: motor programs versus feedback in the development of reaching. J. Mot. Behav. 11: 189-200, 1979.
- JOHNSON, R. A. AND WICHERN, D. W. Applied Multivariate Statistical Analysis. Englewood Cliffs, NJ: Prentice-Hall, 1982, p. 291-358.

- KNUDSEN, E. I., DU LAC, S., AND ESTERLY, S. Computational maps in the brain. Annu. Rev. Neurosci. 10: 41-65, 1987.
- KONISHI, M. Centrally synthesized maps of sensory space. Trends Neurosci. 9: 163-168, 1986.
- LACQUANITI, F., FERRIGNO, G., PEDOTTI, A., SOECHTING, J. F., AND TERZUOLO, C. Changes in spatial scale in drawing and handwriting: kinematic contribution by proximal and distal joints. J. Neurosci. 7: 819-828, 1987.
- MEYER, D. E., SMITH, J. E. K., AND WRIGHT, C. E. Models for the speed and accuracy of aimed movements. *Psychol. Rev.* 89: 449–482, 1982.
- PAILLARD, J. The contribution of peripheral and central vision to visually guided reaching. In: Analysis of Visual Behavior, edited by D. J. Ingle, M. A. Goodale, and R. J. Mansfield. Cambridge, MA: MIT Press, 1982, p. 367-385.
- PRABLANC, C., ECHALLIER, J. F., KOMILIS, E., AND JEANNEROD, M. Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biol. Cybern.* 35: 113–124, 1979.
- SAKITT, B. Visual-motor efficiency (VME) and the information transmitted in visual-motor tasks. *Bull. Psychon. Soc.* 16: 329-332, 1980.
- SAKITT, B., LESTIENNE, F., AND ZEFFIRO, T. The information transmitted at final position in visually triggered forearm movements. *Biol. Cybern.* 46: 111-118, 1983.
- SCHMIDT, R. A., ZELAZNIK, H., HAWKINS, B., FRANK, J. S., AND QUINN,

J. T. Motor output variability: a theory for the accuracy of rapid motor acts. *Psychol. Rev.* 86: 415-451, 1979.

- SHANNON, C. E. A mathematical theory of communication. Bell Syst. Techn. J. 27: 379-423, 1948.
- SIMPSON, J. I. AND GRAF, W. The selection of reference frames by nature and its investigation. *Rev. Oculomot. Res.* 1: 3-20, 1985.
- SOECHTING, J. F. Effect of target size on spatial and temporal characteristics of a pointing movement in man. *Exp. Brain Res.* 54: 121–132, 1984.
- SOECHTING, J. F. Elements of coordinated arm movements in three-dimensional space. In: *Perspectives on the Coordination of Movement* edited by S. A. Wallace. Amsterdam: North-Holland.
- SOECHTING, J. F. AND FLANDERS, M. Errors in pointing are due to approximations in sensorimotor transformations. J. Neurophysiol. 62: 595-608, 1989.
- SOECHTING, J. F. AND LACQUANITI, F. Modification of trajectory of a pointing movement in response to a change in target location. J. Neurophysiol. 49: 548-564, 1983.
- SOECHTING, J. F. AND TERZUOLO, C. A. Sensorimotor transformations and the kinematics of arm movements in three-dimensional space. Proc. Attention and Performance XIII, In press.
- WOODWORTH, R. S. The accuracy of voluntary movement. *Psychol. Rev.* 2, *Suppl.*: 13, 1899.
- WORRINGHAM, C. J. AND STELMACH, G. E. The contribution of gravitational torques to limb position sense. *Exp. Brain Res.* 61: 38–42, 1985.