# Transformation from Head- to Shoulder-Centered Representation of Target Direction in Arm Movements

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## Abstract

■ In a previous study (Soechting and Flanders 1989a) we suggested that subjects used a coordinate system centered at the shoulder while pointing to targets in extrapersonal space. In particular, we suggested that this coordinate system was used to define target location in terms of its distance and the direction from the shoulder. In this paper we examine this suggestion in more detail. We show that when subjects make errors in the distance of a pointing movement, the computed errors in direction will depend on the origin of the coordinate system chosen to measure direction. From an analysis of the computed error, we estimate the origin of each subject's coordinate system. We artificially induced large errors in pointing distance by asking subjects to point half-way to a target on a line from the shoulder or from the head, that is, in directions from two possible centers. The subjects' performance on both these tasks was comparable to the performance of subjects asked to point directly to the target. From this finding we argue that there exists both a head-centered and a shoulder-centered representation of target location within the central nervous system. ■

## INTRODUCTION

When a human subject points to a target, the information that is necessary to make this movement is commonly provided by the visual system. This information must be transformed into patterns of activation of the arm muscles that are appropriate to move the limb to the target. Researchers who have dealt with this problem have found it useful to consider the transformation to be in part a serial process: a series of transformations from the initial representation to intermediate representations to the motor output patterns (Andersen & Zipser 1988; Georgopoulos 1986; Grobstein 1988; Hollerbach 1982; Soechting 1989; Soechting & Flanders 1989a; Sparks 1988). Furthermore, we have found it useful to distinguish between kinematic and dynamic representations of the task (Hollerbach & Flash 1982; Soechting 1989). By kinematic representations we mean the location of the hand in space as well as the joint angles and muscle lengths that correspond to a given orientation of the limb. By dynamic representations we mean the forces, torques, and patterns of muscle activity that move the arm from one orientation to another. We hypothesize that pointing movements are initially represented in kinematic terms, followed by a transformation to movement dynamics and patterns of muscle activation.

Within this conceptual framework, we have recently begun to investigate the different levels of kinematic representations involved in the task of moving the arm to a target and the sensorimotor transformations between these levels of representation (Soechting & Flanders 1989a, 1989b). To do so, we presented subjects with a target, asked them to remember its location, removed the target, and asked them to point to the remembered target location in the dark. (The movements were made in the dark in the absence of a physical target so that subjects could use neither visual nor tactile cues to correct the movements.) We then used the errors in pointing to gain some insight into the computational processes involved in specifying the kinematics of this task.

We found that subjects did make consistent errors in pointing. They tended to point in the right direction but they made considerable errors in distance. In particular, the distance of the finger from the shoulder was proportional to the distance of the target from the shoulder, but the relationship between these two distances was nonlinear. Subjects did not point far enough to distally located targets, missing by as much as 15 cm. We could account for this error readily if we made the following assumptions: (1) The shoulder and elbow joint angles required to reach the target are computed from the target's location relative to the shoulder. (2) This computation involves a linear approximation to the mathematically exact solution, and it is the use of this linear approximation that is responsible for the observed errors in pointing.

In this computation, target location is defined by its distance from and direction relative to the shoulder. Since the visually derived representation of target location is in head-centered coordinates, and a shoulder-centered representation of target location is required by our hypothesis, a transformation of the representation of target location from head-centered to shoulder-centered coordinates is implied.

The reasoning that target location was represented in a shoulder-centered frame of reference was based on errors in pointing distance that will be described in more detail in Results. Errors in pointing direction did not enter into our reasoning, but we tacitly assumed that if distance was defined from the shoulder, so was direction. Although it may appear illogical, the possibility remains that target distance is represented in shoulder-centered coordinates but that direction is represented in head-centered coordinates. Therefore, in this paper we will take up the question of the appropriate frame(s) of reference for the representation of target direction. We will present evidence that direction is defined in shoulder-centered coordinates as well as in head-centered coordinates.

## Experimental Rationale and Analysis

The rationale for the experiments to be described in this paper is illustrated in Figure 1, which shows schematically in a top view the position of a subject's head and shoulder and a target location. We make a distinction between two frames of reference: the frame of reference that the subject uses to represent direction and the frame

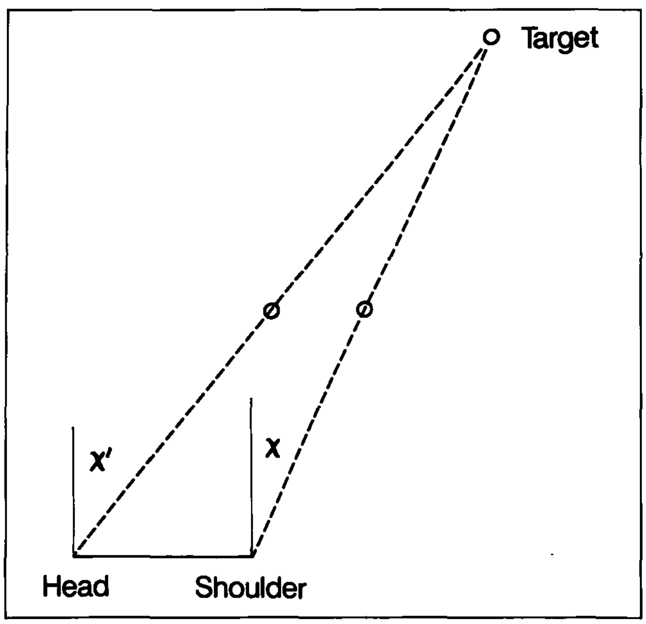


**Figure 1.** Schematic of the task. If the subject points half-way to the target, the finger position will be different if direction is specified from the head or from the shoulder.

of reference in which we measure target location experimentally. If the subject points exactly to the target, then there obviously will be no error in either distance or direction, irrespective of the frame of reference. However, if the subject makes an error in distance (such as pointing only half-way to the target as indicated by open circles in Figure 1), the spot to which the subject points will depend on how the subject defines the direction of the target. In other words, it will depend on the origin of the coordinate system that the subject uses to define direction. For example, if the origin is shoulder-centered, the subject would be expected to point to a spot on the dashed line from the shoulder to the target. If direction is in a head-centered frame, the spot would be on the line between the head and the target.

In the latter case, if the experimenters used a shoulder-centered coordinate system (such as the angle $\chi$) to compare the direction of pointing with the direction of target location, we would find that the subject made consistent errors in direction: the direction of pointing would always be medial to the target direction. Furthermore, the larger the error in distance of pointing, the larger would be the error in direction. If, on the other hand, we had measured direction relative to the head (i.e., in the subject's frame of reference), we would conclude that the subject performed perfectly as far as direction was concerned.

From trigonometry, we can predict precisely the computed error in pointing that is due to our incorrect choice of origin. In this analysis, we will choose the shoulder as the origin and define target direction by azimuth ($\chi$), the mediolateral direction in the horizontal plane, and by elevation ($\psi$), the direction in the vertical plane. We define $\chi$ and $\psi$ to be positive for points located lateral to and above the shoulder. Assume that the subject defines direction to be relative to an origin that is a distance $d_h$ medial to the shoulder and $d_v$ above the shoulder. We define the direction angles measured from the subject's origin to be $\chi'$ and $\psi'$. Finally, assume that the subject points in the correct direction, in his or her frame of reference, and makes only errors in distance. If the subscript p is used to denote the location to which the subject points and the unsubscripted variables the location of the target, then

$$\chi'_p = \chi', \qquad \psi'_p = \psi' \tag{1}$$

but $\chi_p$ and $\psi_p$ (measured from the shoulder) will differ from $\chi$ and $\psi$ by

$$\Delta\chi = \chi_p - \chi, \qquad \Delta\psi = \psi_p - \psi \tag{2}$$

For any origin used by the subject (defined by $d_v$ and $d_h$), this error can be predicted from the following procedure. By the law of sines

$$\begin{aligned} \cos \chi'/r &= \sin(\chi' - \chi)/d_h \\ \cos \chi'_p &= \sin(\chi'_p - \chi_p)/d_h \end{aligned} \tag{3}$$

where $r$ and $r_P$ are the horizontal component of the distance from the target to the shoulder and the distance from the finger to the shoulder, respectively. Since $\chi'_P = \chi'$,

$$r \sin(\chi' - \chi) = r_P \sin(\chi' - \chi_P) \quad (4)$$

and making the assumption that $\Delta\chi$ is small so that

$$\sin \Delta\chi \simeq \Delta\chi, \qquad \cos \Delta\chi \simeq 1 \quad (5)$$

one obtains

$$\Delta\chi = (1 - r/r_P) \tan(\chi' - \chi) \quad (6)$$

By a similar procedure, one obtains for the computed error in elevation

$$\Delta\psi = (1 - R/R_P) \tan(\psi' - \psi) \quad (7)$$

where $R$ and $R_P$ are the radial distances from the shoulder to the target and to the finger, respectively.

We estimated the origin of the frame of reference used by subjects for pointing in the following manner. We always measured target and finger location relative to the shoulder. We then compared the measured errors in pointing azimuth and elevation with those predicted by Eqs. (6) and (7) for different values of $d_v$ and $d_h$. The values of $d_v$ and $d_h$ at which the measured and predicted error agree provide the best estimate of the origin used by the subject in the pointing movement. Quantitatively, the slope of the linear regression between the measured and predicted errors in direction is unity when $d_v$ and $d_h$ coincide with the subject's origin. The 95% confidence limits for this estimate of the origin are given by the range of values of $d_h$ and $d_v$ for which the regression coefficient differs from unity with $p < 0.05$.

## RESULTS

### Pointing to a Virtual Target

Figure 2 illustrates why we originally concluded that the shoulder was the origin ultimately used to represent the location of a point in space for targeted arm movements. The figure shows the results of a multiple regression analysis that predicted the position of the finger for an arbitrary target location when the subject points in the dark (Soechting & Flanders 1989a).

Consider the top row first. In this row we have measured target distance and direction from the shoulder. The light dotted lines represent a range of target locations, at intervals of 20 cm and 30°, while the heavy solid lines denote the predicted finger position for these target locations. Each panel gives the predictions at one value of azimuth (that is in a vertical plane at the indicated angle with a sagittal plane through the shoulder) ranging from −45° medial to 45° lateral to the shoulder. The undershoot in distance is clear. At a distance of 30 cm from the shoulder, the solid arcs are close to the dashed arcs, indicating there were few or no errors in distance for pointing to proximal targets. However, at greater distances (50 and 70 cm from the target), the solid arcs are proximal to the dotted arcs, implying an undershoot that becomes progressively greater with target distance.

It is also clear that the solid arcs (predicted finger position at constant target distance) are centered about the shoulder, since they are parallel to the dashed arcs. The radial distance of finger position depends only on target distance, but *not* on direction, when distance is measured from the shoulder.

The lower row shows the results of the analysis applied to the same data when the origin is chosen to be at the head approximately midway between the eyes (25 cm medial to and 20 cm above the shoulder). The arcs representing finger position at constant target distance from the head are not centered about the head. Instead they appear to be centered about a point below the head. When distance is measured from the head, the radial distance of finger position depends on target distance and *also* on the elevation and azimuth of the target. Thus, using the shoulder as the origin for our frame of reference to describe pointing movements gave a simpler description of errors in distance than did using the head as origin.

There are errors in direction (especially elevation) whether direction is measured from the shoulder or from the head. An inspection of these errors in Figure 2 yields no clear preference for either representation of direction. When azimuth and elevation of the finger's location are plotted against the corresponding target parameters, there are also no obvious differences whether direction is measured from the shoulder or from the head. This is illustrated in Figure 3 which shows typical results from one subject in an experiment in which the subject pointed to a virtual target in the dark. In the top row is plotted the azimuth (left) and elevation (right) of the finger versus azimuth and elevation of the target, measured from the shoulder. Each data point represents the results from one trial. In the lower row, results from the same trials are plotted with direction measured from the head. The 45° line represents perfect performance.

Irrespective of whether direction is measured from the shoulder or from the head, the data points appear to be clustered about the 45° lines. This is so in spite of the fact that the subject made errors in pointing distance similar to those illustrated in Figure 2; when the target was 70 cm from the shoulder she pointed to a spot which was 10 cm proximal to the target. (Recall that the analysis presented in the previous section predicts that directional errors should be sensitive to our choice of origin, provided the subject makes errors in distance.) Given the scatter in the data points for direction, it appears that the errors in distance in this experiment are too small to permit a clear delineation of the origin of the frame of reference.

These qualitative observations are borne out by a quantitative analysis. The slopes of the regression between pointing direction and target direction did not

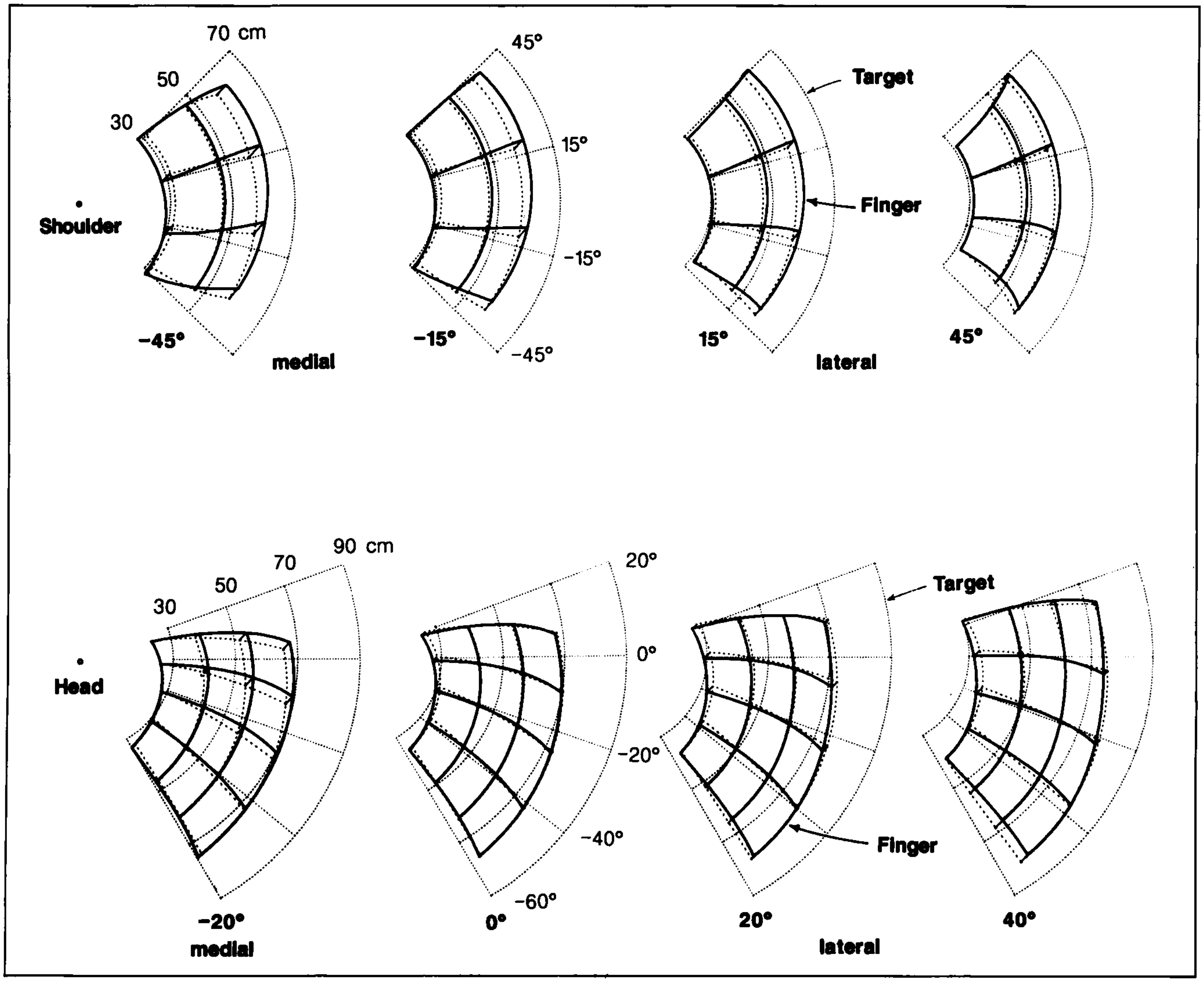


**Figure 2.** Finger location for different target locations when subjects pointed to a virtual target in the dark, described with the shoulder as origin (top row) and a head-centered origin (bottom row). Dotted lines: target position in different vertical planes ranging from 45° medial to 45° lateral to the shoulder (top row) and from −20° to 40° relative to the head (bottom row). Solid lines: finger position corresponding to the target position; dashed lines: projection of finger position onto the plane of target position.

differ for head- and shoulder-centered frames of reference. When direction was measured from the shoulder these values were 0.99 ± 0.02 (95% confidence limits) for azimuth ($\chi$) and 0.99 ± 0.04 for elevation ($\psi$); with direction defined relative to the head these values were 1.04 ± 0.03 and 0.95 ± 0.04, respectively. The average results for eight subjects who were instructed to point to a virtual target in the dark also did not differ significantly. Measured from the shoulder, they were $\chi$, 0.97 ± 0.04 (SE) and $\psi$, 0.94 ± 0.04 and from the head $\chi'$, 0.97 ± 0.05 and $\psi'$, 0.92 ± 0.04.

However, the regression analysis between the measured error in direction and the error predicted by assuming the origin of the coordinate system to be at a point other than the shoulder indicates that the subject's origin lies somewhere between the shoulder and the head. Even though the uncertainty in our estimate is large, the range encompasses neither the head nor the shoulder.

This point is illustrated in Figure 4, which shows results from eight subjects including the subject whose data are presented in Figure 3. Each quadrangle outlines the area for one subject within which the slope of the regression between measured and predicted error does not differ from unity at the 95% confidence level. According to our analysis, the subject's origin for specifying direction might be any point within the quadrangle. The two dots denote the location of the shoulder and of the "head," the latter point defined to be 25 cm medial to and 20 cm above the shoulder and located approximately midway between the two eyes. The quadrangles overlap neither of these points. For the eight subjects, the best

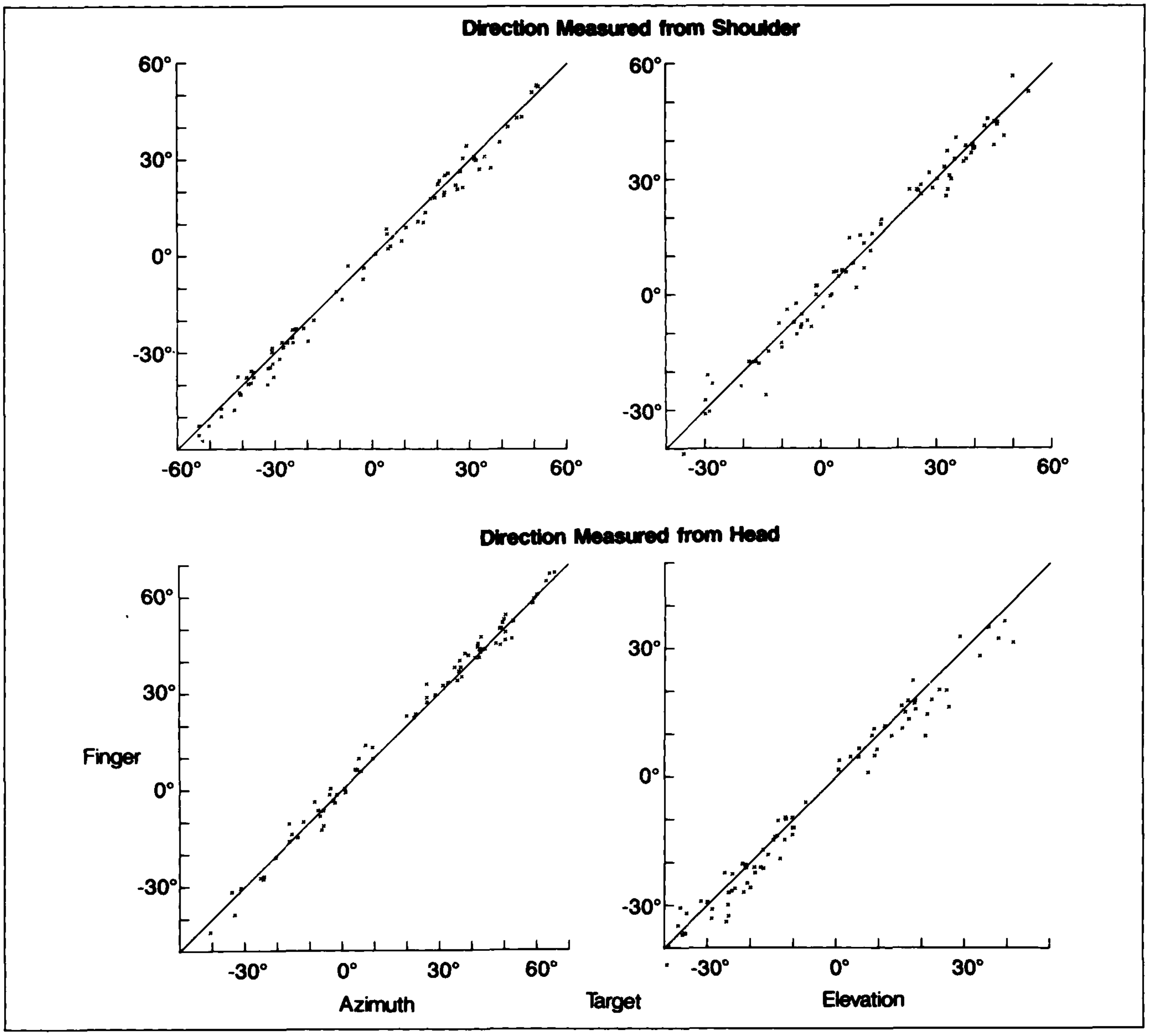


**Figure 3.** Direction of pointing measured from the shoulder (top row) and from the head (bottom row) when a subject pointed to a virtual target in the dark.

estimate of the origin for pointing direction (the point at which the slope of the regression is unity) is 15 ± 6 cm medial to and 17 ± 11 cm above the shoulder.

## Pointing Half-Way to a Virtual Target

To delineate the location of the origin of the coordinate system more precisely, we asked subjects to point half-way to the remembered location of the target. Our rationale was that by inducing larger differences between pointing and target distances, we would accentuate any directional errors arising if we define direction from a point different from the origin which the subject uses to specify direction [see Eqs. (6) and (7)]. Therefore, provided that the directional variability in performance does not increase substantially, the uncertainty in defining the origin of the coordinate system for pointing should be reduced.

As described in Methods, we gave each subject three different instructions in the following sequence: point half-way to the target, point half-way from the shoulder, and point half-way from the head. The first instruction gave diverse results. Each subject apparently interpreted this instruction in a different manner. This conclusion is based on postexperiment interviews with the subjects as well as on the scatter in the estimates of the origin. One

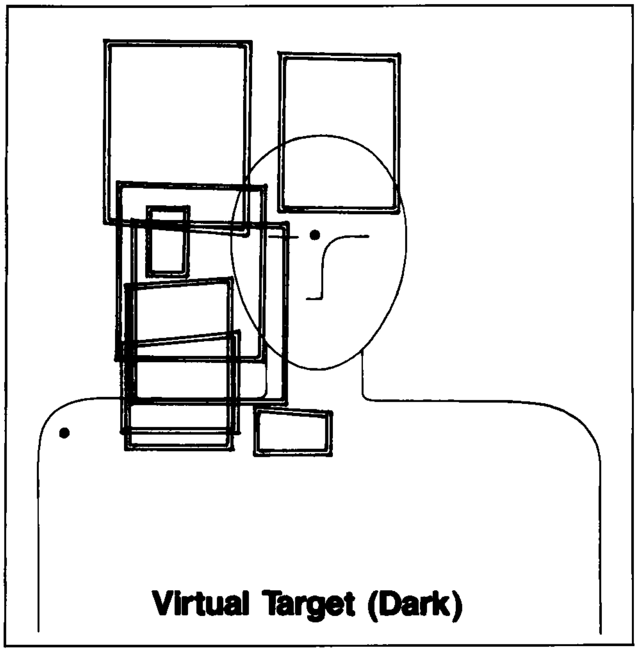


**Figure 4.** Estimate of the origin used by subjects for pointing to virtual targets in the dark. Each box represents the 95% confidence limits of this estimate for one subject.

reported that she moved to a point half-way from the head, and the analysis confirmed this contention. Another stated that she made half the movement, which is difficult to interpret. A third claimed that she moved half-way from the starting point (which was at the level of the waist) to the target; this contention was not borne out by the analysis. Finally, the fourth subject gave a nonspecific answer. Since the subjects interpreted this first instruction in an individual manner, the results of this part of the experiment will not be described further.

The other two instructions led to much more consistent results. Figure 5 shows our estimates of the subjects' origin for specifying the direction of pointing when they were instructed to point to a spot half-way along a line from the target to the shoulder (left) and to head (right). As we had expected, the uncertainty in the estimates of the origin for the direction of pointing decreased, and the four subjects gave reasonably consistent results.

When they were asked to point to a location half-way to the shoulder, they did not succeed precisely in this task. Instead, direction of pointing was aligned with a point medial to the shoulder at about the height of the shoulder's center of rotation. The best estimate for the location of this point averaged 9 ± 3 cm medial and 4.5 ± 4 cm above the shoulder (i.e., 16 cm lateral to and 15.5 cm below the center of the head) for the four subjects. The mediolateral estimate for the location of the origin under this experimental condition agrees reasonably well with the result when subjects were asked to point directly to the target (15 ± 6 cm), while the vertical location differed somewhat more.

When the subjects were asked to point to a location half-way from the head, our estimate of the origin (27 ± 3.5 cm medial to and 17.5 ± 6 cm above the shoulder) coincided closely with the center of the head (between the eyes). When asked to do so, subjects in fact did point to a location on a line between the head and the target.

Figures 6–9 show the data for these two experimental conditions for the same subject whose results were shown in Figure 3. Figure 6 presents the data points for azimuth and elevation when the subject was asked to point half-way from the shoulder. When azimuth is measured from the shoulder, the data points tend to fall below the 45° line, indicating that the subject pointed in a direction medial to the azimuthal direction of the target. This observation implies that the finger and target tended to align with a point whose origin was medial to the shoulder (see Figure 1). Instead, when azimuth is measured from the head, the data points lie above the 45° line, implying alignment of target and finger with a point lateral to the head. This qualitative assessment is in agreement with the quantitative evaluation presented in Figure 5.

For elevation, the data points cluster about the 45° line when elevation is measured from the shoulder but fall below the line when it is measured from the head, implying an origin that is close to shoulder level (see Figure 5).

In Figure 7 we have connected the target location and finger position for each trial from the same experiment, in a top view (left) and viewed from the side (right). Extrapolating these lines back to the frontal plane containing the head and the shoulder and computing the average location at which they intersect this plane provides another estimate of the origin. This procedure gave values similar to those obtained using the regression analysis; however, the uncertainty in the estimates was much larger. On average this procedure gave an estimate for the location of the origin 8 ± 2 cm (SE) medial to and −1 ± 5 cm below the shoulder, when the subjects were asked to point half-way from the shoulder.

Figures 8 and 9 present results from the same subject when she was asked to point half-way from the head. When azimuth and elevation are measured from the head the data points cluster close to the 45° line; they clearly do not when direction is measured from the shoulder. Extrapolating the lines connecting target and finger position back to the frontal plane also gives an intercept that is close to the head (Figure 9). For the four subjects, this procedure gave an estimate that was 28 ± 6 cm medial to and 22.5 ± 5 cm above the shoulder.

Comparing the scatter of the data points in Figures 6 and 8, where subjects pointed half-way to the target, with that in Figure 3, one notes that there is somewhat more variability in the performance when the subject was asked to point half-way from the head or from the shoulder. Details on all four subjects are provided in Table 1,

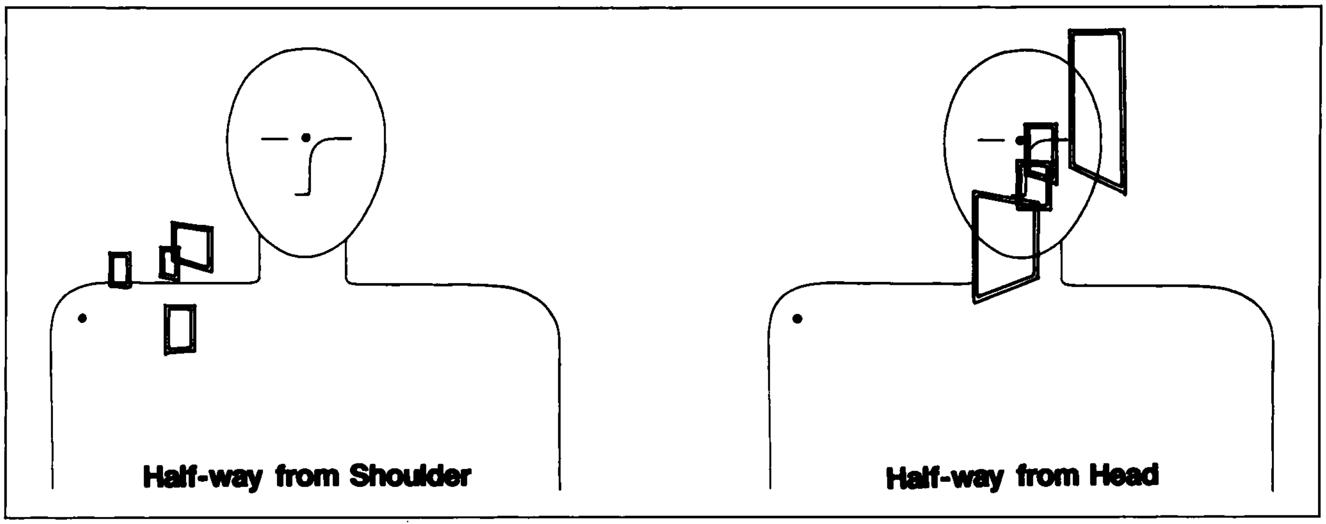


**Figure 5.** Estimate of origin used by subjects when they were instructed to point half-way to a target in the direction from the shoulder (left) and from the head (right).

in which we report the variable error in azimuth and elevation for each subject in each of the three experimental conditions. Variable errors in the two half-way pointing conditions tended to be comparable and slightly larger (generally 15–30%) than those when subjects were instructed to point directly to the target.

As mentioned, our aim in asking subjects to point half the distance was to increase the sensitivity of the analysis for ascertaining the origin from which direction was specified. We were not so much interested in how well subjects were able to bisect a line in three-dimensional space. Therefore, errors in distance were not analyzed as extensively as were directional errors. However, we can report that in all subjects the slope of the regression between finger distance and target distance was consistently less than 0.5 when subjects were asked to point half-way to the target, averaging about 0.4 when they were asked to point half-way from the shoulder and 0.35 for movements half-way from the head.

### Pointing to a Virtual Target in the Light

In the experiments that we have described in a previous publication (Soechting & Flanders 1989a), we also asked subjects to point to virtual targets when the room lights were on. In this experimental condition, they made errors in distance similar to those when movements were made in the dark (Figure 2). Postexperiment interviews with these subjects indicated that they used cues in the visual surround to line up the finger position with the remembered target direction. If so, then the origin for pointing movements predicted by the regression analysis should be centered about the head. This prediction was borne out by the experimental data as shown in Figure 10.

## DISCUSSION

We found that subjects were able to point to a target in the direction defined from the shoulder region as well as they were able to point in the direction of the target from the head. We showed this by asking subjects to point half-way to the target, artificially increasing the distance between finger and target positions.

If we measure the direction of the finger and of the target using the same origin as that used by the subject, there will be no measured constant error in the direction of pointing. However, if we use a coordinate system whose origin differs from that used by the subject, a constant directional error in pointing will be measured. We arbitrarily set the origin at the shoulder and then calculated the point in the frontal plane at which directional errors would be zero. Based on this analysis and the subjects' variable errors under different experimental conditions, we came to the conclusion stated above.

Before discussing the implications of this conclusion, it may be useful to consider the assumptions that underlie the analysis. The main assumption we made was that the error in the direction of pointing was due entirely to our incorrect choice of an origin defining direction. This assumption neglects other sources of error. One source is the variability in the performance of the subject. That is, for a target at a given location, the direction of pointing may vary on repeated trials. Such variability, along with the ratio of target distance to pointing distance, will affect the uncertainty in the estimate of the subject's origin but not the position of the origin itself.

A more important assumption is that the subject does not make consistent errors in pointing direction, as measured from the origin of the subject's intrinsic coordinate system, and that the consistent error we measure is due entirely to our improper choice of an origin. This as-

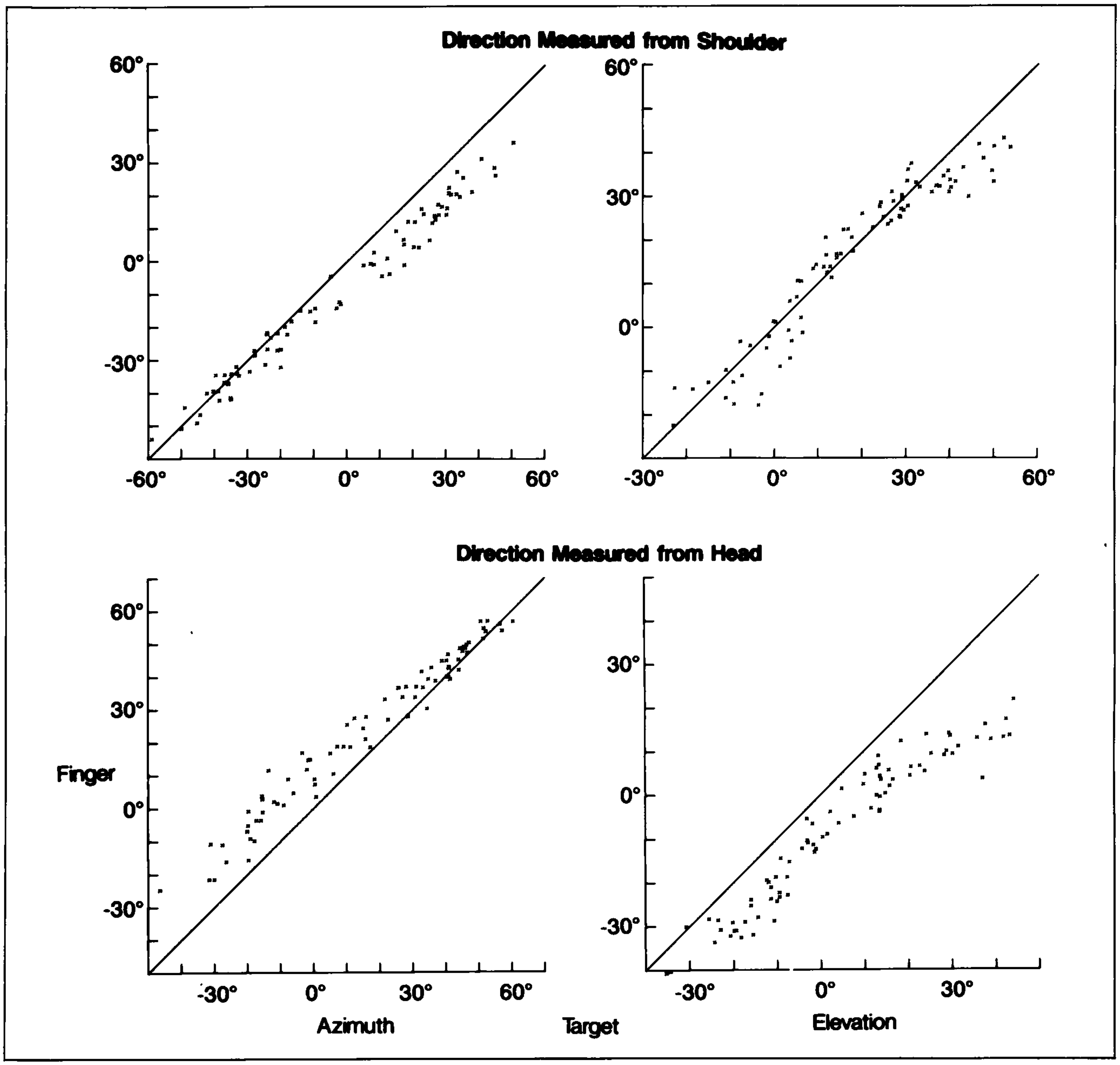


**Figure 6.** Direction of pointing measured from the shoulder (top) and from the head (bottom) when a subject pointed to a spot half-way from the shoulder to the target.

sumption is likely to be incorrect. Subjects do make consistent errors in distance, underestimating distal targets (Figure 2). We have previously suggested that this error in pointing distance arises because subjects use a linear approximation of the nonlinear relationship between target position and the orientation angles at the shoulder and elbow joints that would place the finger on the target (Soechting & Ross 1984; Soechting & Flanders 1989b). These linear approximations involve direction as well as distance. Therefore, some of the directional error in pointing might be due to the use of this approximation, that is, subjects might make directional errors within their intrinsic coordinate system. As can be seen in Figure 3, this component of directional error is small compared to the directional errors induced by shifting the origin when subjects pointed half-way to a target (Figures 6 and 8). Nevertheless, it is possible that such errors in movement production are large enough to cause a bias in the origin of the coordinate system we compute.

One might predict that subjects should be able to point to a location on a line from the head to the target, that is, in a head-centered direction. The task could simply require the subject to imagine the target to be closer

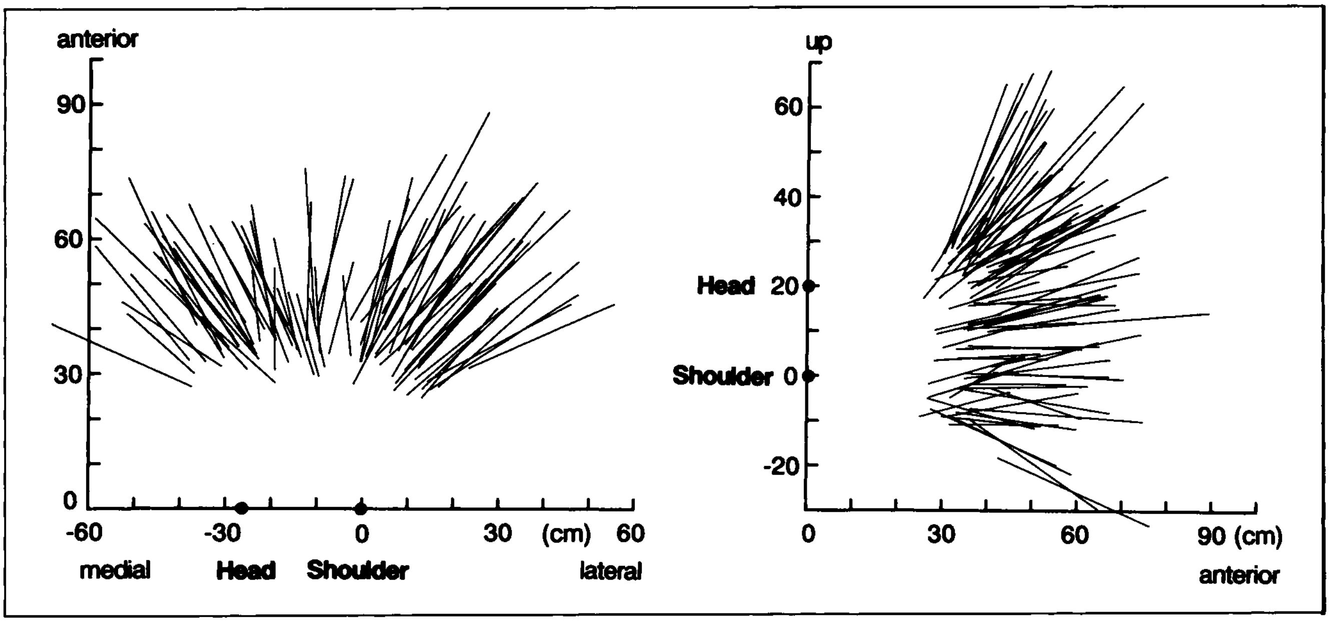


**Figure 7.** Difference between target and finger location viewed from the top (left) and from the side (right). Data are from the same experiment as in Figure 6.

than it appears to be, but at the same retinotopic locus. Moving to a point on a line from the shoulder to the target, at first glance, seems like a more difficult task. Given a target presented visually and represented retinotopically (in a head-centered frame of reference), this task would require the subject to also compute the location of the shoulder in a head-centered frame of reference, to imagine a line between the shoulder and the target and then to compute the direction from the head to a spot on this line. If indeed this were the process subjects used to point half-way from the shoulder, one would expect such additional computations to lead to larger errors and to greater variability in the performance, which we did not observe.

These difficulties disappear if one assumes that pointing movements of the arm automatically evoke a spatial transformation that shifts the origin of the coordinate system used to represent target location from the head to the vicinity of the shoulder. If so, the task of moving half-way from the shoulder becomes much simpler. Direction in a shoulder-centered coordinate system remains unchanged while distance is halved. This hypothesis implies that the computational burden of moving half-way from the head and half-way from the shoulder is about the same. The transformation from head-centered to shoulder-centered coördinates would be involved in both instances, the representation of direction would not need to be modified in either task, distance would need to be halved, before the transformation for movements to a point half-way from the head and after the transformation for movements half-way from the shoulder.

Therefore we hypothesize that one step in the sensorimotor process that leads to a pointing movement of the arm involves a transformation that moves the origin of the coordinate system in which the location of points in extrapersonal space is represented from the center of the head (the eyes) toward the shoulder. Note that our results imply that the origin is not shifted completely to the center of rotation of the shoulder (glenohumeral joint), but to a point that is approximately 10 cm medial to it (Figure 5). However, as we have already mentioned, the subjects' errors in movement production will bias our estimate of the origin. Thus, it is quite possible that the neural representation of target direction is relative to an origin that is closer to the shoulder than our results would indicate.

Although the variability in the estimates of the origin was much greater when subjects were instructed to point to virtual targets in the dark (Figure 4), the results of those experiments are also in accord with our interpretation since the best estimate for the origin of the coordinate system for pointing in this instance was also located between head and shoulder. Taken together with our previous observations concerning distance (see Figure 2), these results indicate that, for pointing movements of the arm, target location (distance and direction) is represented in (approximately) shoulder-centered coordinates. Target location is initially represented in a retinotopic frame of reference, and most likely also one

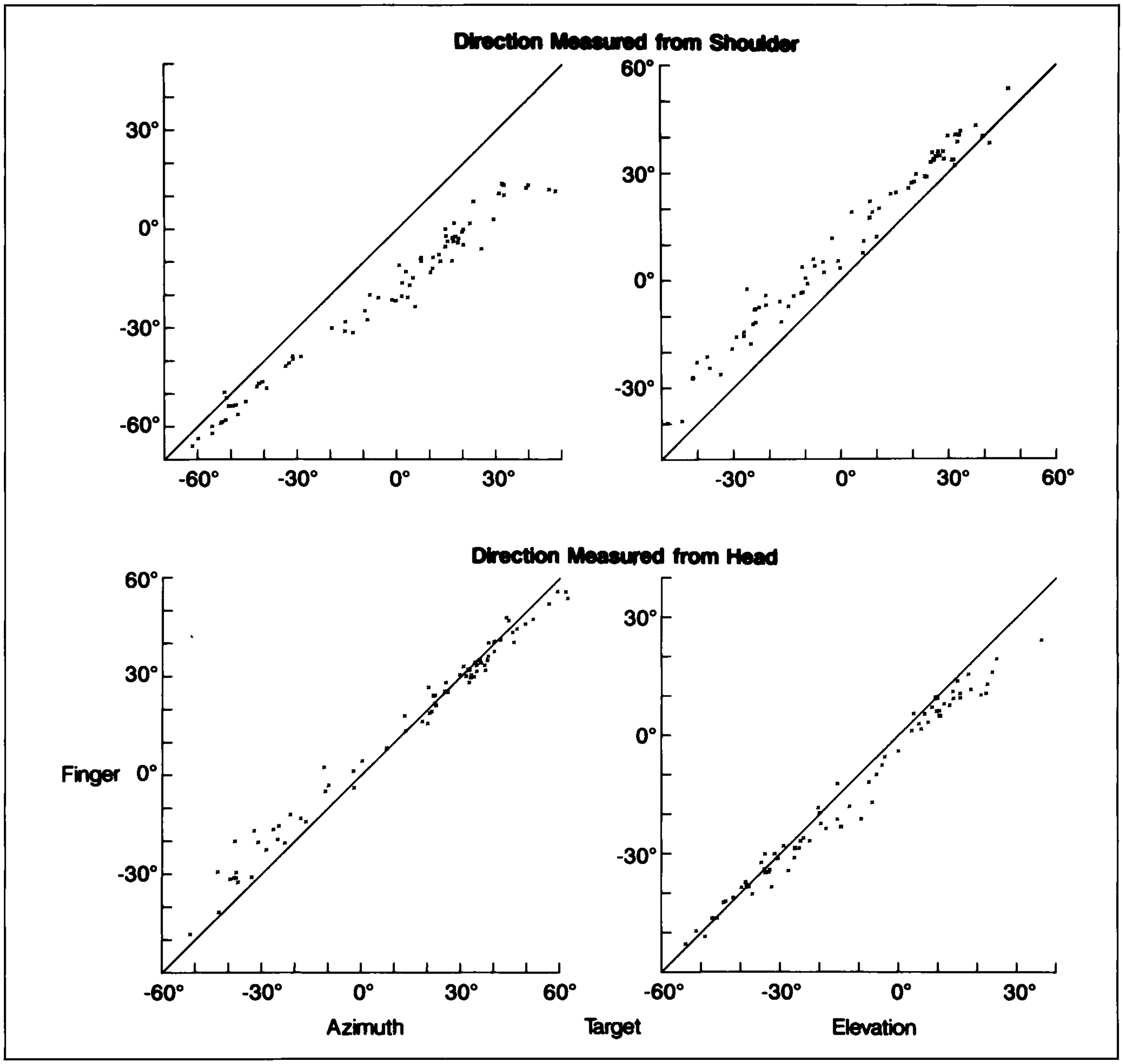


**Figure 8.** Direction of pointing when a subject pointed to a spot half-way from the head to the target.

that is head-centered but fixed in space (Andersen & Zipser 1988; Jay & Sparks 1984, 1987; Mays & Sparks 1980). Therefore our results imply that there is an obligatory transformation from head-centered to coordinates centered at a point closer to the shoulder, at least for arm movements to a target.

The observations concerning pointing movements to virtual targets in the light would appear to contradict this conclusion. For all four subjects in this experimental condition, our estimate of the origin for direction is centered about the head and far removed from the shoulder. Thus, one might conclude that movements where visual feedback is available do not evoke a transformation from head- to shoulder-centered coordinates. However, we believe it is more likely that movements performed in the presence or absence of visual feedback involve the same serial processes, including a shift from head- to shoulder-centered coordinates. We suggest that the difference in the results in the lights-off and lights-on conditions (Figures 4 and 10) arises because subjects make visually mediated corrections to the movement to align the finger with landmarks in the visual surround when this is possible (Georgopoulos, Kalaska, & Massey 1981; Prablanc, Echallier, Komilis, & Jeannerod 1979;

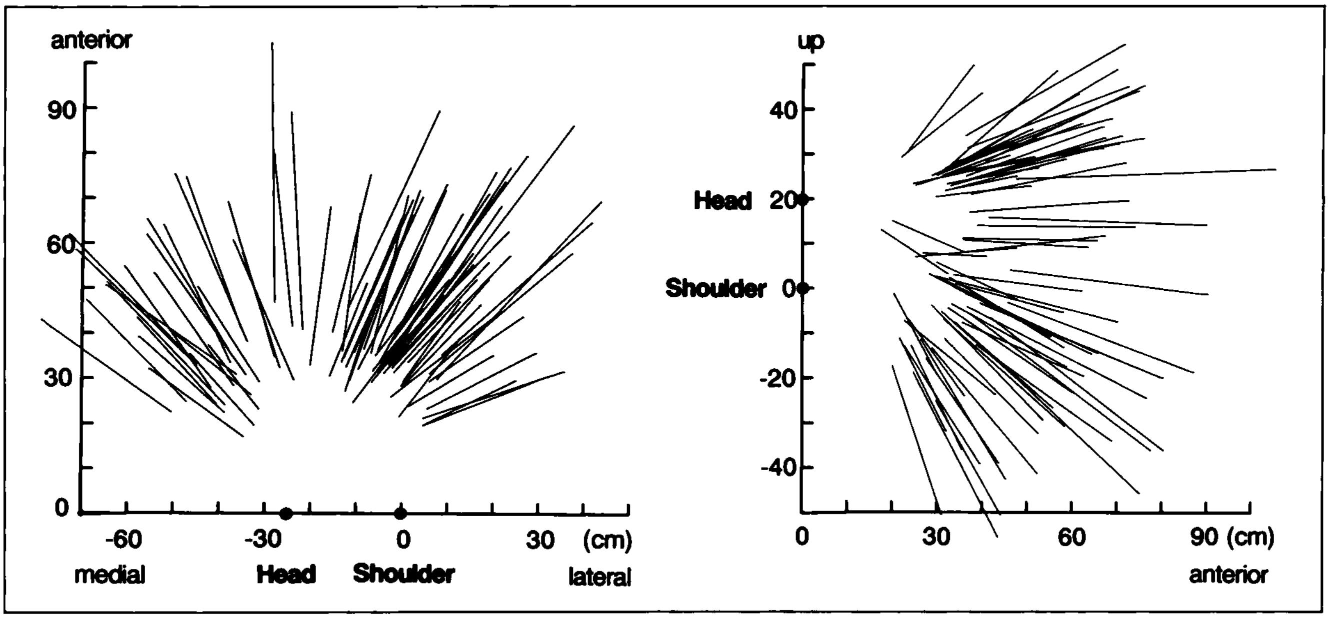


**Figure 9.** Difference between target and finger location for data from the same experiment as in Figure 8.

**Table 1.** Variable Error (Degrees) in Pointing Direction

| | *Azimuth* | | | *Elevation* | | |
|---|---|---|---|---|---|---|
| *Subject* | *VT* | *1/2S* | *1/2H* | *VT* | *1/2S* | *1/2H* |
| 1 | 2.92 | 2.97 | 3.99 | 2.95 | 3.41 | 3.22 |
| 2 | 2.31 | 2.95 | 2.86 | 2.93 | 3.67 | 2.65 |
| 3 | 2.61 | 4.76 | 3.90 | 2.24 | 3.77 | 2.62 |
| 4 | 2.35 | 3.41 | 3.23 | 2.69 | 3.15 | 2.90 |
| Average | 2.55 | 3.52 | 3.49 | 2.70 | 3.50 | 2.85 |

VT, point to virtual target in dark; 1/2S, point half-way from shoulder; 1/2H, point half-way from head.

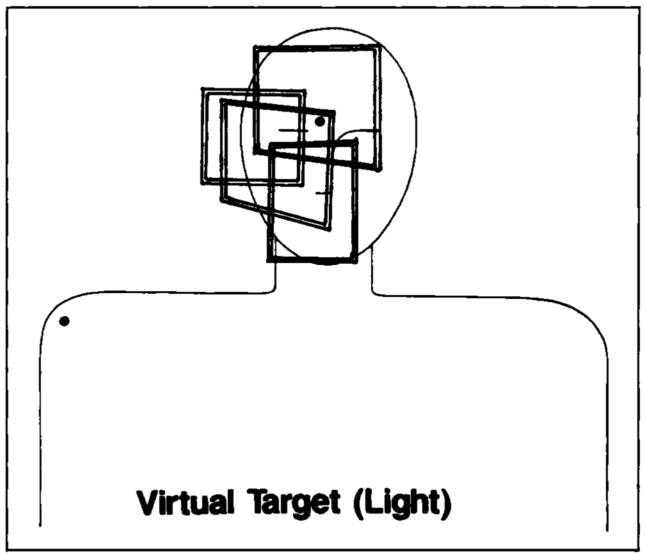


**Figure 10.** Estimate of the origin for pointing to virtual targets in the light.

Prablanc, Pelisson, & Goodale 1986; Soechting & Lacquaniti 1983), thus tending to bias our estimate toward a head-centered frame of reference.

## METHODS

The experimental arrangement and recording system have been described in detail elsewhere (Soechting & Flanders 1989a). In those experiments, subjects stood erect and were presented with a target. They were asked to remember the location of the target, the target was removed and the lights were turned out, and the subjects were instructed to point with their right arm to the remembered target location (Virtual target—dark). Even though subjects made appreciable errors in distance (see Figure 2), as shown under Results, the analysis yielded a large uncertainty in the estimate of the origin for pointing.

Therefore we conducted another set of experiments that was designed to increase the difference between target distance and pointing distance, and hence to yield a better estimate of the origin of the coordinate system for pointing. Each experiment consisted of four blocks of trials, each block encompassing about 80 trials. In each block, target location was varied randomly from trial to trial over a range of directions ±50° mediolaterally and 50° above and below the shoulder.

In the first block of trials we again asked subjects to point to virtual targets in the dark. In the next three blocks we asked them to point half-way to a virtual target, also in the dark. In the second block, no further instructions were given. In the third block, we asked them to point to a location half-way on a line connecting the shoulder and the target, that is in the direction from the shoulder, and in the fourth block, to point in the direction from the head. The task was demonstrated to the subjects for the third and fourth blocks to make sure they understood the instructions.

Four subjects participated in this set of experiments. All were naive to the purpose of the experiment.

### Recording System and Further Analysis

The locations of the finger and of the target were measured ultrasonically with a resolution of 0.1 mm, as was a point on the upper arm located approximately at the center of rotation of the shoulder. The source for the ultrasound was a spark emitted at the tip of a small stylus. One stylus was grasped by the subject and represented finger position, the second constituted the target, and the third was attached to the subject's right upper arm. The measured position of this last stylus was shifted medially so that the position of the "shoulder" was 4 cm medial to the surface of the arm. The position of the target and of the finger was calculated relative to this "shoulder" position.

A multivariate regression analysis between finger position and target position was performed. In this regression analysis we included terms up to cubic order in target position and retained only those terms that were statistically significant (Soechting & Flanders 1989a). This regression analysis was used to predict finger position at an arbitrary target location (Figure 2). It was also used to compute the variable error, which we define as the square root of the variance of the difference between finger location and the polynomial, that is, the portion of the data that could not be accounted for by the polynomial. Full details are given in Soechting and Flanders (1989a).

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## REFERENCES

Andersen, R. A., & Zipser, D. (1988). The role of posterior parietal cortex in coordinate transformations for visual-motor integration. *Canadian Journal of Physiology and Pharmacology*, *66*, 488–501.

Georgopoulos, A. P. (1986). On reaching. *Annual Review of Neuroscience*, *9*, 147–170.

Georgopoulos, A. P., Kalaska, J. F., & Massey, J. T. (1981) Spatial trajectories and reaction times of aimed movements: Effects of practice, uncertainty and change in target location. *Journal of Neurophysiology*, *46*, 725–743.

Grobstein, P. (1988). Between the retinotectal projection and directed movement: Topography of a sensorimotor interface. *Brain Behavior Evolution*, *31*, 34–48.

Hollerbach, J. M. (1982). Computers, brains and the control of movement. *Trends in Neuroscience*, *5*, 189–192.

Hollerbach, J. M., & Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement. *Biological Cybernetics*, *44*, 67–77.

Jay, M. F., & Sparks, D. L. (1984). Auditory receptive fields in primate superior colliculus shift with changes in eye position. *Nature (London)*, *309*, 345–347.

Jay, M. F., & Sparks, D. L. (1987). Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *Journal of Neurophysiology*, *57*, 35–55.

Mays, L. E., & and Sparks, D. L. (1980). Saccades are spatially, not retinocentrically, coded. *Science*, *208*, 1163–1165.

Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). 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. *Biological Cybernetics*, *35*, 113–124.

Prablanc, C., Pelisson, D., & Goodale, M. A. (1986). Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research*, *62*, 293–302.

Soechting, J. F. (1989). Elements of coordinated arm movements in three-dimensional space. In S. A. Wallace (Ed.), *Perspectives on the coordination of movement*, pp. 47–83.

Soechting, J. F., & Flanders, M. (1989a). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology*, *62*, 582–594.

Soechting, J. F., & Flanders, M. (1989b). Errors in pointing are due to approximations in sensorimotor transformations. *Journal of Neurophysiology*, *62*, 595–608.

Soechting, J. F., & Lacquaniti, F. (1983). Modification of trajectory of a pointing movement in response to a change in target location. *Journal of Neurophysiology*, *49*, 548–564.

Soechting, J. F., & Ross, B. (1984). Psychophysical determination of coordinate representation of human arm orientation. *Neuroscience*, *13*, 595–604.

Sparks, D. L. (1988). Saccadic command signals in the superior colliculus: Implications for sensorimotor transformations. *Canadian Journal of Physiology and Pharmacology*, *66*, 527–531.