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Three-dimensional drawings in isometric conditions: planar segmentation of force trajectory

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Summary. Normal human subjects grasped an isometric handle with an unrestrained, pronated hand. They were asked to exert forces continuously to draw lemniscates (figure eights) in specified or self-chosen planes and in the presence or absence of a three-dimensional visual feedback cursor and a visual template. In every condition, the mean plane orientation in the force space differed appreciably between the two loops of the figure, as described previously by Soechting and Terzuolo (1987a) for free drawing arm movements. These findings suggest that the planar segmentation of the motor trajectory is not a consequence of joint motion but arises from central constraints related to the production of motor trajectory in space.

Key words: Force – Trajectory – Segmentation – Human

Introduction

Studies of drawing movements in two-dimensional (2D) or three-dimensional (3D) space have revealed two major principles of organization of motor trajectories, namely the coupling between velocity and curvature (Viviani and Terzuolo 1982; Lacquaniti et al. 1983; Soechting and Terzuolo 1986) and the segmentation of the movement kinematics and plane of motion (Morasso 1983; Viviani and Cenzato 1985; Viviani 1986; Soechting and Terzuolo 1987a, b). Similar results were also observed when subjects were asked to produce curved point-to-point arm movements (Abend et al. 1982; Flash and Hogan 1985). The study of such behavioral properties led to the characterization of the functional constraints of the motor system, that is, it provided information on how the central nervous system may plan and control motor trajectories. In a previous paper (Massey et al. 1992), we showed that the velocity and curvature of force trajectories generated in isometric conditions covary in the same way as during movement (Viviani and Terzuolo 1982; Lacquaniti et al. 1983; Soechting and Terzuolo 1986), which suggests that this covariation originates from central constraints and not from peripheral biomechanical factors associated with the motion of the inertial load of the arm. In the present paper, force trajectories are examined in relation to the problem of segmentation of motor trajectories.

Soechting and Terzuolo (1987a) showed that when subjects draw a lemniscate (figure eight) in free space, the plane of motion of the wrist changes abruptly between segments of the trajectory and lies in a stable plane within each segment. The change of plane occurs usually at the point of inflection of the figure, that is, when the direction of motion changes from clockwise to counterclockwise, or vice versa. With more complex 3D trajectories, the subjects do not produce smooth and continuous changes in the plane of motion, and the trajectories are piecewise planar (Morasso 1983; Soechting and Terzuolo 1987b). These results have been related to the rules that govern the coordination of the upper arm and forearm orientation angles (Soechting and Terzuolo 1986, 1987a, b). It was observed that the modulation of a given set of arm orientation angles, namely the elevation and yaw of the upper arm and forearm (Soechting and Ross 1984), were coupled during free hand drawing and point-to-point movements (Soechting and Lacquaniti 1981; Lacquaniti et al. 1986; Soechting et al. 1986). These arm orientation angles defined also a preferred coordinate system for the proprioceptive recognition of the arm in space (Soechting and Ross 1984; Wormingham et al. 1987). These results led to the hypothesis that the orientation angles of the upper arm and forearm are part of the intrinsic parameters used by the motor system to produce arm trajectories in space (Soechting and Terzuolo 1986).

The rules governing the coordination of arm orientation angles introduce constraints in the relation between extrinsic (spatial trajectory) and intrinsic parameters (joint angles) of the movement, which reduce the number of degrees of freedom of the system. Assuming that complex arm trajectories are segmented, the rules of coordina-

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tion of the arm orientation angles predict that the motion of the wrist is necessarily planar within each segment but can change from one segment to the next (Soechting and Terzuolo 1986). These results have emphasized the role of the arm orientation angles and subsequently of joint motion in the occurrence of planar segmentation within free hand trajectories. However, it is not clear whether the joint motion per se induces the planar segmentation or whether both result from common constraints related to the production of a motor trajectory.

Although the rules governing the arm orientation angles successfully predicted the existence of the planar segmentation, one can ask whether other factors might intervene. For example, dynamic interactions due to inertial, centripetal and Coriolis forces arise during multijoint limb movements (Hollerbach and Flash 1982). Moreover, the measure of steady-state restoring forces in two joints arm postures indicates that the stiffness and the apparent inertia of the hand have a directional property (Hogan 1985; Mussa-Ivaldi et al. 1985). The stiffness and inertial fields are essentially symmetric and can be graphically described by an ellipse which orientation varies according to the posture of the arm (Hogan 1985; Mussa-Ivaldi et al. 1985). Although, these dynamic properties of the arm were measured in steady-state tasks, their results account for kinematic features of multijoint arm movements obtained in simulation studies (Flash 1987) and reaching studies with normal subjects and deafferented patients (Ghez et al. 1990). Therefore, one can hypothesize that according to the position of the arm in space it can be easier to move in certain directions than others, which might lead to a change of plane of the trajectory.

The question is then, whether the planar segmentation is observed in isometric conditions, that is, in the absence of overt joint motion, and when the trajectory is defined in isometric force space. If the planar segmentation is still present in isometric conditions, this would indicate that it does not result from the motion of the arm segments, nor from the dynamic properties of the arm, and would suggest that it arises from central constraints. To provide an answer to this question, we asked subjects to draw lemniscates in isometric force space, in different planes, and in the presence or absence of visual feedback. The results showed that the planar segmentation of the motor trajectory is still present in isometric conditions. Preliminary results have already been presented (Lurito et al. 1991).

Materials and methods

Subjects

Twenty-six healthy, unpracticed human subjects (6 females and 20 males) participated in this experiment. Subjects performed the task with their preferred hand; all subjects but one were right-handed.

Apparatus

The experimental apparatus consisted of a 3D isometric manipulandum and a color video monitor on which stereographic figures and a force-feedback cursor could be displayed. The devices and methods for generating the stereograms were described previously (Massey et al. 1988, 1991). Briefly, the manipulandum was a vertical T-shaped handle 18 cm long mounted on three load cells. The force exerted in each of the three axes (X, Y, and Z; respectively lateral, posterior-anterior, and vertical directions) was digitized and sampled every 10 ms. A stereographic force-feedback cursor could be displayed on the color monitor at a position corresponding to the force exerted on each of the axes; a change of 100 gm-force produced a displacement of the force-feedback cursor of 1 cm. Subjects saw the stereograms of the figure and cursor, when present, through appropriate filters (Massey et al. 1988).

Behavioral task

Subjects sat comfortably with the chin in a chin rest. The manipulandum was placed in front of the subjects and in the midsagittal plane, so that the upper arm was along the trunk and the forearm was approximately horizontal. The color monitor was placed 50 cm away, in front of the subject at eye-level. Subjects grasped the handle with the hand pronated and the arm otherwise unrestrained. They were asked to exert forces continuously, at a self-chosen pace, to draw figure eights either in the frontal (XZ), sagittal (YZ), horizontal (XY), or in a self-chosen preferred plane. The subjects were asked to draw the figure eights in the frontal plane either vertical (8) or lying (∞). In some trials a 3D visual force-feedback cursor and a visual template were displayed on the monitor; however, the subjects were instructed not to attempt to trace exactly the form and size of the figure but, instead, to make continuous rhythmic motions in duplicating the type of the figure. When no display was provided to the subjects, they were instructed verbally about the orientation of the plane in which to draw the figure. The subjects did not perform under all the conditions, and some subjects did several sessions under the same conditions. Each drawing usually lasted 10 s, but the data were recorded during the last 5 s, after the subject had reached a stable rhythm.

Data analysis

X, Y, and Z force components were smoothed using a digital low-pass filter (cut-off 15 Hz). Differentiations were performed digitally using a five point Lagrange polynomial approximation. From the instantaneous tangential velocity vector, we computed the instantaneous tangent unit-vector $\mathbf{t}$ which was then differentiated to obtain the normal unit-vector $\mathbf{n}$.

The instantaneous plane of the trajectory (i.e. osculating plane) was defined by the binormal unit-vector $\mathbf{b}$ (i.e., vector normal to the osculating plane), the components of which $[b_x(t), b_y(t)$, and $b_z(t)]$ were obtained from the cross product of $\mathbf{t}$ and $\mathbf{n}$. Curvature $C(t)$ (i.e. rate of change of the direction of motion) and torsion $T(t)$ (i.e. rate of change of the plane of motion) were computed using respectively:

$$C(t)=\left|\frac{d\mathbf{t}}{dt}\right|/V(t) \qquad (1)$$

and

$$T(t)=\left|\frac{d\mathbf{b}}{dt}\right|/V(t) \qquad (2)$$

where $V(t)$ is the instantaneous speed.

The orientation of the binormal vector was also defined by its spherical coordinates (see Fig. 1)[1]: $\theta(t)$ (i.e. angle from the positive Z

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[1] These coordinates are simply related to the geographical coordinates used by Soechting and Terzuolo (1986, 1987a, b): elevation $\psi=\theta-90°$; and azimuth $\chi=360°-\phi$.

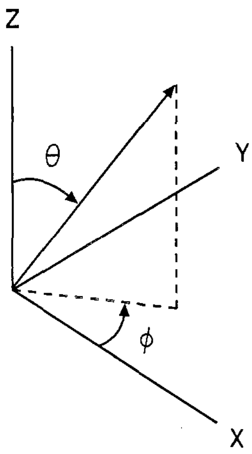

Fig. 1. Spherical coordinates θ (angle from the positive Z axis) and ϕ (angle measured on the horizontal plane and counterclockwise from the X axis) used to describe the orientation of the binormal vector of the plane of the trajectory

axis) and $\phi(t)$ (i.e. angle measured on the horizontal plane and counterclockwise from the X axis; (t) was omitted in the following equations to simplify the notation:

$$\theta = \cos^{-1}\{b_z/(b_x^2 + b_y^2 + b_z^2)^{1/2}\} \tag{3}$$

$$\phi = \begin{cases} \cos^{-1}\{b_x/(b_x^2 + b_y^2)^{1/2}\}, & \text{if } b_y \geq 0 \\ 360^\circ - \cos^{-1}\{b_x/(b_x^2 + b_y^2)^{1/2}\}, & \text{if } b_y < 0. \end{cases} \tag{4}$$

As the direction of the binormal vector is reversed for clockwise and counterclockwise motion, and since we were interested only in the orientation of the plane of the trajectory, we computed the spherical coordinates restricting the binormal vectors of each loop to one side of the unit-sphere. Accordingly, the spherical coordinates of the binormal vector defining the frontal plane were $\theta = 90^\circ$ and $\phi = 90^\circ$, those for the sagittal plane were $\theta = 90^\circ$ and $\phi = 180^\circ$, and those for the horizontal plane were $\theta = 180^\circ$ and ϕ cannot be determined.

We divided the trajectory at the point of inflection between the two loops of the figure, which always corresponds to a minimum of curvature and angular velocity. Then we computed the spherical mean resultant (Mardia 1972) of the binormal vector time series for each repetition of each loop. Thus, for each drawing there were as many repetitions of one loop as there were half cycles of the lemniscate. The spherical standard deviation (SD) across repetitions was computed using the Mardia (1972) definition. The mean angular difference between the two loops was computed using the dot product of the two mean resultants averaged over the repetitions.

Results

The results concerning the general orientation of the plane of the figure eights in the different conditions, the spherical SD of the loops, and the angular difference between the planes of the two loops of the figure are summarized in Table 1. When the subjects were asked to draw the figure eight in the frontal plane, the general orientation of the drawn figure was consistently tilted; the upper part was more distant than the lower one. For the other specified planes, no systematic bias of the drawing plane was observed. The high variability of the spherical coordinates in the self-chosen plane condition indicates that the chosen orientation of the plane was different among subjects. The orientation of the self-chosen plane does not seem to be related to the instructed orientation of the previous condition. However, the most notable result here is that, in almost all the conditions, the orientation of the plane differed significantly between the two loops of the figure eights, similarly to what Soechting and Terzuolo (1987a) have described for free hand movements. Interestingly, the angular difference between the loops was not significantly correlated with the average speed of force drawing.

A typical example of force trajectory produced by a subject when asked to draw a figure eight in the frontal plane is illustrated in the first row of Fig. 2. A perspective view of the force trajectory is shown in the left panel (from the subject's point of view, X is in the lateral direction, Y is in the posterior-anterior direction, and Z is vertical). The projections of the trajectory onto the three cardinal planes are presented in the right panels. The instructed figure is shown as a solid line, whereas the force data sampled every 10 ms are shown as dots. The arrow indicates the direction of drawing. As can be observed in the YZ projection, the figure was substantially tilted from the vertical, with the upper part anterior to the lower one. It can also be observed that the upper and the lower loops of the figure are drawn in planes of different orientation. In the second row of Fig. 2, the XYZ force components are plotted against time. The vertical dotted lines indicate when the points of inflection between the two loops of the figure occurred. An alteration of the Y and Z components from an otherwise close to sinusoidal modulation can be noticed in correspondence to the points of inflection. In the third row of Fig. 2, the curvature and angular velocity are

Table 1. Mean and standard deviation (SD, in parentheses) across subjects of the spherical coordinates (θ, ϕ) of the general plane orientation of the figure eights, the spherical SD of the loops, and the angular difference between the two loops of the figure for the different conditions

Instruction	Visual feedback	θ	ϕ	Spherical SD	Angular difference	N
Frontal 8	+	118 (16)	90 (13)	9.8 (4.2)	19 (8)***	15
Frontal ∞	+	127 (15)	92 (8)	5.6 (3.6)	18 (7)*	3
Frontal 8	–	108 (9)	90 (7)	7.5 (2.0)	16 (10)**	7
Frontal ∞	–	108 (10)	89 (9)	9.1 (2.5)	14 (5)***	6
Sagittal	+	91 (2)	170 (11)	4.5 (1.4)	18 (6)**	4
Sagittal	–	94 (7)	178 (7)	5.7 (3.9)	9 (3)***	8
Horizontal	–	169 (5)	118 (50)	7.0 (2.1)	14 (11)	3
Self-chosen	–	118 (28)	102 (55)	7.6 (2.5)	13 (8)**	6

Units are degrees, n, number of subjects performing in each condition; + and –, presence and absence of visual feedback respectively
t-test: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

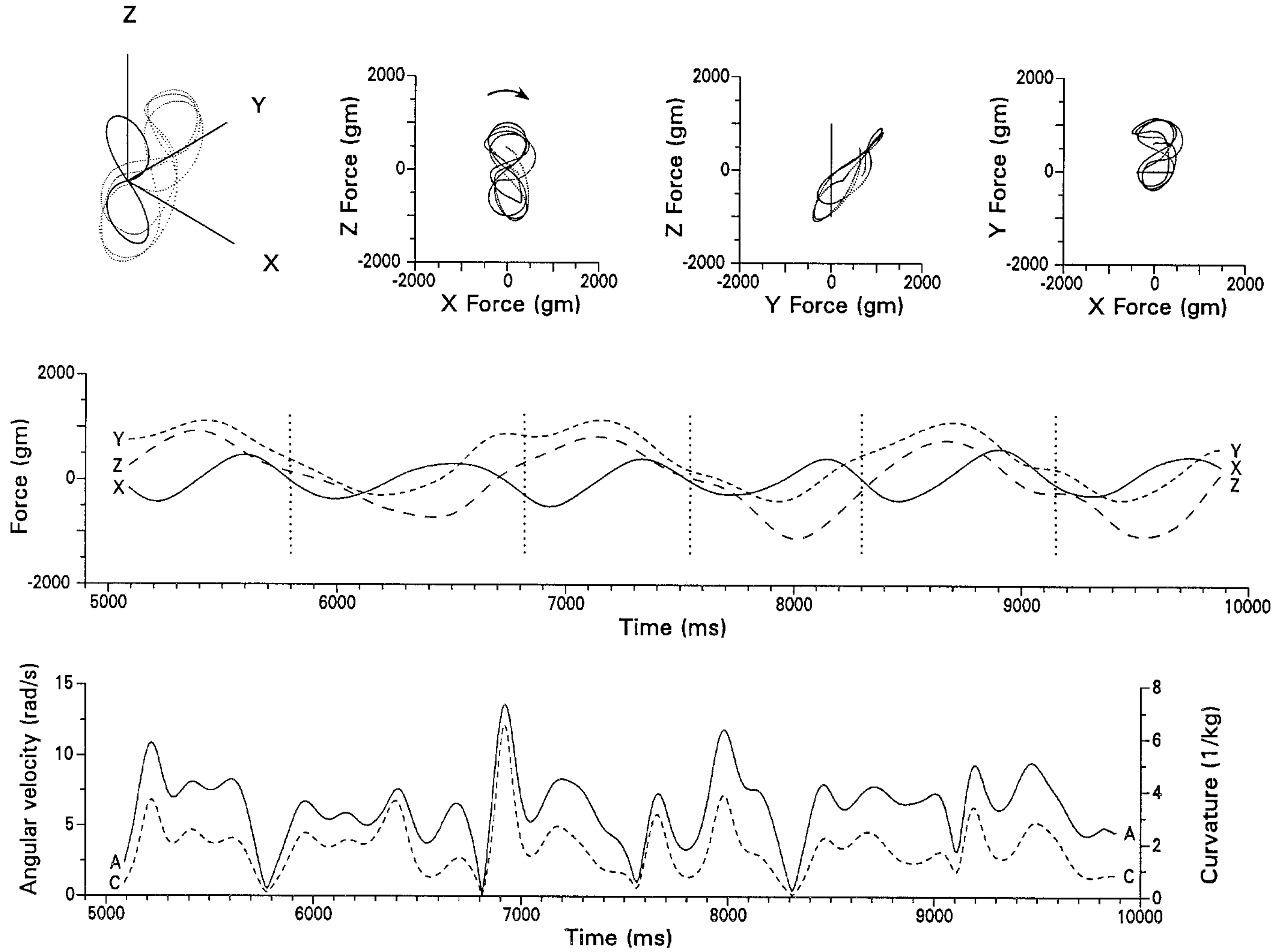

Fig. 2. Force trajectory performed by a subject when asked to draw a figure eight in the frontal plane (XZ). *First row*: spatial plots of the force trajectory. The *arrow* indicates the direction of drawing. *Second row*: XYZ components of force plotted against time. The *vertical dotted lines* indicate when the points of inflection between the two loops of the figure occurred. *Third row*: curvature (C) and angular velocity (A) plotted against time

plotted against time. By definition, the points of inflection are at a minimum of curvature. The time course of the angular velocity covaried with the curvature, as we have described previously (Massey et al. 1992). In the three rows of Fig. 3, the components of the binormal vector are plotted against time. The change of sign of b_y reflects the change of direction of motion from one loop to the other, and therefore corresponds to the point of inflection between the two loops. If the figure was perfectly in the frontal plane, the components b_x and b_z would be equal to zero, but here the absolute values of b_z are large due to the tilt of the figure. In addition, the positive values of b_x are more distant from zero than the negative ones, which indicates that the plane of one loop (lower loop) is rotated more laterally than the other. This can also be observed in the Fig. 4, where in the two upper rows the spherical coordinates θ and ϕ of the binormal vector are plotted against time. These parameters have been corrected due to the change of movement direction, as indicated in Materials and methods. The angle θ has no consistent change from one loop to the other (upper loop 126°, lower loop 127°). By contrast, the angle ϕ of the binormal vector is alternatively close to and away from 90°, that is from the anterior direction (upper loop 101°, lower loop 131°). The spherical SD of the binormal vector was 6.5° for the upper loop, and 8.9° for the lower one. The angular difference between the average plane orientation of the two loops was 24°. In the third row of Fig. 4, the torsion is plotted against time. The torsion has high peaks at the points of inflection when the binormal vector changes sign and has small values between each peak, which indicates that the plane of motion is almost constant within each loop.

The kind of change of plane from one loop to the other was usually consistent during the continuous cycles of the figure, whereas it was not consistent for a given condition, either among subjects, or for repeated trials by the same subject. The subjects that performed repeatedly tended to choose the same direction of motion across trials (e.g., upper loop clockwise and lower loop counterclockwise), but the changes of the planar orientation between the loops could still be different. The changes of planar orientation were not related to the order of the conditions.

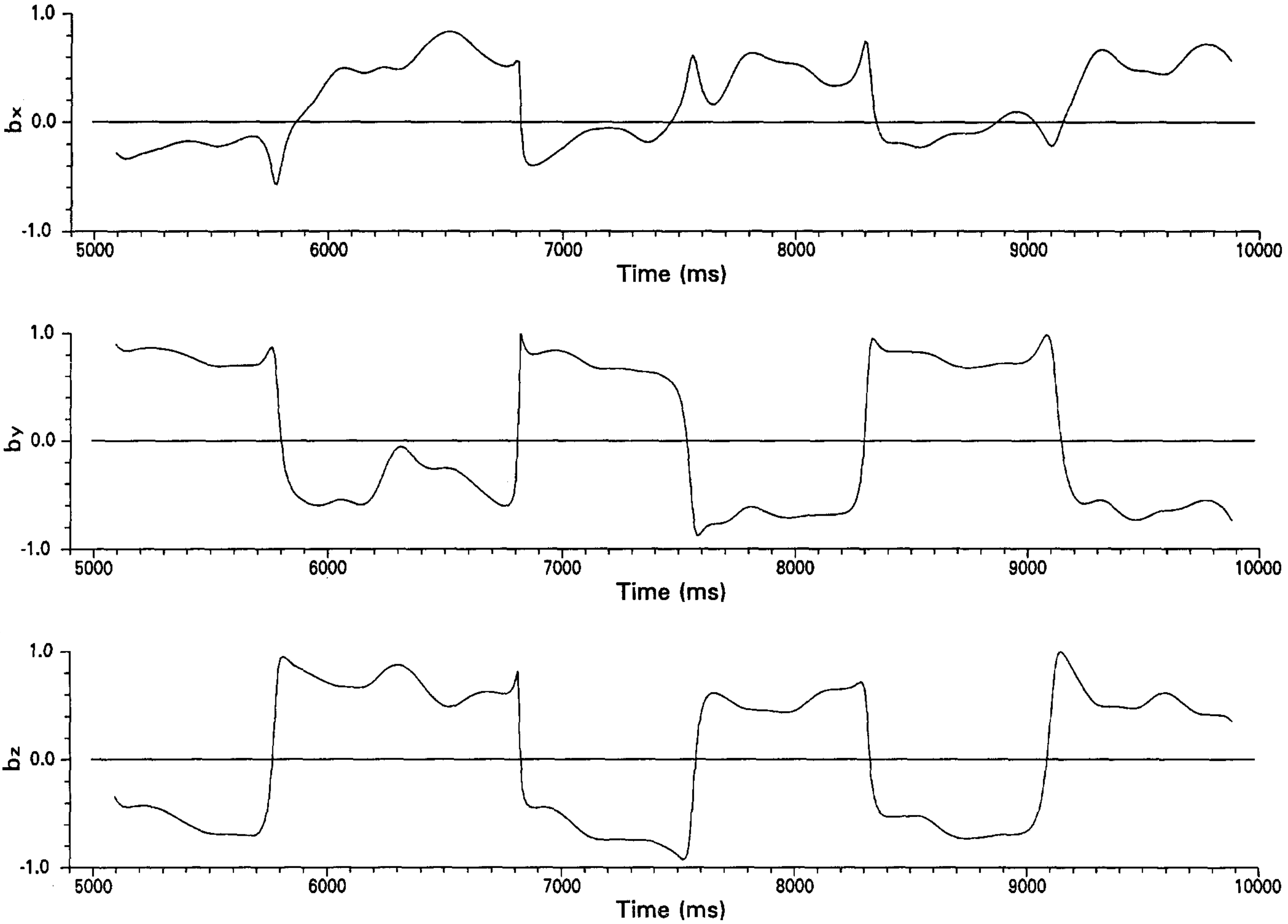

Fig. 3. *XYZ* components of the binormal vector for the data presented in Fig. 2, plotted against time

The following example illustrates a different change of planar orientation between the two loops of the figure eight than the one described previously. The data of one trial for a different subject are presented in the Figs. 5, 6, and 7. In this case, as in the previous one illustrated, the subject was asked to draw a figure eight in the frontal plane. In the first row of Fig. 5, we can observe the same kind of tilt in the plane of the figure as for the case illustrated in Fig. 2. However, by contrast with the previous case, the planes of the two loops do not seem to differ by a lateral rotation but by a change of amount of tilt. Moreover, as described in the previous example, the *Y* and *Z* force components present an alteration of the close to sinusoidal modulation in coincidence with the occurrence of the points of inflection between the two loops (see second row of Fig. 5) and the time course of the curvature and angular velocity were coupled and presented clear minima at the points of inflection (see third row of Fig. 5). In Fig. 6, the plots of the *X*, *Y*, and *Z* components of the binormal vector against time indicate that the positive values of b_z are closer to zero than the negative ones, that is, one loop (lower loop) is more tilted than the other one. In Fig. 7, it can be observed that the angle θ of the binormal vector changes alternately (upper loop 105°, lower loop 126°), whereas the angle ϕ is not very different from one loop to the other (upper loop 89°, lower loop 92°). The spherical SD of the binormal vector was 7.9° for the upper loop, and 9.1° for the lower one. The angular difference between the average plane orientation of the two loops was 21°. The torsion plotted in the third row of Fig. 7 shows that there was little planar variation within each loop of the figure.

Substantial differences between the planar orientation of the loops could be observed, even in the conditions where the subjects drew figures in a plane close to the specified one. Figures 8, 9, and 10 illustrate a case in which a subject was asked to draw a figure eight in the sagittal plane. In Fig. 8, it can be observed that the figure was close to the specified plane. Accordingly, the *Y* and *Z* components of the binormal vector were small compared to the *X* component (see Fig. 9). In the two upper rows of Fig. 10, we can see that the angle θ of the binormal vector was consistently different from one loop to the other (upper loop 77°, lower loop 100°), whereas ϕ remained similar (upper loop 181°, lower loop 186°). The spherical SD of the binormal vector was 2.2° for the upper loop and 2.6° for the lower one. The angular difference between the average plane orientation of the two loops was 24°.

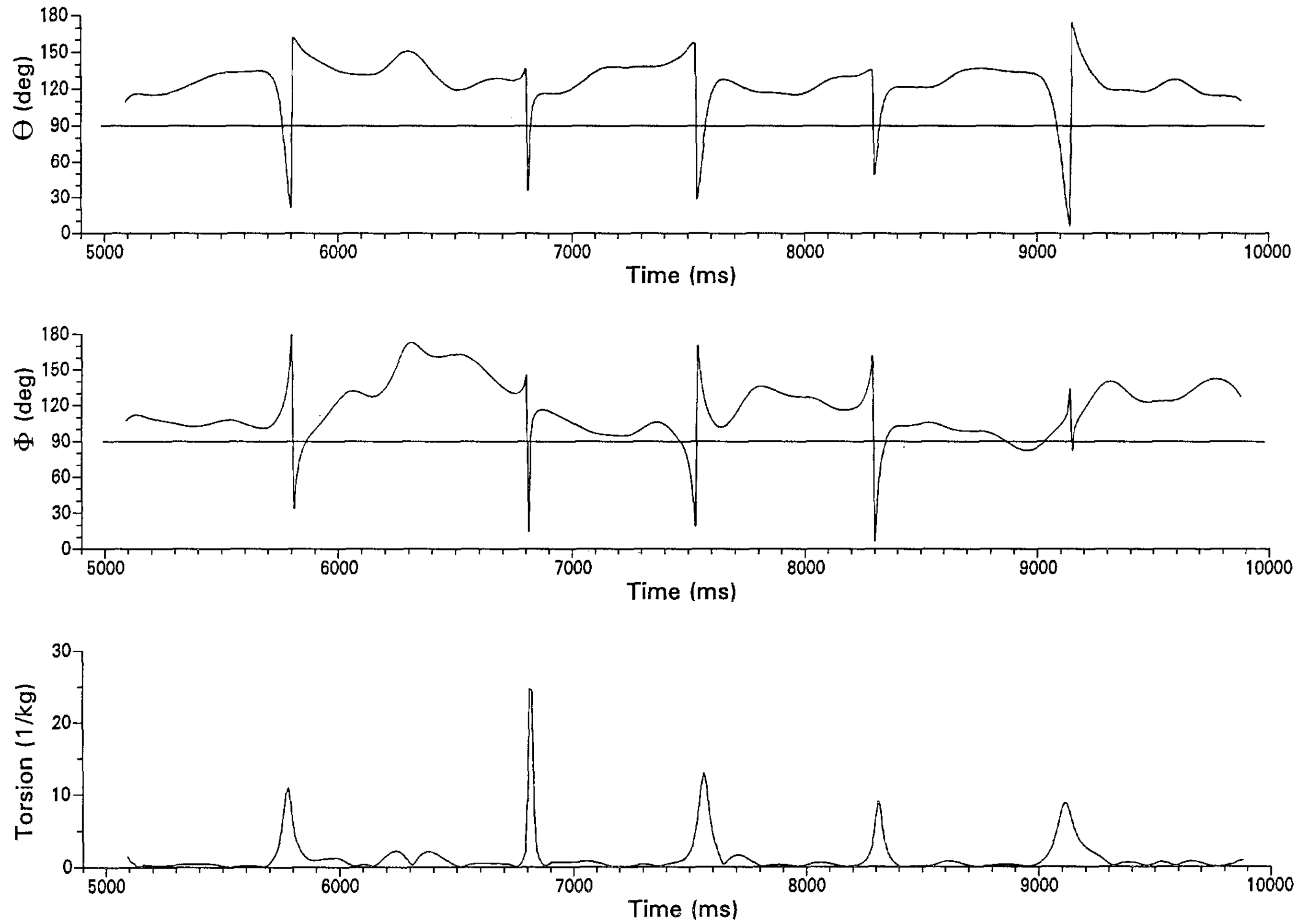

Fig. 4. Spherical coordinates and torsion for the data presented in Fig. 2. *First row*: θ plotted against time. *Second row*: ϕ plotted against time. *Third row*: torsion is plotted against time

Discussion

In this experiment, subjects had to exert isometric forces continuously in order to draw figure eights in different planes, and in the presence or absence of a visual force-feedback cursor. In every condition there was a substantial difference in the plane orientation of the two loops of the figure. Moreover, the angular differences observed in this experiment were in the same range as those obtained by Soechting and Terzuolo (1987a) in a free hand movement experiment.

The results of the present experiment indicate that the planar segmentation of the motor trajectory occurs whether or not the trajectory involves joint motion. Therefore, if not joint motion, nor movement dynamics are the crucial factors producing this effect, another one which is common to movement and isometric conditions must be responsible. One can ask whether the mechanical features of the arm due to the musculoskeletal geometry might be the cause of the planar segmentation of the trajectory. However, this seems unlikely for several reasons. First, similar results were observed in isometric and movement experiments although the mechanical characteristics such as the joint torques and muscles activities are drastically different. Differences in EMG activity between isometric and movement have been described even for simple forearm isometric or movement flexions (Tax et al. 1990). Second, in Soechting and Terzuolo's (1987a) experiment and in ours similar results were observed for different instructed plane orientation. Obviously, the joint torques and muscles activities are different when the trajectories are drawn in different planes (see Soechting and Terzuolo 1987a). Third, we observed different types of change of plane between subjects or for repeated trials by the same subject, although the musculoskeletal geometry of the arm was nearly constant. It seems, then, that joint motion or arm mechanics cannot account for the changes of plane observed in isometric conditions, even if they might contribute to this effect in movement conditions. Consequently, these results suggest that the planar segmentation is due to central constraints related to the production of a motor trajectory. It is, however, not clear at what level these constraints might intervene between the intended spatial definition of the trajectory and the motor output.

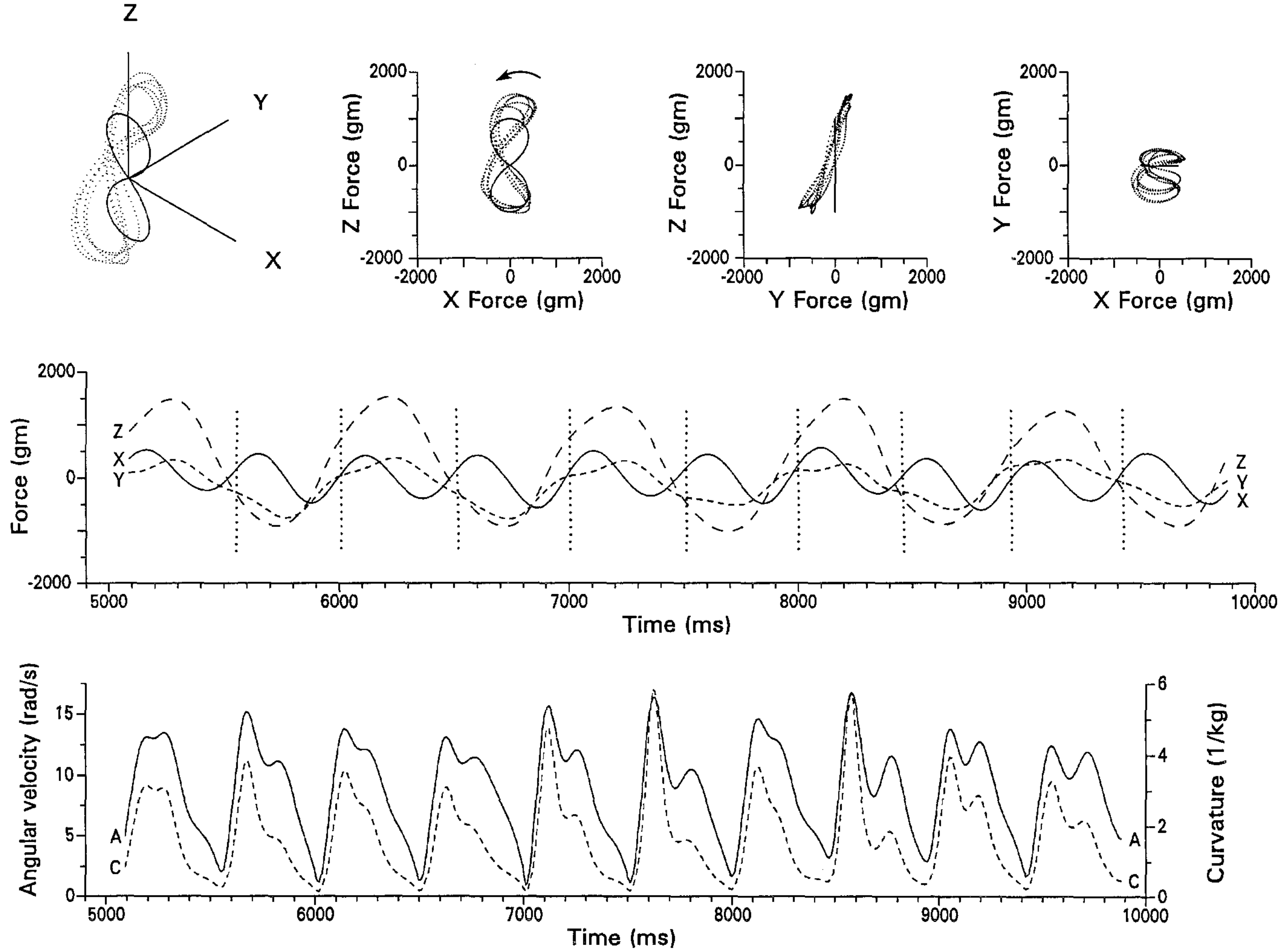

Fig. 5. Force trajectory performed by a different subject when asked to draw a figure eight in the frontal plane (XZ). See legend of Fig. 2

Although biomechanical factors might not be responsible for trajectory segmentation, they may underlie systematic biases, such as the consistent tilt of the figure eights in the anterior-posterior direction when the subjects were asked to draw it in the frontal plane. Such departure from the specified plane could result from the orientation of the stiffness field, which means that it might easier to exert forces in an oblique anterior-posterior plane, than in a strictly frontal plane.

Common factors in the production of movement and isometric drawing trajectories

Although joint motion is absent in isometric conditions, one can hypothesize that the motor implementation of the trajectory still involves a transformation from the intended spatial trajectory into arm orientation angles. Indeed, it can be argued that the motor system is probably adapted to produce movements in space, instead of drawings under isometric conditions. Accordingly, the stage of transformation from extrinsic to intrinsic motor parameters that can explain the occurrence of the planar segmentation during hand movements (Soechting and Terzuolo 1986, 1987a, b), could also account for the same results in isometric condition. Indeed, the rules of coordination of the arm and forearm predict that the plane of motion of the wrist cannot change continuously within a given segment of the trajectory (Soechting and Terzuolo 1986). The necessary assumptions for this prediction are that the modulations of the arm orientation angles are periodic and of the same frequency within a given segment of the trajectory. Soechting and Terzuolo (1987a) provided evidence for these assumptions. They observed that, within a segment of the trajectory, the modulation of the arm orientation angles is close to sinusoidal. From this, it follows that the modulation of the orthogonal components of the wrist trajectory will be also sinusoidal (Soechting et al. 1986). Thus, the sinusoidal-like modulation of the arm orientation angles and of the wrist trajectory components and the constant plane of motion are two views of the same phenomenon (Soechting and Terzuolo 1987b). In

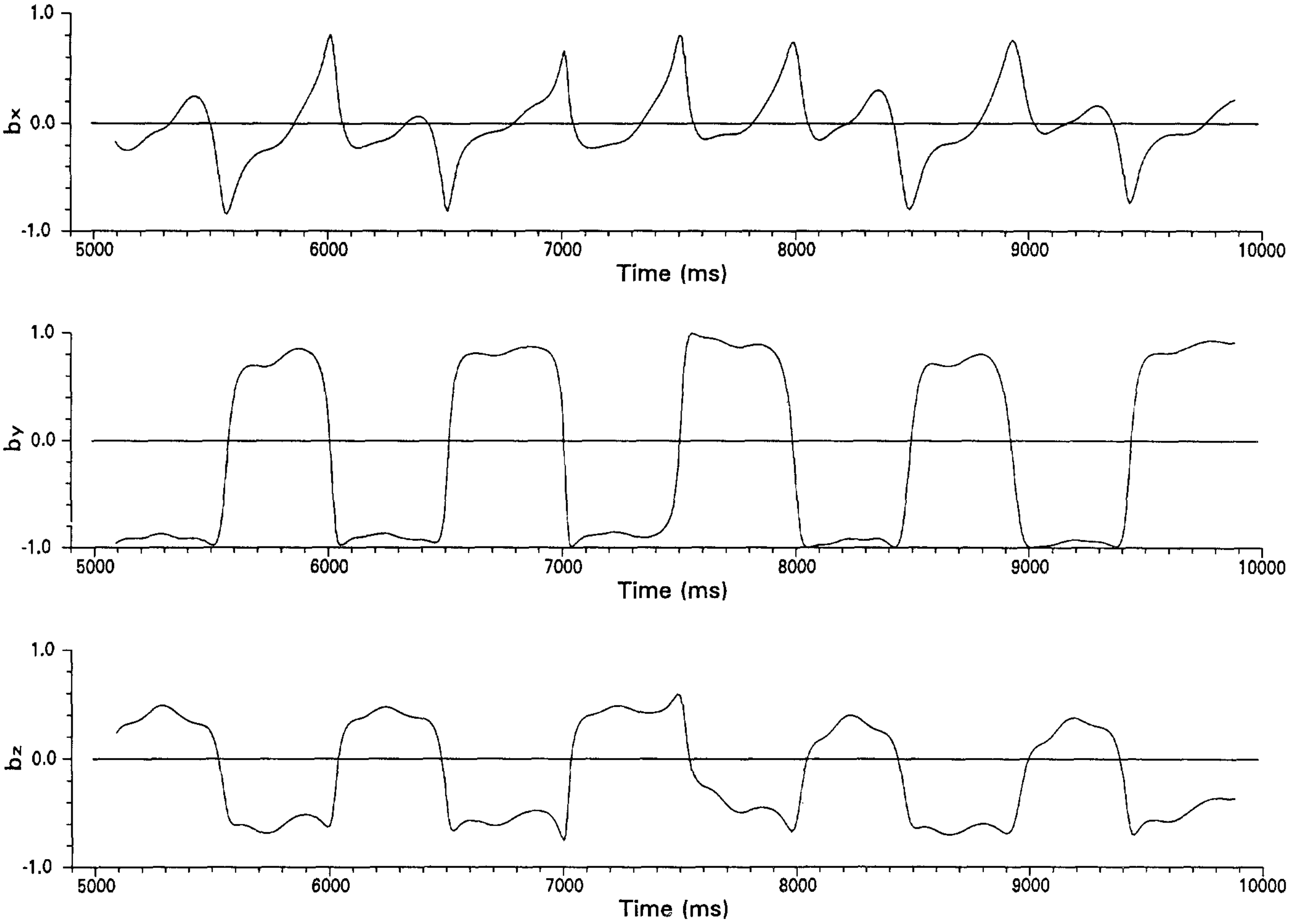

Fig. 6. *XYZ* components of the binormal vector for the data presented in Fig. 5, plotted against time

the isometric conditions, the orientation angles were obviously invariant, as was the position of the wrist, but the time course of the force components within a segment of the trajectory were modulated in a nearly sinusoidal fashion. Consequently, what seems important is that the motor system produces *similar kinds of spatial modulations for wrist movements and isometric forces.*

The results of the present study provide a second case for a fundamental similarity in the control of movement and isometric force trajectories. The first case was provided previously when it was shown that the relation linking curvature and velocity in movement trajectories (Viviani and Terzuolo 1982) is also observed under isometric conditions (Massey et al. 1992). These similarities are remarkable, for the mechanical characteristics in both conditions are drastically different, which means that the implementation (e.g. joint torques, muscles activities) of the spatial trajectory is also different. What is common to both of these cases is the *spatial* aspect of trajectory control. This phenomenon is reminiscent of the motor equivalence concept (Bernstein 1967), which denotes the capacity of the motor system to achieve the same spatial goal in different ways.

Brain mechanisms related to motor equivalence

Several studies in behaving monkeys have been devoted to the relation between single cell activity in various brain areas and production of arm movements in space (see Georgopoulos 1991 for a review). These studies documented consistent changes of neuronal activity that were related to the direction of the movement. Recently, the activity of motor cortical neurons has been recorded while monkeys performed an isometric force pulse in relation to a visually specified direction and in the presence or absence of a force bias (Taira et al. 1991; Georgopoulos et al. 1992). The results showed that the cell activity was directionally tuned as in movement tasks, and that the tuning was not affected by the presence of a force bias. Thus, the activity of motor cortical cells is similarly related to spatial direction in movement and isometric conditions and in the presence or absence of a force bias.

Other studies provide similar links between neural activity and the motor equivalence property. For example, whenever movement direction about a single joint and muscle activity were dissociated by applying an external load, it was found that a good proportion of cells in the

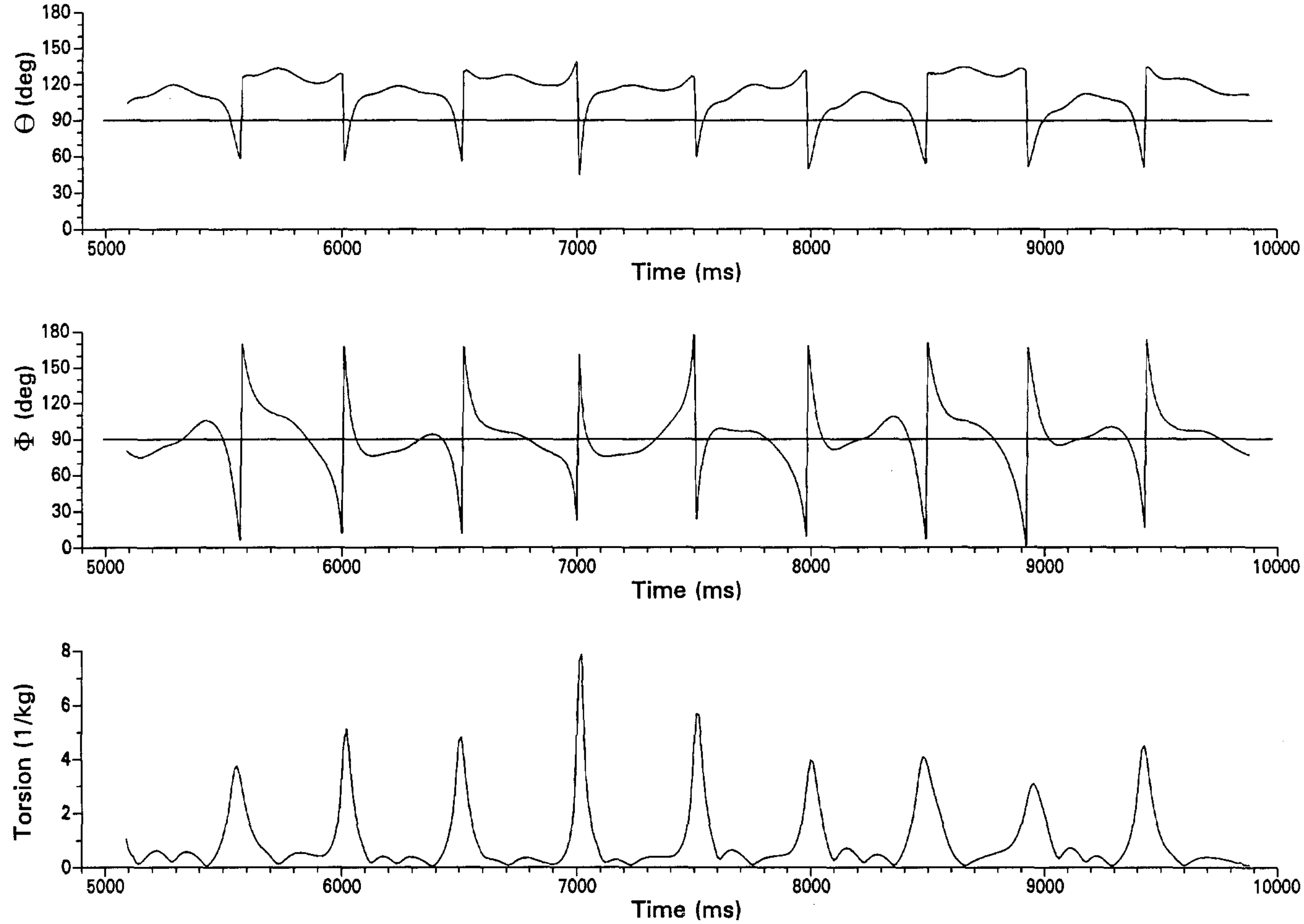

Fig. 7. Spherical coordinates and torsion for the data presented in Fig. 5. See legend of Fig. 4

motor cortex, the supplementary motor area, the cerebellum nuclei and the basal ganglia were related to the movement direction regardless of the muscle pattern activity used to produce such movement (Thach et al. 1978; Mitchell et al. 1987; Kalaska et al. 1989; Crutcher and Alexander 1990). Consequently, these neural activities seem to be related to the movement goal independently of its implementation.

The activity of single cortical motor cells is characterized by a broad directional tuning function, which led to the hypothesis that information about movement direction arises from the combined activity of a neuronal population (Georgopoulos et al. 1983). This has been confirmed in several subsequent studies (Kalaska et al. 1983, 1989; Georgopoulos et al. 1984, 1986, 1988; Fortier et al. 1989; Caminiti et al. 1990). In these studies, it was shown that the neuronal population vector (Georgopoulos et al. 1983), which is a measure of the combined directional tendency of an ensemble of neurons, points in the direction of the upcoming movement. Moreover, the time-varying direction and length of the neuronal population vector, computed from a population of motor cortical neurons, seems to reflect the instantaneous tangential velocity of the movement with a delay of about 150 ms (Georgopoulos et al. 1984; Georgopoulos et al. 1988; Schwartz and Anderson 1990). The 'neural' trajectories reconstructed from the time series of neuronal population vectors correspond well to the actual movement trajectories produced in reaching (Georgopoulos et al. 1988) as well as in 2D drawing tasks (Schwartz and Anderson 1989; Schwartz et al. 1991). Accordingly, Schwartz et al. (1991) have shown that the curvature and velocity of the 'neural' trajectory covaried in the same way as in the actual arm trajectory. These results indicate that this covariation may arise from constraints pertaining to the combined activity of an ensemble of motor cortical neurons. In other words, the behavioral features such as those described by the kinematics of motor trajectories closely reflects properties of the neuronal ensemble.

Although several stages from the intended spatial trajectory to the implementation of the motor output can

Fig. 8. Force trajectory performed by a third subject when asked to draw a figure eight in the sagittal plane (YZ). See legend of Fig. 2

Fig. 9. XYZ components of the binormal vector for the data presented in Fig. 8, plotted against time

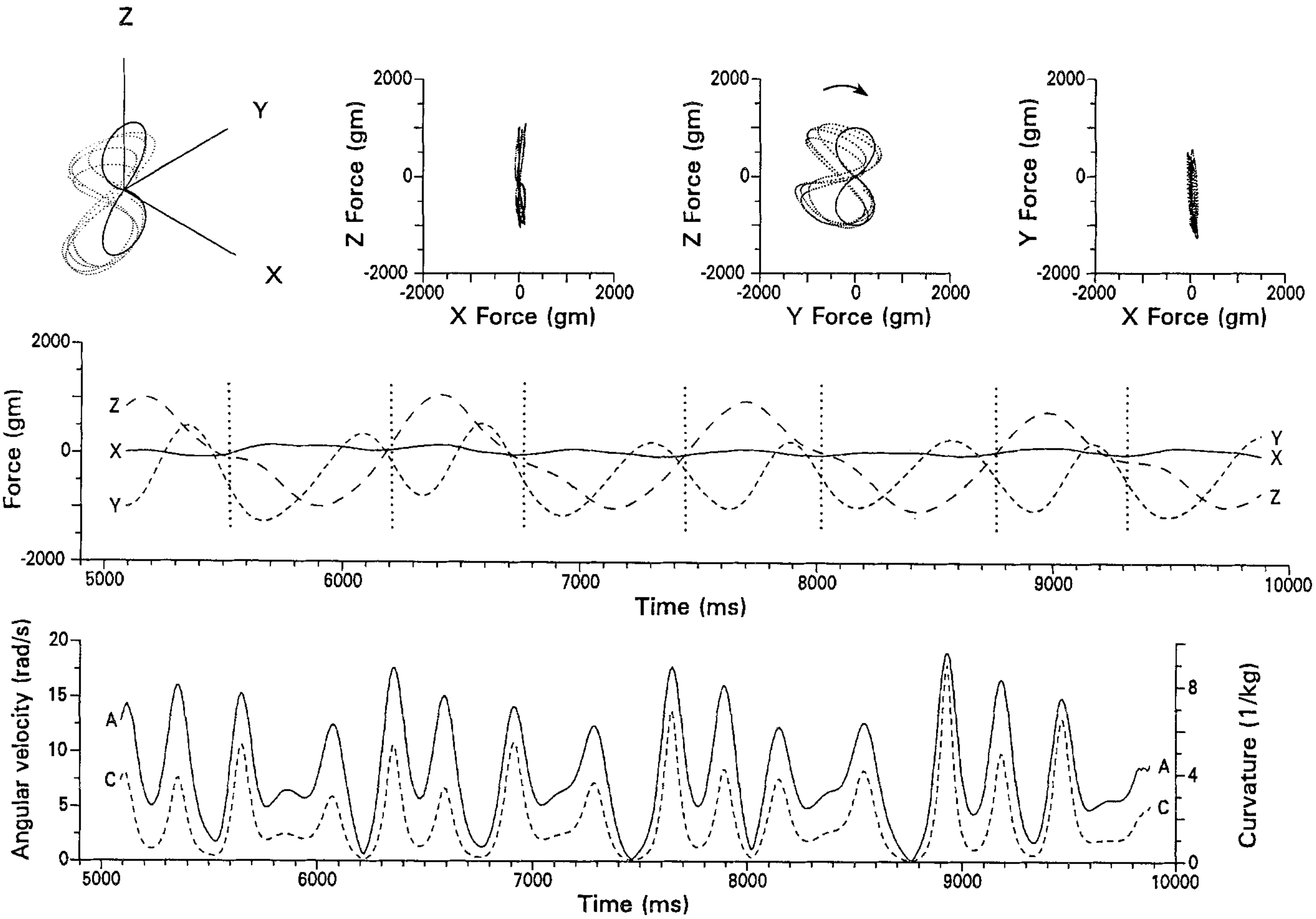
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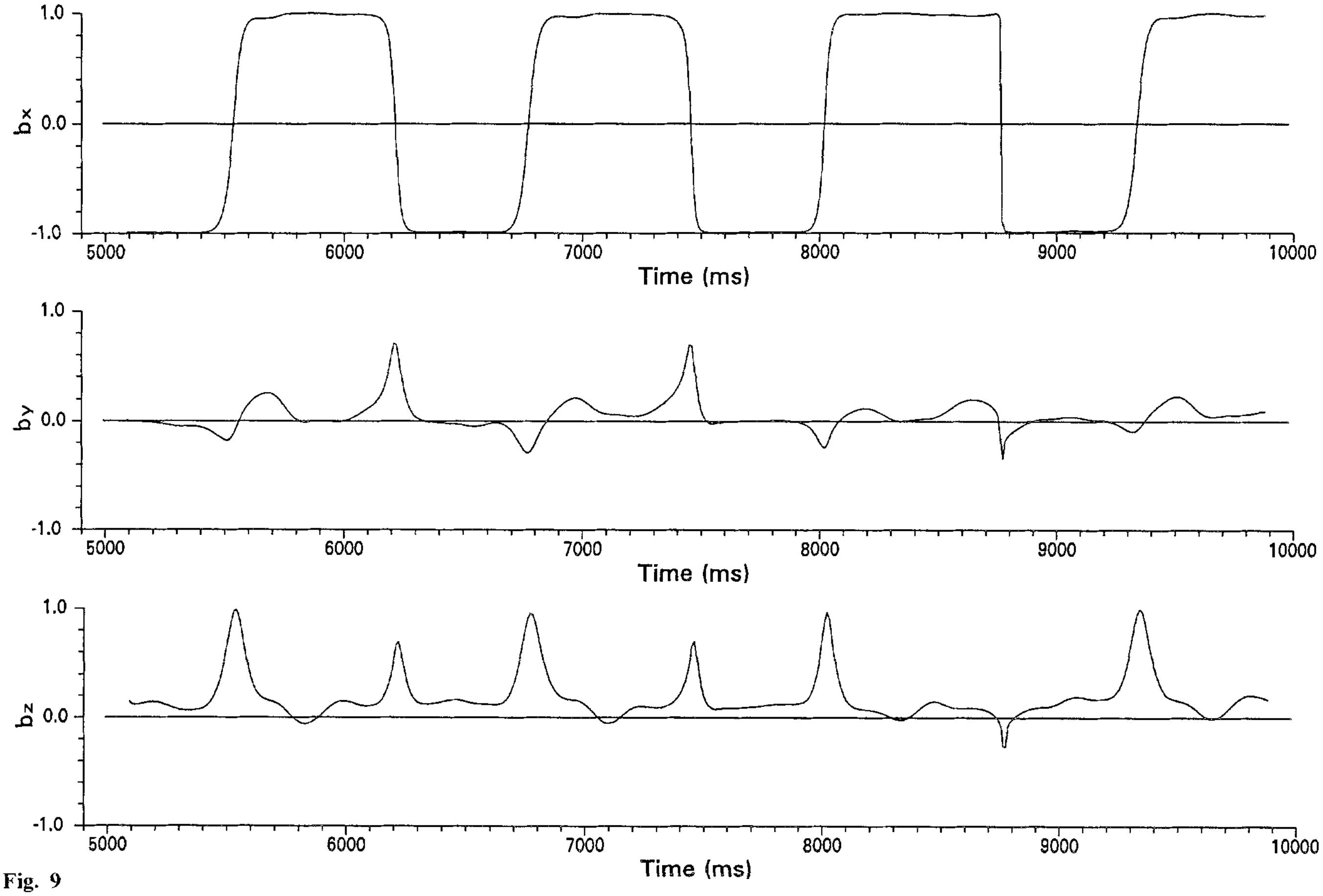
Fig. 8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6000
7000
8000
9000
10000
Time (ms)

Fig. 9

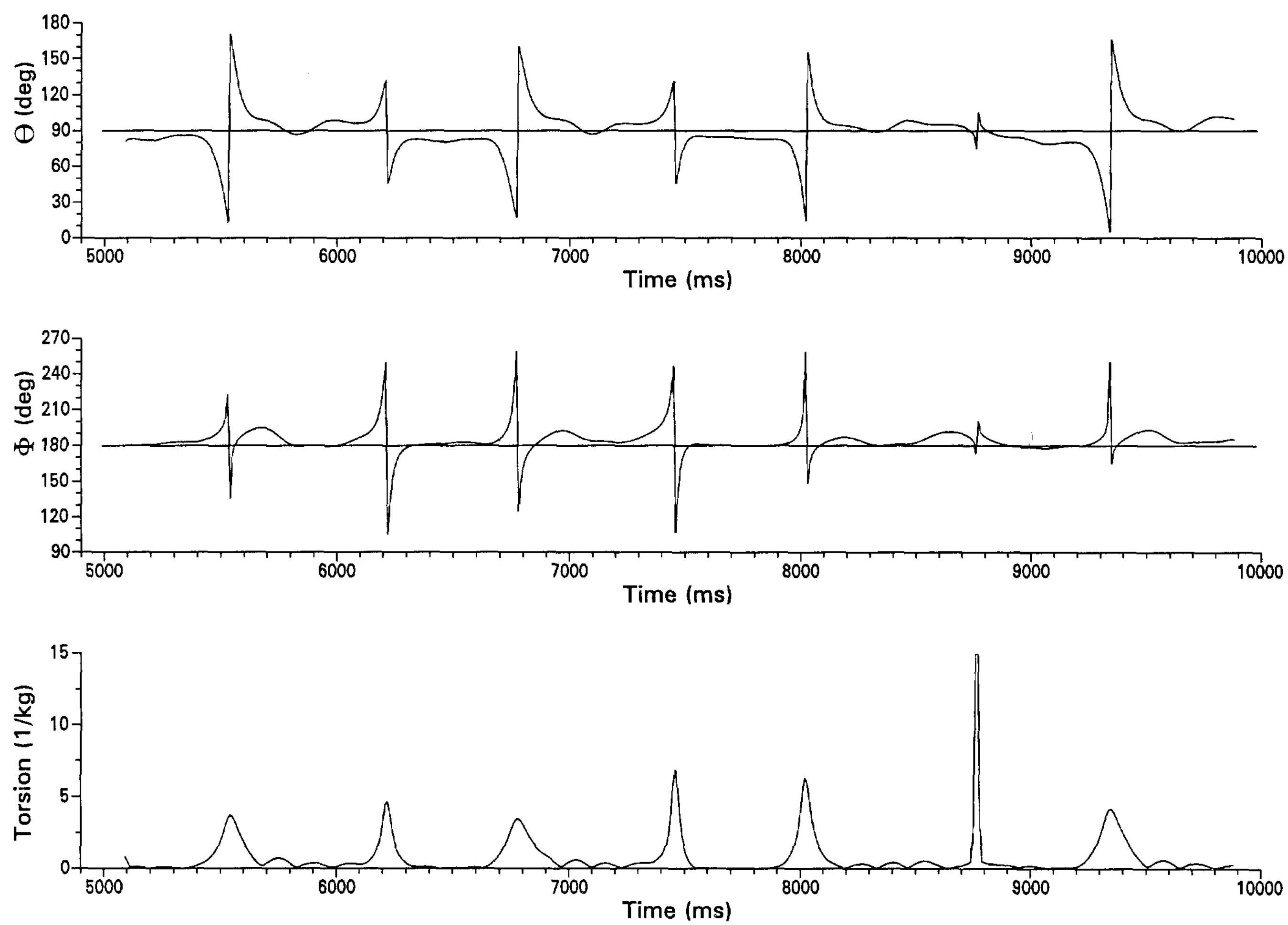

Fig. 10. Spherical coordinates and torsion for the data presented in Fig. 8. See legend of Fig. 4

be responsible for the planar segmentation, the close relation between neuronal activity and movement kinematics discussed above suggest the hypothesis that the planar segmentation results from properties of the population of neurons coding the movement direction. In order to produce a curved trajectory, the activity of the neuronal ensemble must change in time. The planar segmentation obtained in 3D drawing trajectories suggests that the neuronal population vector rotates in a constant plane within a segment of the trajectory, and that this plane can change at the point of inflection, that is, when the direction of motion change. This means that a change of plane orientation tends to occur when the direction of rotation of the neuronal population vector is reversed (e.g., from clockwise to counterclockwise). Although it is unclear now why such change of plane may occur, it can be related to characteristics of the time-varying coding of movement direction by the neuronal population. This hypothesis can be tested in further neurophysiological experiments.

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