# COORDINATION OF ARM MOVEMENTS IN THREEDIMENSIONAL SPACE. SENSORIMOTOR MAPPING DURING DRAWING MOVEMENT 

J. F. Soechting,* F. Lacquaniti $\dagger$ and C. A. Terzuolo* $\dagger$<br>*Laboratory of Neurophysiology, University of Minnesota, Minneapolis, Minnesota, U.S.A. and $\dagger$ Istituto di Fisiologia dei Centri Nervosi, CNR Milan, Italy


#### Abstract

In this paper data are presented concerning the motion of limb segments during drawing movements executed in different planes in free space. The technique used allows the determination of the wrist and elbow positions in space as well as the measurement of the elbow angle of extension. Other kinematic variables are determined trigonometrically. Elbow and shoulder torque is also calculated.

For circles and ellipses, it was found that the motion at the wrist is sinusoidal in two orthogonal dircctions in the planc of motion. Angular motion, when described by a set of angles previously identified psychophysically as constituting an appropriate coordinate system, is also sinusoidal. Although the number of degrees of freedom of the arm affords many possible ways of performing the task, there is a fixed phase relation between the angles of elevation of the upper arm and forearm for naturally executed movements in all planes of space. Also, the phase of the yaw angles of the upper arm and forearm relative to the angles of elevation are related to the plane of motion and to the slant of ellipses in a fixed manner. There is a simple mapping between angular motion and intended wrist trajectory. Because this mapping is not valid for all planes of space, the actual trajectory can deviate from the intended one. However, the subject has no cognizance of the distortion.

The calculated torque deviates substantially from sinusoidal and does change significantly when the same movement is executed in different planes. Results of simulations and mathematical analysis indicate that the fixed phase relationship between angles of elevation leads to a minimal distortion from sinusoidal motion at the wrist in an average sense and that the characteristic distortions observed in the sagittal plane result inevitably from this constraint on the phase relations. The results support the assumption that the topology of the sensorimotor map used for the production of the movement and for its perception is the same. The problem of invariant relationships between kinematic parameters is discussed and the suggestion is made that they represent a general constraint, leading through learning and practice to an optimal solution in an average sense.


In order to pursue experimentally the problem of motor coordination of the human arm, one can use the following observations to provide a starting point: (1) although the number of possible degrees of freedom theoretically would allow arm movements to be performed in a variety of ways, it has been shown ${ }^{4,9,19,21,23}$ that normally any given motor task is performed in a unique and stereotyped manner. Also, for some tasks the movement can be characterized by invariant relations in the space and time domains. ${ }^{8,19,22}$ In particular, shoulder and elbow motions are coupled in the sense that the angular motion at the two joints maintains certain fixed relations. Also, a law relating curvature of the trajectory at the hand and movement speed has been described for drawing movements. ${ }^{12}$ (2) Perceptually, there appears to be a preferred coordinate representation describing the orientation of limb segments in space. ${ }^{16,20}$

In order to generalize these observations and to approach experimentally the problem of motor coordination in three-dimensional space, one can start with the simplifying assumption that invariant relations hold true for all naturally executed and highly practiced movements and furthermore, that the same mapping between motor and sensory events is involved in the production and perception of a
movement. Such mappings have been developed theoretically by Pellionisz and Llinás ${ }^{14}$ and dealt with in detail for the vestibular system by Robinson. ${ }^{15}$ Although in these two instances, the mapping is by means of tensor transformations between different coordinate systems, other types of transformations are not meant to be excluded.

Given the simplifying assumption stated above, it appears appropriate to begin by studying movements with highly specified and repeatable aspects of their trajectories. Drawing of circles and ellipses are such types of tasks since it is reasonable to expect that subjects should be able to transfer the drawing of such figures from the ordinary planes (frontal and horizontal) to other planes without a significant degradation of performance.

This study will focus on shoulder and elbow motions during the execution of such tasks.

## METHODS

## Motor tasks

Right-handed subjects were asked to draw, in free space, geometrical figures such as circles or ellipses with their right arm. They were asked to confine their movements within a cube measuring 50 cm to a side. With this exception, the amplitude of the movement was not specified precisely, nor was the exact location of the movement trace within the
available space. They were asked to perform the movement repetitively ( 5 -10 cycles) at a self-determined frequency (generally from 0.7 to 1.2 Hz ). The subjects were asked to draw the figures in the frontal plane, in the sagittal plane or in planes oblique to these two principal planes. For the ellipses it was specified that the major axes be oriented either vertically, horizontally or slanted obliquely to the horizontal. Finally, movement direction. clockwise or counterclockwise. was also specified.
Since we were able to monitor motion at the shoulder and elbow joints only, the subjects were asked to keep their wrist rigid and thus produce the geometric figure by motion resiricted to the proximal joints. Most movements were performed with the eyes open, but in some instances subjects were asked to produce the specified movement with their eyes closed. In some cases the subjects were asked to carry a 1 kg weight in their hand while making the drawing movement.

## Recording system

The position of the elbow and of the wrist in space was obtained by means of a pair of ultrasound emitters and a set of three orthogonal, linear microphones. ${ }^{18}$ The two emitters were pulsed in an alternating fashion and their perpendicular distance from the microphones was recorded with a spatial resolution of 0.1 mm . Temporal resolution was 20 ms . The two emitters were located 10 cm laterally to the wrist and to the elbow. In addition, elbow angle of flexion-extension was measured goniometrically. ${ }^{2}$ Electromyograms of biceps and anterior deltoid muscles were recorded in a conventional manner using surface electrodes, sampled at 500 Hz and full-wave rectified.

## Kinematic analysis

The angular orientation of the upper arm and of the forearm was computed from the position of the two emitters and the measured elbow joint angle. In Fig. 1, the points s, $e$ and $w$ denote the position of the shoulder, elbow and wrist, respectively. The Cartesian coordinate system $X Y Z$ is fixed in space with its origin at the shoulder, $X$ corresponding to the anterior direction, $Y$ to the lateral direction and $Z$ the vertical. The elbow joint angle of flexion-extension is given by $\phi$.

Assuming that the shoulder is fixed, that is, there is no translation of its center of rotation, the arm has four degrees of motion; three at the shoulder joint and one at the elbow joint. Therefore four angles are necessary to fully describe the motion of the arm. They can be defined in a number of different ways. ${ }^{1.29}$ The angular measures we have chosen are also defined in Fig. 1. They are: $\theta$ and $\beta$, the angular elevation of the upper arm and forearm, respectively, and $\eta$ and $\alpha$. upper arm and forearm yaw. Angular elevation is measured in a vertical plane relative to the vertical, yaw in the horizontal plane relative to the $X$ axis. For a lateral rotation, yaw is defined to be positive. Thus, as illustrated in Fig. $1, \eta$ is positive and $\alpha$ is negative. These angles ( $\eta$ and $\theta$ for the upper arm, $\alpha$ and $\beta$ for the forearm) were identified previously psychophysically as the preferred coordinate system for recognition of the orientation of the arm in space. ${ }^{20}$ Therefore, they appear to be the logical choice to describe arm movement as well. They will be referred to as orientation angles.

Using this coordinate system, the position of the elbow and of the wrist is:

$$
x_{0}=f_{1} \sin \theta \cos \eta
$$

elbow:

$$
r_{e}=t_{1} \sin \theta \sin \eta
$$

$$
z_{e}=f_{1} \cos \theta
$$

$$
x_{w}=x_{\mathrm{e}}+\ell_{2} \sin \beta \cos \alpha
$$

wrist:

$$
\begin{equation*}
y_{\mathrm{w}}=y_{\mathrm{e}}+\ell_{2} \sin \beta \sin \alpha \tag{2}
\end{equation*}
$$

where $f_{1}$ and $f_{2}$ are the length of the upper arm and forearm. respectively.

The angles $\alpha$ and $\beta$ could be calculated directly from the location of the two emitters:

$$
\begin{align*}
& \tan \alpha=\Delta y \Delta x  \tag{3}\\
& \tan \beta=-\left(\Delta x^{2}+\Delta y^{2}\right)^{1 / 2} / \Delta z
\end{align*}
$$

$\Delta x, \Delta y$ and $\Delta z$ being the difference in the $x, y$ and $z$ components of the location of the two emitters.

In order to calculate the orientation angles $\eta$ and $\theta$ of the upper arm, the location of the center of rotation at the shoulder had to be determined. This was done graphically by asking the subject to move his arm back and forth in the sagittal plane and recording the trajectory of two points on the upper arm. There was an additional complication, however; the emitters did not measure directly the position of the elbow and the wrist in space, but rather that of points located 10 cm laterally to these landmarks. Since the position of the emitter for the elbow ( $x, y, z$ ) is given by Soechting ${ }^{17}$

$$
\begin{align*}
& x=x_{\mathrm{e}}-a(\sin \zeta \cos \theta \cos \eta-\cos \zeta \sin \eta) \\
& y=y_{\mathrm{e}}-a(\sin \zeta \cos \theta \sin \eta-\cos \zeta \cos \eta)  \tag{4}\\
& z=z_{\mathrm{e}}+a \sin \zeta \sin \theta
\end{align*}
$$

(where $a$ is the distance from the elbow to the emitter), the true position of the elbow can be determined once the angles are known. The true position of the wrist is given similarly.

The angle $\zeta$ is the angular rotation about the axis of the humerus required to bring the plane of the arm (shoulder elbow-wrist) from the vertical to its actual orientation. The angle $\zeta$ can be calculated according to:

$$
\begin{equation*}
\sin \zeta \sin \theta=n_{z} \tag{5}
\end{equation*}
$$

where $n_{z}$ is the $z$-component of the perpendicular to the


Fig. I. Definition of angular coordinates used to describe the orientation of the arm in space. The points $s$, e and $w$ denote the location of the shoulder, elbow and wrist. while $X, Y$ and $Z$ define a Cartesian coordinate system fixed in space, corresponding to the anterior, lateral and vertical directions. The orientation of the arm is defined by the angular elevation of the upper arm ( $\theta$ ) and of the forearm ( $\beta$ ) and the angles of yaw ( $\eta$ and $\alpha$ ). Angular elevation is measured relative to the vertical ( $Z$ ) axis in a vertical plane, yaw in the horizontal plane relative to the anterior $(X)$ direction. The anatomical angle of elbow flexion-extension is defined as $\phi$.
plane of the arm. Furthermore, the pair of angles $(\zeta, \phi)$ cannot be specified independently of $(\alpha, \beta)$. Rather, they are related by:

$$
\begin{aligned}
& \cos \phi=\cos \beta \cos \theta-\sin \beta \sin \theta \cos (\alpha-\eta) \\
& \sin \zeta \sin \phi=\sin \beta \sin (\alpha-\eta) .
\end{aligned}
$$

Details are given in Soechting. ${ }^{17}$
The angles $\eta, \theta$ and $\zeta$ were calculated according to the following procedure. The positions of the emitters at the elbow and the wrist were specified in terms of the angles $\eta$, $\theta, \zeta$ and the measured elbow angle $\phi$. An iterative procedure was then used to obtain the values of $\eta, \theta$ and $\zeta$ to minimize the difference between the measured and the calculated positions of the emitters. Note that the angles $\eta, \theta, \zeta$ can be determined uniquely knowing simply the location of the center of rotation at the shoulder and the location of the two emitters. Since we also measured elbow angle $\phi$, the system is over-determined and thus permits an estimate to be made of the error introduced by assuming a fixed center of rotation at the shoulder. On average, the root mean square error at each emitter was about 0.5 cm . Once the angles had been calculated, the actual position of the elbow and of the wrist in space was estimated according to the equations (4) and (2). (Only the calculated positions of the wrist and elbow will be used, rather than the measured positions of the emitters.) As a second estimate of the uncertainty of our calculations, we determined the root mean square difference between the measured and calculated values of the elbow angle $\phi$; this error typically ranged from $2^{\circ}$ to $4^{\circ}$. The major source of error is that there is inevitably some translation of the center of rotation of the shoulder joint, given its anatomy.

## Torques

The torque required to produce the observed motion was calculated according to equations ( $2-13$ ) and (2-29) to (2-31) of Soechting, ${ }^{17}$ following smoothing and numerical differentiation of the joint angles, the mass of each limb segment and its moments of inertia having been estimated on the basis of total body weight and other anthropometric data. ${ }^{3}$

Since the shoulder has three degrees of freedom, torque at the shoulder is a vector quantity. In this paper we shall represent its components in a Cartesian frame of reference fixed in space ( $X Y Z$ coordinates of Fig. 1). The direction of the lines of action of muscies acting at the shoulder joint will not be fixed in this frame of reference, however. Instead, muscles whose insertion is on the humerus will have lines of action which are approximately constant in a reference frame fixed to the arm. Thus torque estimates will also be given for this frame of reference. For the sake of convenience we have chosen a Cartesian coordinate system which is aligned with the spatially fixed frame of reference when the upper arm is vertical and the arm lies in the sagittal plane. A transformation from torques represented in one frame of reference to their representation in another frame of reference is achieved by means of multiplication by the rotation matrix between the two coordinate systems (equations $1-3$ of Soechting). ${ }^{17}$

## Phase and disiortion analysis

As we shall show in Results, the movement of the wrist in space, as well as the changes in orientation angles $\eta, \theta, \alpha$, $\beta$ which produced it, were approximately sinusoidal. Therefore it was possible to quantify the modulation of angular motion in terms of mean value, amplitude and phase of the fundamental. To this end, the period of the oscillations was calculated from the times at which the vertical component of the wrist velocity crossed zero. Mean, amplitude and phase of the fundamental for each parameter were then calculated by Fourier analysis. The distortion from a true sinusoid was defined conventionally as the root mean square difference between the fundamental component and the
experimental value, normalized by the latter's variance. Distortion can thus range from 0 to $l$. The values reported in this paper are for the velocities of each of the variables.

This report summarizes the results of five experiments involving three subjects.

## RESULTS

## Circles and ellipses drawn in different planes

Circular or ellipsoidal motion at the wrist results from a combination of approximately sinusoidal oscillations in the vertical and horizontal directions. ${ }^{7,12}$ This has been verified to be true also for movements in free space. Figure 2 shows typical results from one subject who was asked to draw a circle in the frontal plane. The trajectories described by the wrist and the elbow in the execution of this task are shown in three-dimensional plots in Fig. 2A. The projections of the trajectories onto the horizontal $(X Y)$ and sagittal planes $(X Z)$ are indicated by dashed lines. The direction of the movement is denoted by arrows; in this instance the movement was performed in a clockwise direction as viewed by the subject.

The trajectory of the movement of the wrist was primarily in the frontal plane and in this plane it approximated a circle, as may be appreciated in the left-most panel of Fig. 2C which describes the projection of the wrist onto the frontal plane ( $Y Z$ ). However, the amplitude of the movement in the vertical direction was somewhat larger than that in the horizontal direction; thus the trace may be described more accurately as an ellipse with moderate eccentricity. Furthermore, there was little cycle-tocycle variability in the position of the wrist or of the elbow. The distortion of the velocity (as defined in Methods) of the sinusoidal oscillations of the wrist for the vertical $(Z)$ and horizontal ( $Y$ ) directions were 8 and $10 \%$, respectively, the two components of the movement being $88^{\circ}$ out of phase.

Figure 2B shows that the sinusoidal movement at the wrist resulted from sinusoidal changes in the orientation angles, that is $\theta$ and $\eta$ which define the angular elevation and the yaw of the upper arm, and $\beta$ and $\alpha$ which define the elevation and yaw of the forearm, respectively. The panel also shows changes in the measured angle of elbow flexion-extension $(\phi)$. The distortions in $\alpha, \beta$ and $\theta$ were comparable to those computed for the motion at the wrist, the values ranging from 10 to $13 \%$. The distortion in the angle of yaw of the upper arm $(\eta)$ was somewhat larger ( $30 \%$ ); it can be appreciated in Fig. 2B as an asymmetry in the rising and falling phases, the rate of increase in $\eta$ being greater than its rate of decrease. In this instance, the distortion in $\phi$ was modest (14\%).

The deviation from sinusoidal motion and the phase relations between different angles can also be appreciated in the angle-angle plots shown in Fig. 2 C . For true sinusoidal motion such plots should describe an ellipsoidal or straight-line relationship


Fig. 2. Circle drawn in free space in the frontal plane. (A) depicts the trajectory of the wrist (left) and of the elbow (right) in three-dimensional space. The dashed lines indicate the projections of these trajectories onto the horizontal and sagittal planes and the arrows indicate the direction of motion (clockwise as viewed by the subject). Variations in the orientation angles and in the elbow angle are shown in (B). The upper left panel in (C) shows the projection of the wrist trajectory on the frontal plane. In this figure, as in succeeding figures, a three-dimensional perspective view of wrist trajectory is presented (solid line in (A)) as well as its projection onto the principal plane of motion (C). The other panels in C show the variation of upper arm yaw ( $\eta$ ), forearm elevation ( $\beta$ ) and yaw ( $\alpha$ ) as a function of upper arm elevation ( $\theta$ ). Note that the changes in each of these angles is approximately sinusoidal. The phase relations between angles are given by the polar diagram in each panel, i.e. $\eta$ lags $\theta$ by $134^{\prime}$, while $\alpha$ lags $\theta$ by $104^{\circ}$ and $\beta$ and $\theta$ are $179^{\circ}$ out of phase.
between the angles. For example, if the sinusoidal modulation of two angles (at the same frequency) is in phase with each other, or $180^{\circ}$ out of phase, the relationship should be rectilinear. If there is a phase difference of $90^{\circ}$, the relationship should be ellipsoidal with the major axis oriented vertically or horizontally. A deviation from an ellipsoidal shape indicates a deviation from sinusoidal motion.

Since angular elevation of the upper arm 0 and of the forearm $\beta$ are close to sinusoidal, the approximately rectilinear relationship between these angles indicates a phase difference close to $180^{\circ}$. The calculated value ( $179^{\circ}$ ) is shown schematically by the arrow in the polar diagram in the insert. Yaw of the forearm ( $\alpha$ ) lags $\theta$ by $104^{\circ}$. The distortion in $\eta$ manifests itself as a flattening of the upper half of the ellipse; $\eta$ lagged $\theta$ by $134^{\circ}$.

The results shown in Fig. 2 are typical of data obtained from all three subjects when they were asked
to draw a circle in the frontal plane. In all cases, the values of the distortions from sinusoidal motion of the orientation angles were comparable to those of the vertical $(Z)$ and horizontal $(Y)$ components of the motion at the wrist, the distortion in yaw of the upper $\operatorname{arm}(\eta)$ being greater than that in the other angles (see Table 1). Furthermore, the phase relations between the angles were close to those shown in Fig. 2, namely a phase lead of $\beta$ relative to $\theta$ of about $180^{\circ}$ and a phase difference between $\alpha$ and $\theta$ of about $110^{\circ}$. (A more detailed analysis of these phase relations will be provided later.)

The behavior illustrated in Fig. 2 was unaffected by a number of experimental procedures. Indeed the results were no different when the subjects performed the task with their eyes closed, except that the cycle-to-cycle variability of the movement was greater. Also, the trajectory of the movement and the changes in orientation angles which gave rise to it were not

Table 1. Distortion of wrist velocity (in \%) and in the velocity of the orientation angles (relative to that in wrist velocity)

| Subject | Plane | $N$ | $Z$ | $\theta / Z$ | $\beta / Z$ | $\phi / Z$ | $X$ |
| :---: | :---: | ---: | :---: | :---: | :---: | :---: | :---: |
| A | Frontal | 12 | $16.8 \pm 5.1$ | $1.10 \pm 0.29$ | $1.57 \pm 0.32$ | $3.10 \pm 1.26$ |  |
|  | Oblique | 12 | $18.2 \pm 5.9$ | $0.99 \pm 0.17$ | $1.41 \pm 0.17$ | $3.64 \pm 1.04$ | $15.4 \pm 3.5$ |
|  | Sagittal | 6 | $18.2 \pm 6.1$ | $2.71 \pm 1.27$ | $1.32 \pm 0.15$ | $1.53 \pm 0.81$ | $34.6 \pm 16.7$ |
|  | Frontal | 21 | $12.0 \pm 4.0$ | $1.60 \pm 0.49$ | $1.42 \pm 0.43$ | $2.36 \pm 1.68$ |  |
| B | Oblique | 7 | $13.6 \pm 2.6$ | $2.12 \pm 0.84$ | $1.79 \pm 1.19$ | $1.82 \pm 0.82$ | $34.6 \pm 14.0$ |
|  | Sagittal | 11 | $14.4 \pm 3.5$ | $3.15 \pm 1.72$ | $1.21 \pm 0.53$ | $0.98 \pm 0.27$ | $27.2 \pm 6.9$ |
|  | Frontal | 4 | $10.9 \pm 1.6$ | $1.18 \pm 0.45$ | $1.99 \pm 0.73$ | $4.15 \pm 0.95$ |  |
| C | Oblique | 4 | $11.4 \pm 2.9$ | $1.02 \pm 0.54$ | $1.81 \pm 0.16$ | $5.25 \pm 1.65$ | $57.3 \pm 16.6$ |
|  | Sagittal | 5 | $8.4 \pm 1.8$ | $1.16 \pm 0.28$ | $2.17 \pm 0.80$ | $4.41 \pm 2.54$ | $31.4 \pm 18.9$ |
|  |  |  | $Y$ | $\eta / X$ | $\eta / Y$ | $\alpha / X$ | $\alpha / Y$ |
| A | Frontal | 12 | $17.4 \pm 8.4$ |  | $2.02 \pm 0.74$ |  | $1.53 \pm 0.67$ |
|  | Oblique | 12 | $18.3 \pm 4.4$ | $1.67 \pm 0.39$ | $1.42 \pm 0.40$ | $1.28 \pm 0.23$ | $1.09 \pm 0.25$ |
|  | Sagittal | 6 |  | $0.70 \pm 0.09$ |  | $0.99 \pm 0.14$ |  |
|  | Frontal | 21 | $13.3 \pm 4.0$ |  | $3.26 \pm 1.47$ |  | $1.57 \pm 0.42$ |
|  | Obliquc | 7 | $20.8 \pm 4.9$ | $1.26 \pm 0.47$ | $1.77 \pm 0.38$ | $0.81 \pm 0.38$ | $1.28 \pm 0.56$ |
|  | Sagittal | 11 |  | $1.02 \pm 0.49$ |  | $0.97 \pm 0.34$ |  |
|  | Frontal | 4 | $14.7 \pm 2.1$ |  | $2.03 \pm 1.29$ |  | $1.01 \pm 0.09$ |
| C | Oblique | 4 | $37.4 \pm 21.4$ | $0.50 \pm 0.22$ | $1.15 \pm 0.97$ | $0.47 \pm 0.12$ | $1.07 \pm 0.96$ |
|  | Sagittal | 5 |  | $0.99 \pm 0.58$ |  | $0.93 \pm 0.39$ |  |

affected when the subject carried a 1 kg weight in his hand. Finally, no differences were found when the subject traced a path in space by following the perimeter of a hoop.

Figure 3 summarizes the findings from which these conclusions were drawn. In this instance, the subject was tracing the outline of a circle in the frontal plane by following the perimeter of a hoop while carrying a 1 kg weight. Note that $\theta, \alpha$ and $\beta$ show little distortion also in this case and that the phase of $\beta$ relative to $\theta$ is again $179^{\circ}$. The differences in the phases of $\eta$ and $\alpha$ relative to $\theta$ in Figs 2 and 3 stem from the fact that the direction of the movement was reversed (counterclockwise in Fig. 3 and clockwise in Fig. 2). Here $\alpha$ leads $\theta$ by $103^{\circ}$ compared to a phase lag of $104^{\circ}$ in Fig. 2. Similarly, $\eta$ leads $\theta$ by $144^{\circ}$ compared to a phase lag of $134^{\circ}$ in Fig. 2. Thus the difference in direction of movement, clockwise vs counterclockwise, results in a change in the sign of the phases of the yaw angles ( $\eta, \alpha$ ) relative to the elevation angles $(\theta, \beta)$.

Mathematically, going from a clockwise rotation to a counterclockwise rotation is equivalent to going backwards rather than forwards in time, since $z_{\mathrm{w}}=A \cos t$ and $y_{\mathrm{w}}=A \sin t$. In terms of the orientation angles, this is equivalent to inverting the sign of the phase angle, from positive to negative and vice versa. Note that the distortion in $\eta$ is unaffected by changing the direction of the movement. In Fig. 2, the falling phase of $\eta$ is faster than the rising phase; in Fig. 3 it is the rising phase which is faster. In both cases, it is the upper part of the $\eta-\theta$ ellipse which is flattened.

Figure 4 shows the results of one trial in which the subject was asked to draw a circle in the sagittal plane. Also, in this case there is little cycle-to-cycle variability in the movement at the wrist or at the elbow, but the trajectory described by the wrist
deviates appreciably from a circular motion. This can be seen in Fig. 4A and more appreciably in the upper left panel in Fig. 4C which shows the projection of the wrist motion onto the sagittal plane. Specifically, there is a flattening of the proximal portion of the trajectory of the wrist, the proximal and distal portions of the movement being asymmetric. In this casc the anteroposterior $(X)$ component of wrist velocity deviated appreciably from sinusoidal ( $32 \%$ distortion) and was $60 \%$ larger than that in the vertical component. Nevertheless, the orientation angles were modulated in approximately sinusoidal fashion (Fig. 4 B ); the distortions in the angular elevation ( $\theta, \beta$ ) were about the same as that in the vertical component of wrist motion (a ratio of 0.98 for $\theta$ and 1.02 for $\beta$ ), while the distortion in the yaw angles ( $\eta, \alpha$ ) was appreciably less than that for the horizontal component of the movement (ratios of 0.67 and 0.78 , respectively).

As for the phase relations of $\beta$ and $\alpha$ relative to $\theta$, they are the same when the subject is asked to draw a circle in the sagittal or in the frontal plane. This can be seen by comparing Fig. 4C with Fig. 2C. In both cases, $\beta$ is about $180^{\circ}$ out of phase with respect to $\theta$, while $\alpha$ lags $\theta$ by about $110^{\circ}$. The phase of $\eta$ (yaw at the shoulder) relative to $\theta$ is different however, $\eta$ leading by $138^{\circ}$ (Fig. 4) compared to a phase lag of $134^{\circ}$ in Fig. 2.

The distortion of the trajectory of the wrist when subjects were asked to draw circles or ellipses in the sagittal plane, namely the flattening described above, was observed in all three subjects. It should be stressed that they were unaware of any systematic distortion in the trajectories and convinced that their performance in the sagittal plane was as good as that in the frontal plane.



Figure 5 shows another example for the ellipse. Note that the proximal portion of the trajectory at the wrist actually becomes concave, the distortion in the $X$-component of the motion at the wrist being $75 \%$. However, the distortion in the orientation angles is much less. Their phase relations are similar to those shown in Fig. 4 for the circle. The increased extent of the motion in the vertical direction is achieved, as might be expected, by increasing the amplitude of the modulation in the angles of elevation ( $\theta, \beta$ ) compared to the yaw angles.

Figure 5 illustrates one more point. Sinusoidal changes in the orientation angles are not necessarily accompanied by a sinusoidal modulation in the anatomical angle of elbow flexion-extension ( $\phi$ ). (As was shown in Methods, $\phi$ is nonlinearly related to the orientation angles.)

Figure 6 shows that the phase relations between angles which we have described depend on the choice of angular coordinates. The phases between angular elevation of the forearm ( $\beta$ ) and of the upper arm ( $\theta$ ) and between $\phi$ and $\theta$ are represented as polar histograms, this figure summarizing results from all the experiments. Trials have been classified according to whether they were primarily in the frontal plane, the sagittal plane or in a vertical plane oblique to the two principal planes. Regardless of the plane of motion,
the modulation in $\beta$ and $\theta$ is about $180^{\circ}$ out of phase, with a variability of $\pm 15^{\circ}$ about the mean. By contrast, the phase of the elbow joint angle $\phi$ relative to $\theta$ is almost uniformly distributed over the range of $+90^{\circ}$ to $-90^{\circ}$, going through $180^{\circ}$ (Fig. 6B). This is true even for trials in which wrist motion was mainly in the frontal plane.

One possible reason why the modulation in $\beta$ and $\theta$ should consistently be close to $180^{\circ}$ out of phase is presented in Fig. 7 and in the Appendix. (Recall that circular or elliptical motion results from sinusoidal vertical and horizontal motion at the wrist.) The plot of Fig. 7 shows the distortion in the vertical component of the velocity of the wrist as a function of the phase difference between $\beta$ and $\theta$. In this simulation, $\beta$ and $\theta$ were assumed to vary sinusoidally, that is:

$$
\begin{align*}
& \theta=\theta_{0}+\theta_{1} \cos t \\
& \beta=\beta_{0}+\beta_{1} \cos (t+\delta) \tag{6}
\end{align*}
$$

The distortion from a sinusoid for the vertical component of wrist velocity was then computed using cquation (2).

A large range of possible combinations of mean values $\left(\theta_{0}, \beta_{0}\right)$ and amplitudes $\left(\theta_{1}, \beta_{1}\right)$ was explored. The figure shows that the average distortion as well as the maximum distortion are minimum at a phase


Fig. 5. Ellipse drawn in the sagittal plane.


Fig. 6. Distribution of the phase of forearm angular elevation ( $\beta$ ) and elbow angle ( $\phi$ ) relative to upper arm elevation ( $\theta$ ). Data for all trials (circles and ellipses) are plotted as polar histograms with a bin-width of $5^{\circ}$. Trials are grouped according to the plane of motion: frontal (Front.), sagittal (Sag.) or oblique (Obl.) to these two planes. A movement was considered to be in the frontal plane if the amplitude of wrist motion in the lateral direction was at least twice that of motion in the anteroposterior direction and in the sagittal plane if anteroposterior motion was at least twice as great as lateral wrist motion. All other movements were considered to be in an oblique plane. Note that the phases of $\beta$ relative to $\theta$ are clustered around $180^{\circ}$, while the phases of $\phi$ relative to $\theta$ are distributed over a wide range of values.


Fig. 7. Distortion from sinusoidal motion of the vertical component of wrist velocity as a function of the phase difference between upper arm and forearm elevation. Curves show average and maximum distortions calculated assuming sinusoidal angular motion in $\beta$ and $\theta$. Distortion is defined to be the root mean square difference between the fundamental component of vertical wrist velocity and the calculated values, normalized by the latter's variance. Distortion can therefore range from 0 to $100 \%$. The mean values and the amplitudes of the modulation in this simulation ranged as follows: $25^{\circ} \leq \theta_{0} \leq 65^{\circ}, 5^{\circ} \leq \theta_{1} \leq 25^{\circ}$, $55^{\circ} \leq \beta_{0} \leq 105^{\circ}, 5^{\circ} \leq \beta_{1} \leq 35^{\circ}$. All combinations of these four parameters (in increments of $10^{\circ}$ ) were used in computing the average.
difference $\delta$ of $180^{\circ}$. The minimum distortion (not shown in the figure), was less than $2 \%$ at all values of $\delta$.

In the Appendix we show mathematically that a phase difference of $180^{\circ}$ between $\beta$ and $\theta$ leads to a minimum in the distortion in a global sense. That is to say, for a given choice of $\left(\theta_{0}, \beta_{0}\right)$ and $\left(\theta_{1}, \beta_{1}\right)$ some value of the phase lag $\delta$ other than $180^{\circ}$ may actually lead to a smaller distortion in the vertical component of wrist motion. However in an average sense, that is given all possible combinations of the parameters in equation (6) does a $180^{\circ}$ phase difference lead to a solution which is optimal for minimizing distortion.

The yaw angle $\alpha$ of the forearm also showed a consistent phase relation with respect to the angles of elevation $\theta$ and $\beta$. This is illustrated in Fig. 8A, where the distribution of the phase difference between $\alpha$ and $\beta$ has been plotted. Note that there is a clustering in the distribution about a phase lead of $70^{\circ}$ and a phase lag of $70^{\circ}$. The former corresponds to trials in which the movement proceeded in a clockwise fashion (Fig. 2), the latter to movements in a counterclockwise direction.

The phase of the yaw angle $\eta$ of the upper arm was not as consistently related to the other variables. This is apparent in Fig. 8B, where the distribution of the phase difference between the two yaw angles is shown. Nevertheless, a weak trend is obvious. For movements in the frontal plane, $\eta$ and $\alpha$ are approximately in phase (with a distribution of $\pm 30^{\circ}$ ) while they are out of phase for wrist movements in the sagittal plane.

## Slant

It is apparent from equations (1) and (2) that the vertical extent of motion at the wrist depends only on


Fig. 8. Distribution of the phase of forearm yaw $(\alpha)$ relative to forearm elevation $(\beta)$ and of the phase differences between the two yaw angles. Data are for circles and ellipses whose major axes were either vertical or horizontal.
the two angles of elevation $(\theta, \beta)$, while its horizontal extent depends also on the yaw angles. The results presented in Fig. 7 have already indicated that one could account for the consistent phase difference of about $180^{\circ}$ between $\theta$ and $\beta$ by the fact that it leads to a minimum in the distortion of the vertical component of the wrist velocity. We used a similar procedure to see if the phase difference of $\alpha$ relative to $\theta\left( \pm 110^{\circ}\right)$ and to $\beta\left( \pm 70^{\circ}\right)$ could lead to a minimum in the distortion in the horizontal component of the movement. The results of the simulation did not bear out this hypothesis. Instead, as we shall show, the phase of $\alpha$ relative to $\theta$ and $\beta$ is related to the slant of the movement.

For an ellipse, we define slant as the angle which its major or minor axis makes with the horizontal. One factor which determines slant is the phase between the horizontal and vertical components of wrist displacement. For example, a phase of $\pm 90^{\circ}$ between these components will lead to circles and to ellipses with a slant of $90^{\circ}$. This was the case in all the examples presented so far. A phase difference of $0^{\circ}$ or $180^{\circ}$ between $X$ (or $Y$ ) and $Z$ will lead to straight-line movements. Other values will lead to ellipses of varying degrees of slant.

Figure 9 shows one example in which the subject was asked to produce a slanted ellipse in the frontal plane, while Fig. 10 illustrates an example in which the instruction was to produce a slanted ellipse in an oblique plane. With regard to the former, note that the subject was quite successful in this task, that the variations in the orientation angles were close to sinusoidal, $\beta$ and $\theta$ being $180^{\circ}$ out of phase. However, the phase lead of $\alpha$ relative to $\theta$ is considerably different $\left(142^{\circ}\right)$ from the value of $110^{\circ}$ reported in Fig. 8. This is also true for the example shown in Fig.
10. The subject was less successful on this trial, however. While the projection of the wrist movement on the frontal plane is close to ellipsoidal (Fig. 10C), its projection onto the sagittal plane is highly distorted, as is the modulation in the shoulder angles $(\eta, \theta)$.

Figure 11 summarizes the results of experiments in which the effect of slant on the phase of $\alpha$ relative to $\theta$ and $\beta$ was investigated. Each point represents the results of one trial; the straight line was fitted by eye to the data points. Note that the line intersects the origin, and that a slant of $90^{\circ}$ gives a phase lead of $\alpha$ relative to $\beta$ of $\pm 70^{\circ}$, in agreement with results shown in Fig. 8A.

## Torque

So far we have shown that an approximately sinusoidal motion at the wrist can result from a sinusoidal motion of the orientation angles. The data presented in Figs 12 and 13 will now show that the torque at the shoulder and elbow joints required to produce such a sinusoidal motion can be far from sinusoidal. Torque was calculated according to procedures summarized in Methods and detailed in Soechting. ${ }^{17}$ We present the components of shoulder torque in two frames of reference: one fixed in space and one fixed to the humerus and rotating with the arm (see Methods). When the upper arm is vertical and the shoulder, elbow and wrist lie in the sagittal plane, the two frames of reference coincide. Remember also that torques described in a frame of reference fixed to the arm should show better correspondence with the pattern of activity of shoulder muscles.

In general, the variations in torque were far from sinusoidal. In some instances, for example elbow torque $T_{\mathrm{e}}$ in Fig. 12 and the $X$-component of


Fig. 9. Slanted ellipse in the frontal plane.


Fig. 10. Slanted ellipse in an oblique plane.


Fig. 11. Dependence of the phase relation between forearm yaw ( $\alpha$ ) and elevation ( $\beta$ ) on the amount of slant. Slant is quantitated by means of the phase relation between the horizontal ( $X$ or $Y$, whichever is larger) and vertical components of wrist velocity. Each data point represents the results of one trial and the straight line has been fitted to the data points by eye.
shoulder torque ( $T_{\mathrm{sx}}$ ) in Fig. 12D, the changes were approximately triangular. In other cases ( $T_{\mathrm{e}}$ in Fig. 13), torque appeared to change in approximately a step-wise fashion while yet in others ( $T_{\mathrm{sy}}$ in Fig. 13D), a significant 2 nd harmonic component was apparent. Finally, we note that there is reasonable qualitative agreement between the pattern of activity of biceps and elbow torque $T_{\mathrm{e}}$ (torque tending to flex the forearm is shown as positive), and between anterior deltoid and the $Y$-component of shoulder torque $T_{\mathrm{sy}}$ in the frame of reference fixed to the arm (here torque tending to produce forward flexion at the shoulder is shown as positive). Furthermore, the relative timing of components of torque, and between biceps and anterior deltoid, depends on the plane in which the movement is performed. Thus, biceps and anterior deltoid activity are approximately in phase in Fig. 12, and out of phase in Fig. 13.

## Simulation

In the presentation of the results so far, we have focused on the fundamental component of the mod-


Fig. 12. Variation in shoulder and elbow torque required to produce circular motion in the frontal plane. Trajectories of the wrist and elbow are shown in (A); the projection of wrist trajectory onto the frontal and saggital planes is given in (B). (C) and (D) describe the variation in torque at the elbow ( $T_{\mathrm{e}}$ ) and the $X, Y$ and $Z$ components of shoulder torque ( $T_{s}$ ) as well as full-wave rectified electromyographic activity of biceps and anterior deltoid muscles. Torque is described in two frames of reference: one fixed in space (Spat. Ref.) (C) and one fixed to the arm (Arm Ref.) (D). Full details are given in the text. Changes in orientation angles during the movement are shown in (E).


Fig. 13. Variation in shoulder and elbow torque required to produce circular motion in the sagittal plane.
ulation in the orientation angles. In some instances, the distortion in the angular measures was negligible (for example $\theta, \beta$ and $\alpha$ in Figs 2 and 3); in other instances the distortion was large enough that it could conceivably have an appreciable effect on the motion at the wrist ( $\eta$ in Figs 2 and $3, \eta$ and $\theta$ in Fig. 10). An analysis of the distortions is presented in Table 1. It may be seen that the distortion in $\theta$ and $\beta$ ranged from one to two times the distortion in the vertical component of the wrist movement. The distortions in $\alpha$ and $\eta$ were also comparable in magnitude to those of the horizontal components of wrist motion, that in $\eta$ usually being larger. Note that for movements in the sagittal plane, the distortion in the yaw angles was often smaller than the distortion in the anteroposterior direction of the wrist movement. The trajectories of circles and ellipses drawn in the sagittal plane being highly distorted (Figs 4 and 5), with a flattening of their proximal portions, it thus seems unlikely that the distortion in wrist motion originates from a distortion in the angular motion of the limb.

To settle this point more directly, we performed some simulations. We started with pure sinusoidal angular motions, specifying the mean values for each angle and the amplitude and phase of the modulation. We made one other assumption, namely that
the length of the upper arm and of the forearm was equal, thus incorporating the length of the hand in the forearm segment. (Indeed in the experiments the subjects were asked to keep the wrist rigid.) The resulting distal motion was then calculated according to equations (1) and (2).

Another reason for doing the simulations was the following. The experimental data suggest that: (1) the phase between $\beta$ and $\theta$ is $180^{\circ}$ irrespective of the plane of motion; (2) one factor governing the plane of wrist motion is the phase difference between the two yaw angles $\eta$ and $\alpha$ (in phase in the frontal plane and $180^{\circ}$ out of phase in the sagittal plane), and (3) slant is regulated by means of the phase difference between $\alpha$ and $\theta$. However, the mean and the amplitudes of the angular motions were different for movements in different planes or with different slants. In the context of these conclusions, we wanted to see if the observations concerning the phase relations could be reproduced when the angular motions were pure sinusoids and when all but one or two parameters were kept fixed.

Figure 14 shows that the principal plane of the motion at the wrist is altered by changing the phase between $\eta$ and $\alpha$. The phase of each of the angular motions, relative to $\theta$, is indicated schematically next to each plot of wrist motion in three-dimensional
space. (In Fig. 14A, $\eta$ leads $\theta$ by $90^{\circ}$ while it lags $\theta$ by $90^{\circ}$ in Fig. 14C.) In the first instance, the circular motion is in the frontal plane: as $\eta$ and $\alpha$ move towards $90^{\circ}$ out of phase, the motion is in an oblique plane (Fig. 14B), while in Fig. 14C (where $\eta$ and $\alpha$ are close to $180^{\circ}$ out of phase) the circle is in the sagittal plane. To obtain these results, the mean angle of a was changed, from $-20^{\circ}$ in Fig. 14A, to $-60^{\circ}$ in Fig. 14 C , in addition to changing the phase of $\eta$ relative to $\theta$. All other parameters remained fixed.

To obtain the ellipses in the frontal and sagittal planes shown in Fig. 15, we doubled the amplitude of the modulation in $\beta$ and $\theta$ compared to Fig. 14. All other parameters were unchanged from those used in Fig. 14. Note that the ellipse in the sagittal plane shows the flattening of the proximal portion of the trajectory characteristic of the experimental data (see Figs 4 and 5). Such a deviation is not obvious in Fig. 14C. Note, however, that in the simulations presented in Figs 14 and 15 , the amplitude of the modulation in $\beta$ was about 1.4 times that in $\theta$, a value typical of circles drawn in the frontal plane. When subjects were asked to draw a circle in the sagittal plane, the amplitude of the modulation in $\beta$ was much larger than that in $\theta$ (about 3.8 times as large, on average). When the values used in the simulation were closer to the experimental values, the simulation gave a much more pronounced distortion for circles drawn in the sagittal plane, in agreement with experimental results.

Figure 16 shows that the slant of an ellipse can be determined by changing the phase of $\alpha$ relative to the other angles. In Fig. 16A, $\alpha$ leads $\theta$ by $110^{\circ}$; this phase lead was reduced to $30^{\circ}$ in Fig. 16B. All other parameters were unchanged.

Note that geometry and anatomy do not dictate a unique solution, since the arm has four degrees of freedom ( $\eta, \theta, \alpha, \beta$ ) while the motion at the wrist has only three ( $X, Y, Z$ ). Thus, there is no unique orientation of the arm for a given position of the wrist in space. Uniqueness was achieved by introducing the constraint that $\beta$ and $\theta$ be $180^{\circ}$ out of phase. Figure 17 shows that close to circular motion can still be achieved when this constraint is removed. In these instances we chose a phase lead of $\beta$ relative to $\theta$ of $90^{\circ}$. The resulting motion at the wrist shows a larger distortion than that observed in Fig. 14, as might be expected from the results presented in Fig. 7. (We did not make any systematic attempt to find a combination of parameters which would minimize the distortion. Further improvement could of course be achieved if the requirement that the angular motion be sinusoidal is relaxed.)

Finally, Fig. 18 shows that even when the angular motion is truly sinusoidal, shoulder and elbow torques can show appreciable distortion. The data are for wrist motion in the frontal plane (Fig. 18A and B) and in the sagittal plane (Fig. 18C and D). The same parameter values as in Fig. 14A and C were used and a frequency of 1 Hz was assumed. It is remarkable that although the simulation uses sinusoidal functions while distortions are present in the experimental data, one can find a strong similarity between the main features of the torque in the two cases. In particular, the relations in amplitudes and phases of the components of the torque in the two frames of reference are similar for the computed and experimentally derived data (compare Fig. 12C-D with Fig. 18A-B, and Fig. 13C-D with Fig. 18C-D).


Fig. 14. Simulation of wrist trajectories assuming sinusoidal motion of the orientation angles. The plots show hand trajectory in three-dimensional space (upper row) and its projection onto the frontal and sagittal planes (lower row). The motion is primarily in the frontal plane (A), in an oblique plane (B) and in the sagittal plane ( C ). The change in the plane of motion was brought about by changing the phase of $\eta$ relative to $\theta$ (shown diagramatically in the polar diagrams in the upper row) from $90^{\circ}$ (A) to $180^{\circ}$ (B) and to $-90^{\circ}(\mathrm{C})$. The mean value of $\alpha$ was also changed: $-20^{\circ}(\mathrm{A}),-40^{\circ}(\mathrm{B})$ and $-60^{\circ}(\mathrm{C})$. All other parameters were kept constant and the phases of $\beta\left(180^{\circ}\right)$ and $\alpha\left(110^{\circ}\right)$ relative to $\theta$ correspond to the mean values found experimentally.


Fig. 15. Simulation of ellipsoidal motion in the frontal (A) and sagittal (B) planes. The amplitude of the modulation of $\theta$ and $\beta$ was doubled relative to the values used in Fig. 14; all other values are the same as those used to obtain Fig. 14A and C. Note the flattening of the proximal portion of hand trajectory in the sagittal plane.

More importantly, for movements in the sagittal plane, the distortion (with the appearance of a second harmonic in $T_{s y}$ ) is similar in the two cases.

## DISCUSSION

We begin this discussion by considering whether or not the experimental data agree with the two propositions which make up the simplifying hypothesis stated in the Introduction. One of these propositions
is that the same mapping between motor and sensory events is utilized in the production and perception of a movement. On this topic, the first point to be stressed is the following: only those variables which show invariant relations (such as the phase relations between orientation angles) when the wrist trajectory is traced in different planes can be thought to contribute to both perceptual and motor aspects of the task. Thus the results presented here indicate that the anatomical elbow angle of flexion-extension per se, is


Fig. 16. Simulation of slant by changing the phase of $\alpha$ relative to $\theta$ [from $110^{\circ}$ in (A) to $30^{\circ}$ in (B)]. All other parameters are the same in both parts of the figure.


Fig. 17. Hand motion in the frontal (A) and sagittal plane (B) obtained by relaxing the constraint that $\theta$ and $\beta$ be $180^{\circ}$ out of phase. A phase lead of $90^{\circ}$ of $\beta$ relative to $\theta$ was used in these simulations, and the phase of $\eta$ relative to $\theta$ was changed from $45^{\circ}$ to $-135^{\circ}$, as was the mean value of $\alpha$ from $-20^{\circ}$ to $-60^{\circ}$.



Arm Ret.



Fig. 18. Shoulder and elbow torques required to produce sinusoidal motion of the orientation angles. Torque required to produce circular motion of the hand in the frontal (A)-(B) and sagittal plane (C)-(D) was calculated using the same parameter values as in Fig. 14A and C, and assuming a frequency of 1 Hz . Torques are plotted in a spatially fixed frame of reference (Spat. Ref.) and one fixed to the arm (Arm Ref.)
not one of the participating variables, since its phase relative to the angle of elevation of the upper arm is random from trial to trial (Fig. 6B). Note also that the distortion of the changes in this angle is much larger than that of the orientation angles, namely angular elevation of the upper arm and forearm. The latter two, together with the yaw angles, were identified previously as defining a preferred coordinate system for the recognition of the orientation of the arm in space under static conditions. ${ }^{20}$ Given the present experimental findings it now seems reasonable to assume that the same coordinate system is also utilized under dynamic conditions. Consequently, the data presented in this paper are consistent with the first proposition of the simplifying assumption.

An observation pertinent to this topic was that circles and ellipses are characteristically distorted (Figs 4 and 5) when they are traced in the sagittal plane, while the distortions of the orientation angles are in the same range as those for movements in other planes (in which such a distortion of the wrist trajectories is not present, cf. Fig. 2). Furthermore, the subjects had no cognizance of such a distortion.

From these observations some inferences can bc drawn about the topology of the sensorimotor mapping which lies at the basis of the execution of the task in planes other than the ones in which it has been learned. Indeed, it can be contended that there is an identity between sinusoidal changes of the orientation angles and anticipated circular or elliptical trajectories of the wrist. Given the geometrical relations between orientation angles and wrist position [equations (1) and (2)] and the presence of the constraints found experimentally (namely the phase
relations described in Figs 6A and 8A), this identity is realized when circles and ellipses are drawn in the frontal plane. In other words, the main elements of the topology of the sensorimotor mapping would be: sinusoidal motion of orientation angles maps into sinusoidal motion in the horizontal and vertical direction at the wrist, the phase of shoulder yaw angle is involved in determining the plane of motion and the phase of the elbow yaw angle determines slant. The mapping is subject to the general constraint that the two angles of elevation be $180^{\circ}$ out of phase. Even though the identity between anticipated and actual trajectories breaks down when the plane of the motion is changed, the sensorimotor mapping would remain the same since there is no cognizance of the distortion.

If this interpretation is accepted, there would be a simple way to transfer a motor skill acquired in one plane to other planes and eventually from one body segment to another. To this end, analogous sensorimotor maps would need to exist, and this, we contend, lies at the basis of the phenomenon of motor equivalence. ${ }^{6,13}$

Experiments designed to characterize the topology of the mappings are now conceivable, since our data indicate that from such maps a true representation of geometric space does not emerge, ${ }^{5}$ in contrast with the assumption of some recent theoretical work. ${ }^{14} \mathrm{We}$ would instead predict that the trajectories should be distorted in a characteristic manner once the map has been established. Experimentally then, the approach would be to use the error itself to identify some features of the mapping, as was found when the wrist motion is translated from the frontal to the sagittal plane.

In this case, a main feature of the mapping is that the phase relations between certain angles are the same for trajectories traced in different planes of space. These invariant relations among orientation angles are in keeping also with the second proposition of the simplifying hypothesis stated in the Introduction. Thus the hypothesis is self-consistent and justified by the data.

The meaning to be attached to the term "invariance" needs to be discussed, however. The question is: is the invariance the expression of a law which is strictly obeyed, or is it to be understood as a constraint of more general nature, providing for a convergence (through learning and practice) to approximate the rule expressed by the invariant relation?

The present data, as well as other observations on this subject, ${ }^{10,11,12,23}$ indicate that the latter interpretation is more appropriate. Restricting ourselves to consider motor coordination in three-dimensional space, the experimental data together with the analysis presented in the Appendix indicate that as the phase difference between the modulation of the angular elevation of the arm and forearm approaches $180^{\circ}$, the deviation from a sinusoid of the vertical component of the wrist motion becomes a minimum.

This is true only in an average sense. That is, given a set of mean values and amplitudes of modulation, a phase difference other than $180^{\circ}$ may lead to a minimum distortion and thus an optimal performance. On the other hand, under all conditions the experimental values were found to cluster around $180^{\text {, }}$, thus suggesting very strongly that normal subjects conform to this general constraint. Given the meaning attached to "invariance" stated above and the analytical results of the Appendix, the possibility remains that in exceptional subjects (such as the painter Giotto) the general rule becomes a strict law with specific solutions for optimal performance in each particular case (e.g. plane of motion).

One last point deserves mention. The idea has been expressed previously that trajectory determines dynamics (i.e. forces or torques) of the movement. ${ }^{23}$ Data presented here reinforce this viewpoint. Indeed, the torques required to maintain the described kinematic invariances of the motion were strikingly different in the case of circles and ellipses drawn in the frontal and sagittal planes (Figs 12 and 13). Thercfore, while invariances can be defined readily among kinematic parameters, there is no such counterpart in terms of torque.

Acknowledgements-The authors thank Drs C. Maioli and P. Viviani for a critical reading of this paper. The work was supported by USPHS Grant NS-15018, NSF Grant BNS8418539 and the CNR.

## APPENDIX

In this appendix we show mathematically that a phase difference of $180^{\circ}$ between $\beta$ and $\theta$ leads to a distortion in the vertical component of wrist motion which is minimum in a global sense.

By equations (1) and (2):

$$
\begin{equation*}
z_{w}=/(\cos \theta-\cos \beta) \tag{A.1}
\end{equation*}
$$

We assume

$$
\begin{align*}
& \theta=\theta_{0}+\theta_{1} \cos t \\
& \beta=\beta_{0}+\beta_{1} \cos (t+\delta) \tag{A.2}
\end{align*}
$$

and we make a small angle approximation

$$
\begin{equation*}
\sin \theta \simeq \theta \cdot \cos \theta \simeq 1-\theta^{2} / 2 \tag{A.3}
\end{equation*}
$$

Substituting (A.2) and (A.3) into (A.1) and making use of trigonometric identities, we obtain:

$$
\begin{aligned}
z_{\mathrm{w}} & =\text { constant }+\ell\left\{\beta_{1} \sin \beta_{0} \cos (t+\delta)-\theta_{1} \sin \theta_{0} \cos t\right\} \\
& +\ell / 4\left\{\beta_{1}^{2} \cos \beta_{0} \cos 2(t+\delta)-\theta_{1}^{2} \cos \theta_{0} \cos 2 t\right\} . \quad \text { (A.4) }
\end{aligned}
$$

The second term in (A.4) represents the desired fundamental component of the modulation in $z$, the third term the error. The distortion will be minimized if the third term (harmonic) becomes as small as possible compared to the second term (fundamental). One can define the distortion by integrating it over one cycle of the movement:

$$
\begin{equation*}
D=\frac{\int_{0}^{2 \pi}\{\text { harmonic }\}^{2} \mathrm{~d} t}{\int_{0}^{2 \pi}\{\text { fundamental }\}^{2} \mathrm{~d} t} \tag{A.5}
\end{equation*}
$$

The distortion, as a function of the phase angle $\delta$, will be
a minimum provided:

$$
\begin{equation*}
\mathrm{d} D / \mathrm{d} \delta=0 \tag{A.6}
\end{equation*}
$$

After integration (A.5) and differentiation (A.6), one finally obtains

That the derivative of $D$ be zero is a necessary condition for the distortion to be a minimum, but not a sufficient one. In other words, the distortion $D$ may achieve a local minimum when $\delta$ is $180^{\circ}$, but there may be another solution which will yield a smaller distortion. Other solutions, for

$$
\begin{gather*}
\frac{\mathrm{d} D}{\mathrm{~d} \delta}=\frac{\left[\beta_{1}^{2} \theta_{1}^{2} \cos \beta_{0} \cos \theta_{0}\right] \sin 2 \delta}{\left[\beta_{1}^{2} \sin \beta_{0}\right]^{2}+\left[\theta_{1}^{2} \sin \theta_{0}\right]^{2}-2 \beta_{1}^{2} \theta_{1}^{2} \sin \beta_{0} \sin \theta_{0} \cos \delta} \\
-\frac{1}{2} \frac{\beta_{1}^{2} \theta_{1}^{2} \sin \beta_{0} \sin \theta_{0}\left\{\left[\beta_{1}^{2} \cos \beta_{0}\right]^{2}+\left[\theta_{1}^{2} \cos \theta_{0}\right]^{2}-2 \beta_{1}^{2} \theta_{1}^{2} \cos \beta_{0} \cos \theta_{0} \cos 2 \delta\right\} \sin \delta}{\left\{\left[\beta_{1}^{2} \sin \beta_{0}\right]^{2}+\left[\theta_{1}^{2} \sin \theta_{0}\right]^{2}-2 \beta_{1}^{2} \theta_{1}^{2} \sin \beta_{0} \sin \theta_{0} \cos \delta\right\}^{2}} \tag{A.7}
\end{gather*}
$$

Note that (A.7) is identically zero provided:

$$
\sin \delta=0 \quad \text { and } \quad \sin 2 \delta=0
$$

that is, if $\delta=0$ or $\delta=180^{\circ}$. The solution $\delta=0$ corresponds to a local maximum (see Fig. 7).
which (A.7) is zero and which lead to a smaller distortion can exist, but they will depend on the values taken on by $\beta_{0}$, $\theta_{0}$ and $\beta_{1}, \theta_{1}$, It is only in this sense that solution $\delta$ equal to $180^{\circ}$ represents a global or average minimum.

## REFERENCES

1. Benati M., Gaglio S., Morasso P., Tagliasco V. and Zaccaria R. (1980) Anthropomorphic robotics. I. Representing mechanical complexity. Biol. Cybern. 38, 125-140.
2. Chao E. Y., An K. N., Askew L. J. and Morrey B. F. (1980) Electrogoniometer for the measurement of human elbow joint rotation. J. Biomech. Engng 102, $301-310$.
3. Evans F. G. (1961) Biomechanical Studies of the Musculo-skeletal System. Thomas, Springfield.
4. Georgopoulos A. P., Kalaska J. F. and Massey J. T. (1981) Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty and change in target location. J. Neurophysiol. 46, 725-743.
5. Greene P. H. (1972) Problems of organization of motor systems. Prog. theor. Biol. 2, 304-338.
6. Hebb D. O. (1949) The Organization of Behavior. A Neuropsychologic Theory. Wiley, New York.
7. Hollerbach J. M. (1981) An oscillation theory of handwriting. Biol. Cybern. 39, 139-156.
8. Hollerbach J. M. (1984) Dynamic scaling of manipulator trajectories. J. Dyn. Syst., Measmnt. and Cntrl. 106, $102-106$.
9. Hollerbach J. M. and Flash T. (1982) Dynamic interactions between limb segments during planar arm movement. Biol. Cybern. 44, 67-77.
10. Lacquaniti F., Soechting J. F. and Terzuolo C. A. (1982) Some factors pertinent to the organization and control of arm movements. Brain Res. 252, 394-397.
11. Lacquaniti F., Soechting J. F. and Terzuolo C. A. (1986) Path constraints on point-to-point arm movements in three-dimensional space. Neuroscience 17, 313-324.
12. Lacquaniti F., Terzuolo $C$. and Viviani P. (1983) The law relating the kinematic and figural aspects of drawing movements. Acta psychol. 54, 115-130.
13. Lashley K. S. (1930) Basic neural mechanisms in behavior. Psychol. Rev. 37, 1-24.
14. Pellionisz A. and Llinás R. (1980) Tensorial approach to the geometry of brain function: cerebellar coordination via a metric tensor. Neuroscience 5, 1125-1136.
15. Robinson D. A. (1982) The use of matrices in analyzing the three-dimensional behavior of the vestibulo-ocular reflex. Biol. Cybern. 46, 53-66.
16. Soechting J. F. (1982) Does position sense at the elbow reflect a sense of elbow joint angle or one of limb orientation? Brain Res. 248, 392-395.
17. Soechting J. F. (1983) Kinematics and dynamics of the human arm. Laboratory of Neurophysiology Report, pp. 1.17. University of Minnesota, Minneapolis, MN.
18. Soechting J. F. (1984) Effects of target size on spatial and temporal characteristics of a pointing movement in man. Exp. Brain Res. 43, 121-132.
19. Soechting J. F. and Lacquaniti F. (1981) Invariant characteristics of a pointing movement in man. J. Neurosci. 1, 710-720.
20. Soechting J. F. and Ross B. (1984) Psychophysical determination of coordinate representation of human arm orientation. Neuroscience 13, 595-604.
21. Terzuolo C. A. and Viviani P. (1980) Determinants and characteristics of motor patterns used for typing. Neuroscience 5, 1085-1103.
22. Viviani P. and Terzuolo C. (1980) Space-time invariance in learned motor skills. In Tutorials in Motor Behavior (eds Stelmach G. E. and Requin J.), pp. 525-533. North-Holland, Amsterdam.
23. Viviani P. and Terzuolo C. (1982) Trajectory determines movement dynamics. Neuroscience 7, 431 -437.
