

Perceptuomotor Compatibility in Pursuit Tracking of Two-Dimensional Movements

Paolo Viviani
Pierre Mounoud
Department of Psychobiology
University of Geneva

ABSTRACT. In a previous article, we reported an investigation of visuomanual pursuit tracking of unpredictable two-dimensional targets. This article extends the study to the tracking of predictable stimuli. In both investigations, the target trajectory was elliptical. The experimental factors we varied were the orientation of the major axis of the ellipses (horizontal or vertical), the period of the movement (9.65 to 1.61 s), and the law of motion (natural vs. transformed). In the natural condition (L), the motion results from the combination of harmonic functions, as would be the case if the target were generated by a human. In the transformed (T) condition, the law of motion departs systematically from this natural model. The main results of the study are as follows: (a) Satisfactory performance is achieved only in the natural condition. Pursuit movements obey the same constraints observed in spontaneous movements. (b) Predictability affects significantly the average delay between target and pursuit. (c) Each component of the pursuit movements depends on both components of the targets. Thus, two-dimensional tracking generalizes significantly the classical one-dimensional condition. (d) The simple model developed previously to describe performance with unpredictable targets can be generalized to cover the present case as well.

A PREVIOUS ARTICLE (Viviani, Campadelli, & Mounoud, 1987) reported a study of visuomanual pursuit tracking of unpredictable two-dimensional targets. As argued there, the two-dimensional version of this task represents a significant generalization of the paradigm used in almost all investigations of the tracking skill. Indeed, pursuit movements are rather peculiar among all human motor actions, because they are at the same time under voluntary control and yet constrained both spatially and temporally by an external driving input. Ideally, perfect pursuit requires that the motor control system be used as a general-purpose processor for replicating faithfully any visual input. Whatever its internal structure, the processor should be able to prevent its inner working from manifesting itself in the operating characteristics. In actual fact, of course, such an independence of the operating characteristics from the internal structure is never fully achieved. Eye movements represent perhaps the most typical case in which the few possible types of motor patterns all carry a clear imprint of the

underlying control processes. More generally, however, there is a growing body of evidence to suggest that voluntary movements possess certain unique features that sharply distinguish them from motions that can be produced by mechanical contraptions. These features are likely to reflect both the inner working of the motor control system and the physical properties of the effectors. In particular, in free hand movements, the law of motion depends on the geometry of the trajectory in a way that cannot be predicted from biochemical considerations alone (Flash, 1987; Flash & Hogan, 1985; Lacquaniti, Terzuolo, & Viviani, 1983; Soechting & Terzuolo, 1986; Viviani & Terzuolo, 1982; Wann, Nimmo-Smith, & Wing, 1988). With respect to visuomanual pursuit, therefore, the general question can be raised as to the extent to which the intrinsic properties of the control system interfere with the perceived kinematical and geometrical properties of the visual stimulus. Classical one-dimensional targets (sine waves, steps, ramps, etc.) are intrinsically inadequate to tackle this question, because the geometry of these movements is far too simple. Curved trajectories in the plane represent, instead, the simplest situation in which the notion of geometrical form can be brought to bear in the context of visuomanual coordination.

Several results of the previous study are summarized here:

1. Unpredictable targets whose velocity satisfies the constraints present in human movements can be pursued with good accuracy and in a surprisingly consistent manner.

2. The strategy used to pursue these targets can be represented adequately by a simple velocity feedback scheme that includes a central processing delay.

3. Targets whose velocity is constant—a condition that is never verified in natural movements—can also be tracked in a consistent manner. The feedback scheme can be applied to this case too, but the results suggest that coping with these “unnatural” targets requires a change in the operating characteristics of the motor control system.

Several questions were left unanswered by the experiments with unpredictable targets. The first question that remains open in the two-

This research was supported by Research Grant 1.073.0.85 of the Fonds National Suisse de la Recherche. The experiments were conducted at the Istituto di Fisiologia dei Centri Nervosi - CNR, Milan, with which the first author was formerly associated. We are grateful to Dr. Paola Campadelli for collaborating in the early stages of this project. We also wish to thank Anatol Feldman, Alan Wing, and an anonymous reviewer for suggesting a number of improvements to the original manuscript. Correspondence concerning this article can be sent to Dr. Paolo Viviani, FAPSE, University of Geneva, 24 rue du General Dufour, 1211, Geneva 4, Switzerland.

dimensional case is the influence of predictability on motor performance. It has often been argued (cf. Poulton, 1974; Wickens, 1986) that the pursuit response to periodic targets is partly controlled by a central anticipation of their future course. In the one-dimensional case, the law of motion and its derivatives provide the only basis for such an anticipatory component of the response. In the case of planar trajectories, the direction of the movement also changes in an orderly manner and, therefore, could be anticipated. The extent to which this is actually the case is not known; nor do we know whether such an anticipation of the changes in direction can be carried out independently of a concurrent anticipation about the target kinematics. Finally, we also ignore the question of whether the correlation that might exist between the law of motion and the geometry of the trajectory can itself provide guidance for predicting the future course of the target.

The second issue that deserves further attention is also related to the fact, mentioned above, that voluntary hand movements obey certain constraints in the relation between their form and kinematics. Remember that the constant velocity condition explored in the previous study violates these constraints but is still compatible with a reasonably good tracking performance. The question then arises, whether a more drastic departure of the target motion from the regularities present in spontaneous movements can ultimately result in a measurable disruption of the performance.

A third issue concerns the validity of the feedback scheme used to represent the pursuit performance. The range of average velocities explored in the experiments with unpredictable targets was rather narrow (10.42–16.67 cm/s). It is open to question, therefore, whether the conclusions reached by applying the scheme within such a narrow range remain valid when one considers the full spectrum of velocities observed in natural movements. In particular, the paramount importance given to the velocity feedback deserves special attention because, with a few exceptions (e.g., Jagacinski & Hah, 1988; Miller, Jagacinski, Navalade, & Johnson, 1982), models of pursuit tracking tend to emphasize instead the feedback of position information (cf. Poulton, 1974).

The fourth and final question arises as a result of recent findings on the generation of hand trajectories. There is, in fact, the following evidence:

1. The useful workspace for movements involving wrist, elbow, and shoulder joints is not homogeneous from the point of view of the control strategy (Flash, 1987; Hollerbach & Atkeson, 1986).

2. At least one of the parameters that are relevant to the description of the movement (the mechanical and reflex stiffness) depends on the position in the workspace and the direction of the displacement (Mussa-Ivaldi, Hogan, & Bizzi, 1985).

3. When the available degrees of freedom exceed the requirements of the desired end-point trajectory, specific constraints are injected by

the motor control system into the relation between elbow and shoulder angles (Soechting, Lacquaniti, & Terzuolo, 1986; Soechting & Terzuolo, 1986). These constraints result in equally specific distortions of the actual trajectory.

Taken together, these findings suggest the possibility that, in the pursuit-tracking task, the hand-arm system may respond differently to target motions in different directions and different positions within the workspace. Complex targets, such as those used in the previous experiments, are not well suited to expose this possible influence, because local efforts may cancel out. The pursuit-tracking experiment reported in this article addresses all four issues evoked above. A closed geometrical form—the ellipse—provided in all cases a predictable and simple target trajectory (Issue 1). Two factors of the experimental design were related to the kinematics of the target. The first factor was the instantaneous modulations of the velocity along the trajectory. It has been shown—both in adults (Lacquaniti et al., 1983) and children (Viviani & Schneider, 1990)—that a stable relation exists between the tangential velocity and the radius of curvature of elliptic movements. A power law provides a satisfactory quantitative description of such a relation. In half of the trials, the velocity of the templates satisfied this internal constraint of natural movements. In the other half, the constraint was grossly violated (Issue 2). The second factor was average velocity of the target over one cycle. The period of one motion cycle was varied over a 1–7 range (Issue 3). The third experimental factor was the orientation of the major axis of the ellipse, which defines both the main direction of the movement and the range of covariation of the joint angles (Issue 4).

In comparison with the one-dimensional case, the analysis of two-dimensional pursuit tracking requires the development of specific methodological tools. Here, these matters will be dealt with briefly and only insofar as they are necessary to make the presentation self-contained. The reader is referred to the previous article (Viviani et al., 1987) for a detailed discussion of these methodological issues.

Methods

Subjects. Ten subjects (7 males and 3 females, age range: 25–42 years) volunteered for the experiment. They were all right-handed and had normal or corrected-to-normal vision.

Apparatus. The experimental apparatus and the data acquisition were identical to those described in detail in the previous article (Viviani et al., 1987). Briefly, the visual target was produced by a computer-controlled laser beam that was rear-projected on a transparent digitizing table. Subjects pursued the target with the standard hand-held cursor of the table. The instantaneous position of both the target and the cursor were sampled at 60 Hz, with a nominal accuracy of 0.025 mm.

Targets. In all cases, target trajectories were ellipses with the same form (labeled G for *Geometric*; eccentricity, $\Sigma_g = 0.9$; perimeter, $P = 58.905$ cm). In half of the targets (type H), the major axis of the ellipse was horizontal; in the other half (type V), it was vertical. Each type of target could follow two different laws of motion [the law of motion is the function $l = l(t)$ which describes the increase in time of the curvilinear coordinate l along the trajectory].

The first law of motion (to be called L for *Lissajous*) is the one that obtains when the elliptic trajectory is generated by composing vectorially two sinusoidal functions as follows:

$$x_g(t) = A_{xg} \cdot \sin(\Omega t),$$

$$y_g(t) = B_{yg} \cdot \cos(\Omega t),$$

where Ω is the rhythm of the movement. The eccentricity Σ_g of G is defined as

$$\Sigma_g = \sqrt{1 - (A_{yg}/A_{xg})^2}, \text{ if } A_{xg} \geq A_{yg} \text{ (type H),}$$

$$\Sigma_g = \sqrt{1 - (A_{xg}/A_{yg})^2}, \text{ if } A_{xg} \leq A_{yg} \text{ (type V).}$$

The second law of motion (to be called T for *transformed*) was defined by the following condition: At any instant, t , the tangential velocity along the trajectory must be equal to the tangential velocity that would have, at the same instant, a point tracing a Lissajous ellipse (called D for *dynamic*) whose major axis was rotated by 90° with respect to that of the actual target. The time course of the x and y components of the target in conditions L and T is contrasted in the upper two panels of Figure 1A. For each speed condition (see below), the cycle period of L- and T-type targets is the same. Therefore, the average tangential speed and its time profile are identical in the two cases (see the third panel in Figure 1A). Whereas in L-type targets, however, the maximum tangential velocity occurs where the radius of curvature is maximum, and the minimum tangential velocity occurs where the radius of curvature is minimum, the position of the same minima and maxima along the trajectory is interchanged in type-T targets. Thus, both the time course and the polar distribution of the angular velocity ($A = V/R$) are different in the two cases (Figure 2). The general mathematical procedure for generating elliptic trajectories whose law of motion is that of any Lissajous ellipse is described in Appendix A.

In all cases, pursuit movements were recorded for 19.3 s. The number of complete movement cycles within this period could be 2, 4, 6, 8, 10, 12, and 14, which correspond to the following average velocities: 6.10, 12.20, 18.31, 24.42, 30.52, 36.62, and 42.73 cm/s, respectively. One extra cycle was always inserted at the beginning of the trial to allow subjects to attain a steady performance. This initial cycle was not recorded. Twenty eight different target types resulted from the combination of the two orientations, the two laws of movement, and the seven average velocities.

Procedure. Each subject followed each target type five times. Thus, one complete experiment comprised 140 trials. To avoid fatigue, we administered the trials in two sessions. Half of the subjects were presented with a random permutation of all targets with 2, 6, and 10 cycles in the first session and of all targets with 4, 8, 12, and 14 cycles in the second session. The session sequence was inverted for the other half. For both sessions, a different permutation was used for each session. Two of the subjects (the authors) were aware of the experimental design. Of the 8 other subjects to whom no information was provided, some realized in the course of the experiment that the same target was presented several times. The average interval between repetitions was too large for any motor learning to occur, however. The assignment was introduced verbally, and we stressed the fact that a good performance consisted of "keeping the target as close as possible to the cross-hair of the cursor for as long as possible." Before each session, subjects practiced for a few trials at each of the velocities included in that session. No constraints were imposed on either the general body posture adopted during the task or the arm segments involved in the tracking movements. At the beginning of a trial, subjects placed the cursor cross-hair on the laser spot that indicated the starting point of the target. This point was always in the 3-o'clock direction, but the distance from the center of the table provided a clue to the target type (H or V) about to be presented. Two s after an acoustic warning signal, the target spot started moving, and the subject had to track the spot for as many cycles as were presented in the trial. The pace of the presentation was controlled by the experimenter, and, on the average, trials were 10 s apart. Short periods of rest were inserted at the subject's request. Subjects could also ask to repeat a trial if they felt that in the course of the recording they had lost the necessary concentration.

Results

Qualitative analysis. Throughout this section, we will contrast the tracking performance in the two kinematic conditions, L (Lissajous) and T (Transformed). Thus, we begin by emphasizing the nature of the difference between these conditions. As detailed under Methods, the average speed and time course of the velocity profile for a given rhythm are identical in both conditions. L-type targets result from the combination of pure harmonic functions, whereas the horizontal and vertical components of T-type targets contain higher harmonics (Figure 1A). Nevertheless, both components remain fairly smooth and, each one independently, well within the range of commonly observed spontaneous movements of the hand.

A quantitative difference also exists in the distribution of the angular velocity (Figure 2). The main qualitative difference, however, concerns the relation between the geometry and the kinematics of the targets. It can be shown (Viviani & Cenzato, 1985) that in L-type targets, the tan-

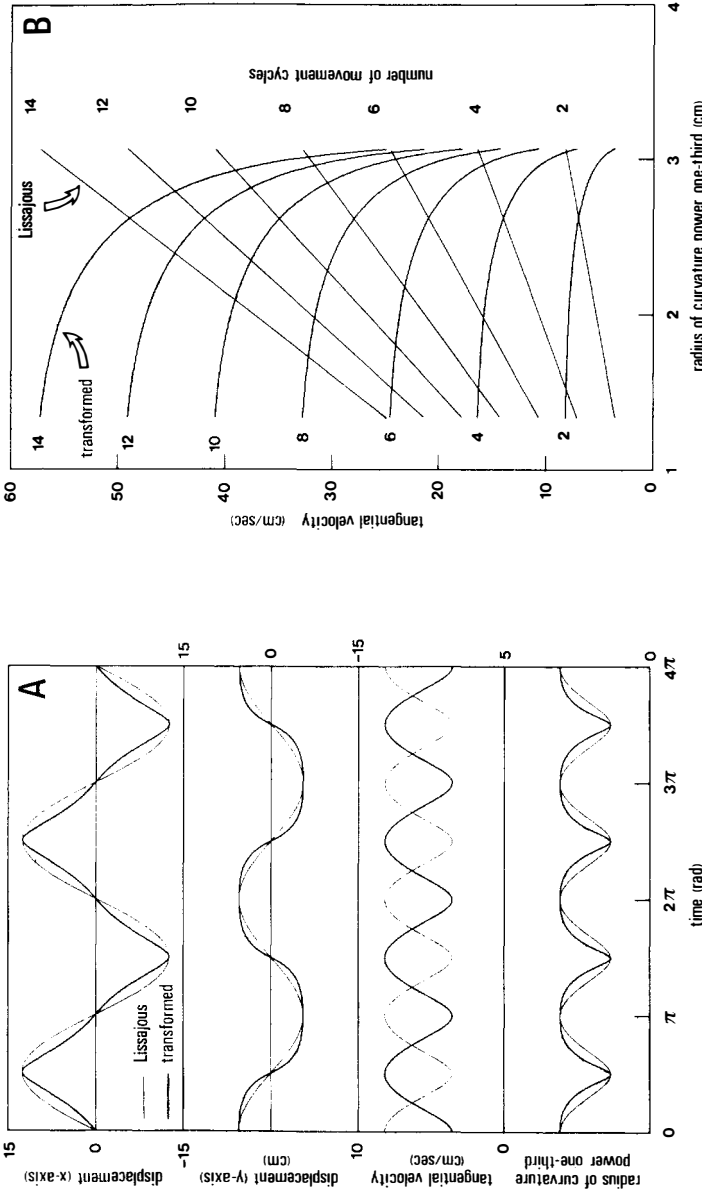


Figure 1. Description of the stimuli. A. Two complete cycles of the stimuli in the time domain (the example illustrates the case of a type-H target at the slowest velocity). Thin lines describe the parametric representation of an L-type ellipse, which is obtained by composing sine and cosine functions. Thick lines describe a T-type ellipse. Horizontal and vertical components for T-type ellipses were computed as described in Appendix A. L- and T-type targets follow the same trajectory. Thus, the radius of curvature (R) oscillates between the same values. Moreover, the profiles of tangential velocity (V) in the two cases are identical to within a 90° shift. Both components of T-type targets contain harmonic components, which are not present in L-type targets. Either of them could be pursued easily in a one-dimensional condition, however. B. Relation between radius of curvature and tangential velocity. At all rhythms, the tangential velocity of Lissajous targets is a linear function of the cube root of R , and the slope of the relation is inversely proportional to the period, T , of the movement. Most spontaneous hand movements comply with the same constraint. For T-type targets, the $V - R$ relation is entirely different and highly nonlinear. Thus, the main difference between experimental conditions L and T is the nature of the covariation between kinematics and geometry.

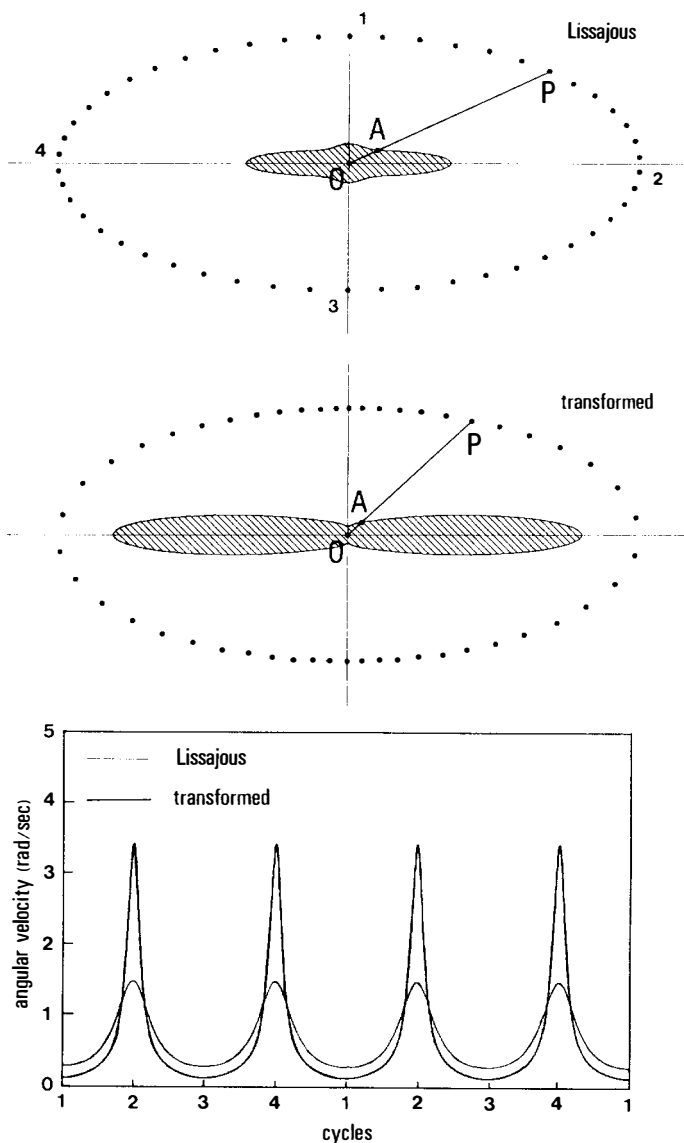


Figure 2. Angular velocity for the two types of targets. The lower plot compares the time course of the angular velocity for an L-type (thin line) and a T-type (thick line) target. The example shown (H-type at the slowest velocity) is the same as that in Figure 1. In the two upper plots, the angular velocity is displayed in the form of polar diagrams, to emphasize its relation to the geometry of the trajectory ($AO =$ angular velocity at point P). Notice that, despite the surface difference between the two plots, the average angular velocities are identical in both cases. A visual impression of the difference between the profiles of tangential velocities is provided by plotting only a few points of the trajectory equally spaced in time.

gential velocity, $V(t)$, is related to the instantaneous radius of curvature, $R(t)$, by the formula

$$2 \pi V(t) = \Omega \cdot P^{2/3} F(\Sigma_g) \cdot R^{1/3}(t),$$

where $\Omega = 2\pi/T$ is the rhythm of the movement, P is the perimeter of the ellipse, and F is a mildly varying function of the eccentricity Σ_g . For any choice of the parameters Ω , P , and Σ_g , $V(t)$ is an increasing linear function of $R^{1/3}$. For T-type targets, however, the $V - R^{1/3}$ relation decreases monotonously and is highly nonlinear. Figure 1B contrasts the two relations for all tested values of the rhythm.

We did not search individual performances for statistical evidence of motor learning. Qualitative analysis of the performance indices (see below) failed to show any systematic effect across subjects of the order in which the various condition were administered, however. In most cases, a stable performance was reached after the very first familiarization trial. Moreover, even the two authors, who had much more practice with the experimental conditions than the other subjects, did not fare better in negotiating the difficult T condition (see later). The two experimental factors that have the largest effect on the tracking performance are the rhythm, Ω , and the kinematic condition (L vs. T). Typical examples are used to illustrate the main qualitative findings in the space (Figure 3), and time (Figure 4) domains. Each trace in Figure 3 represents the average trajectory for one cycle, computed from all the data available in the indicated condition (for instance, in the 8-cycles condition, averages are computed on a $5 \times 8 = 40$ cycles). As the rhythm of the target increased, the entire pursuit trace rotated in the direction of the target movement. A few control trials, recorded in 3 subjects, showed conclusively that the angle of rotation was inverted when the direction of the target movement was inverted. To various degrees, all subjects presented this peculiar effect in condition T. In condition L, instead, a systematic rotation was observed only with targets oriented horizontally, and, on the average, its amplitude was smaller. It is remarkable that, although the angle of rotation at the highest rhythm could be as large as 17° , no subject attempted to compensate for the systematic errors that resulted from such rotation. Indeed, no one was ever reported to have noticed these errors. In condition L, the average perimeter and the eccentricity of the pursuit track matched quite accurately those of the target. In condition T, however, both these parameters decreased when the rhythm increased. In most subjects, pursuit traces of Lissajous targets were reasonable approximations of an ellipse, at all rhythms. Departures from the intended form included occasional distortions and a tendency at the highest rhythms to flatten out the least curved portions of the trajectory. These types of distortions occurred also in the transformed condition, but their amplitude was larger. In addition, within the low–medium range of rhythms, we also observed another type of distortion that was, instead, quite systematic and manifested itself as an antisymmetric

bending of the most curved portions of the trajectory (see upper right panel in Figure 3).

Gross qualitative differences between performance in the two conditions emerged in the time domain. Figure 4 shows the polar representation of the instantaneous delay, δ , between the target and the pursuit for the same set of experimental parameters of Figure 3. The delay is defined and calculated as in the case of random targets (Viviani et al., 1987). For each radial direction, the indicated quantity, δ , is proportional to the time that elapses between the moments when the target and the pursuit pass through homologous points on the trajec-

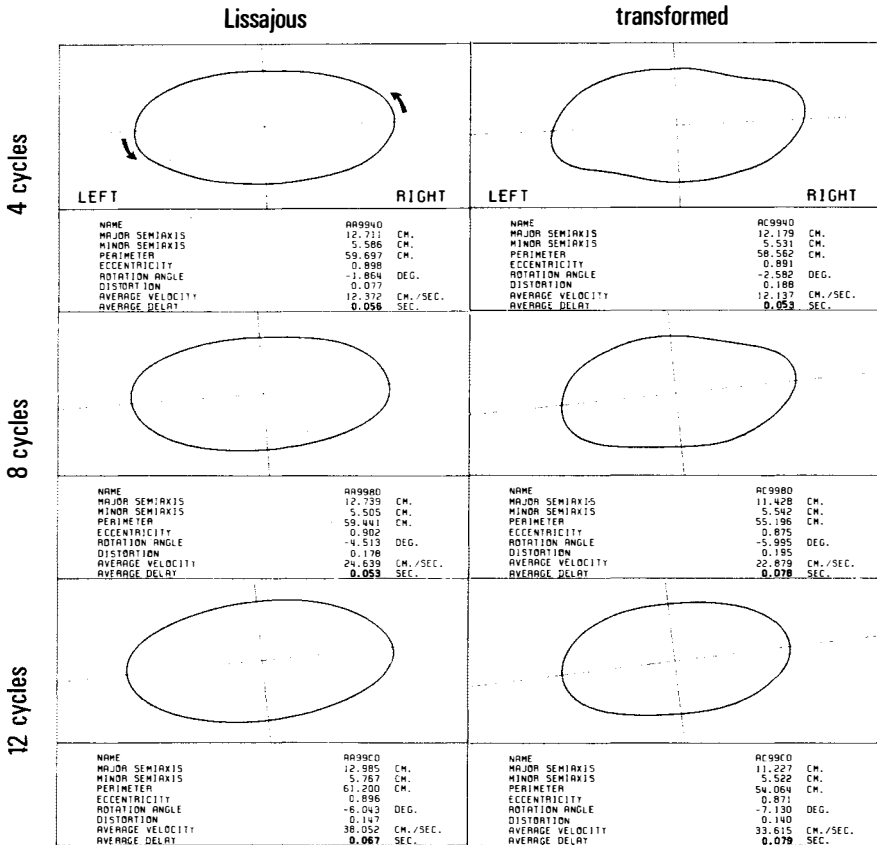


Figure 3. Pursuit trajectories. Data for one representative subject. For the three indicated rhythms, left and right plots illustrate some of the typical features of the pursuit trajectories in the two experimental conditions. Also shown inset are the quantitative parameters used to characterize the performances. As a general rule, pursuit trajectories in the T condition are more distorted, smaller, and less eccentric than those in condition L. A conspicuous rotation of the axes of the pursuit ellipse is present in both conditions.

tory. When the polar plot lies within the elliptic reference, as in two of the examples on the right, the pursuit is in advance with respect to the target. Delays were almost constant for all directions and all rhythms in condition L. Instead, they oscillated considerably and systematically in condition T, the oscillations being related to the velocity profile but not to the orientation of the major axis of the target. Obviously, the peculiar modulation of the tangential velocity prevented the subjects from maintaining a constant level of accuracy in the execution of the task.

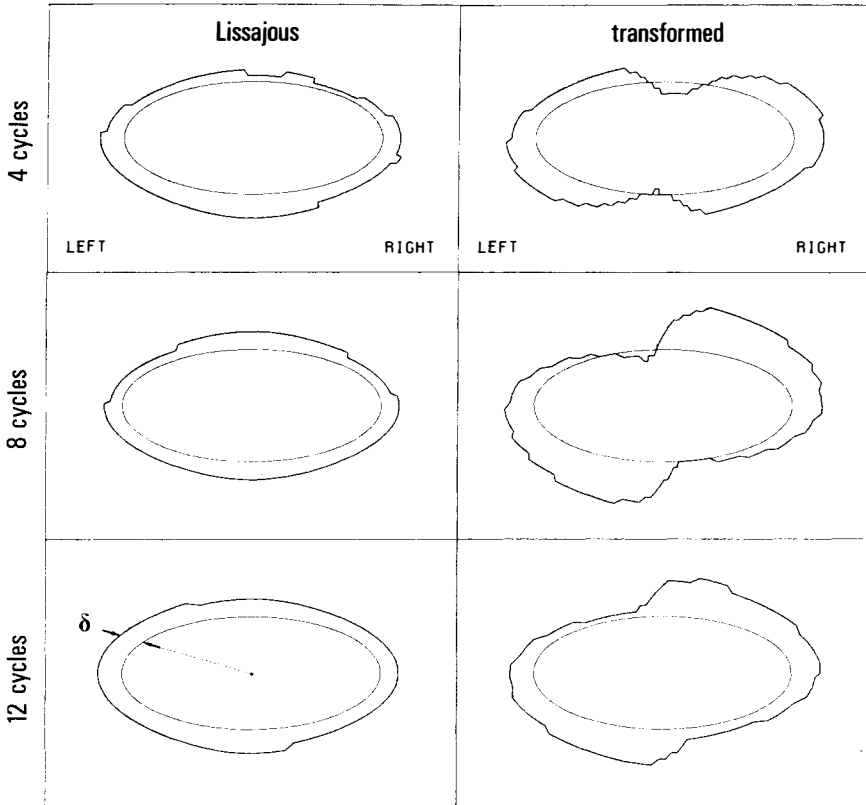


Figure 4. Temporal delays. Data for the same subject as in Figure 3. For the three indicated rhythms, left and right plots illustrate the typical profiles of the instantaneous delay in the two experimental conditions. The results shown are averages over all the cycles within a trial and all the trials for the same condition. As indicated in the lower left panel, the delay at any one point of the trajectory is proportional to the radial distance between the target trajectory and the polar plot. Portions of the plot laying within the outline of the target correspond to regions of the trajectory in which the pursuit is ahead of the target (negative delay). At all rhythms and in all subjects, the delay in condition L is fairly constant across movement cycles. Large modulations of the delay appear instead in condition T.

Finally, the effect of the relation between geometry and kinematics on tracking performance is dramatized by plotting the $V - R^{1/3}$ relation for the pursuit movement. Because individual plots are qualitatively similar, this relation has been calculated from the average pursuit trajectory over all subjects and all cycles of movements within a trial. In condition L (Figure 5) the data points for one complete cycle are almost indistinguishable from the superimposed straight lines that represent the behavior of the target (cf. Figure 1B). The agreement is equally good whether the major axis is horizontal (panel A) or vertical (panel B). In condition T, the situation was quite different. Each panel in Figure 6 displays the $V - R^{1/3}$ plot for the indicated rhythms and for the two orientations of the major axis of the ellipse (A, horizontal; B, vertical). These plots demonstrate large, systematic departures of the pursuit movements from the $V - R^{1/3}$ covariation that characterizes the targets. The differences depend on both the rhythm of the movement and the orientation of the axis. The results for the highest rhythms (10, 12, and 14 cycles) suggest that subjects modulated the velocity in accordance with the Lissajous model over a large portion of the 1st and 3rd quadrant, but with a considerable hysteresis. Efforts to comply with the kinematics of the target were only partially successful over small segments of the 2nd and 4th quadrants.

To summarize, these qualitative results demonstrate that, when the relation between the kinematics and the geometry of the target differs from that which is characteristic of the Lissajous model, the tracking task becomes unusually difficult. A serious deterioration of performance results, both in the space and temporal domain, but it is much more marked in the latter. In the next section we provide a quantitative analysis of these findings.

Quantitative analysis. The parameters of the pursuit trace to be considered are the perimeter, P , the angle of rotation, Θ , the eccentricity, Σ , the distortion with respect to the elliptic form, D , and the average delay, δ . The perimeter was calculated by integrating numerically the data points of the average complete cycle. Θ and Σ were estimated by the corresponding parameters of the least squares best-fitting ellipse of the pursuit trace. The distortion was defined as the least mean quadratic error resulting from the fitting routine. Table 1 summarizes the results of a $2 \times 2 \times 7$ (Orientation \times Kinematic Condition \times Rhythm) analysis of variance (ANOVA) of these quantitative parameters, with 10 replicates (subjects) per cell.

As mentioned in the previous paragraph, the performance parameters and their variations as a function of the rhythm were mostly affected by the kinematic modality. To some extent, however, they were also subject specific. This is particularly obvious for the average delay, δ (Figure 7). The left panel in this figure compares the results of each subject in the two Lissajous conditions (\circ = H targets; \bullet = V targets); the right panel shows the corresponding results for the transformed conditions. The bottom lines in each panel show the population

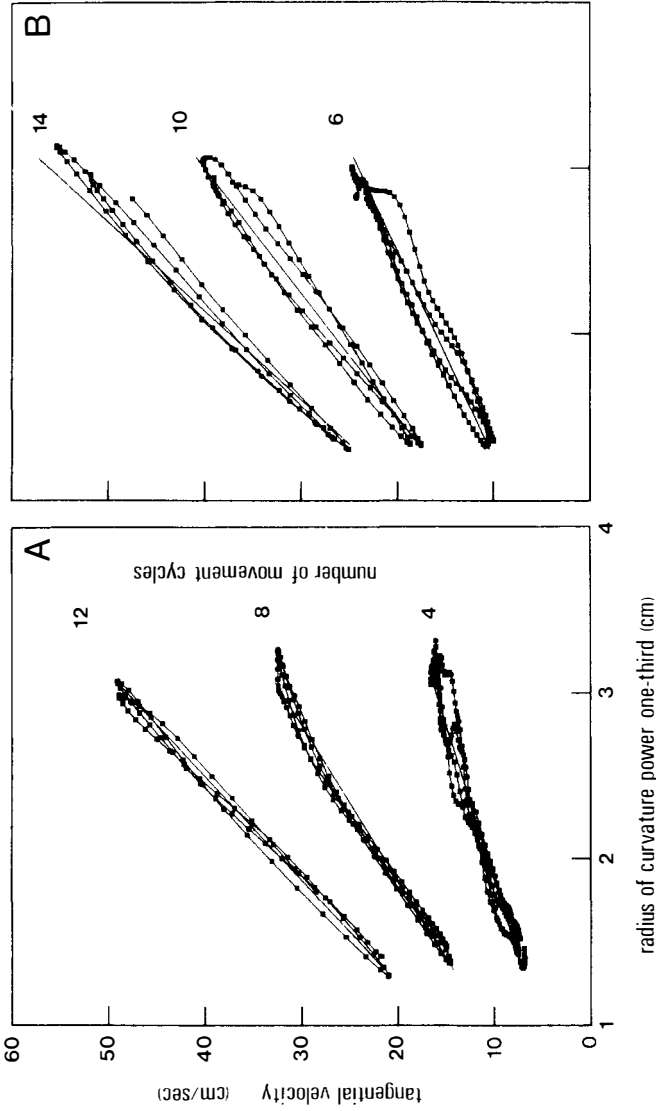
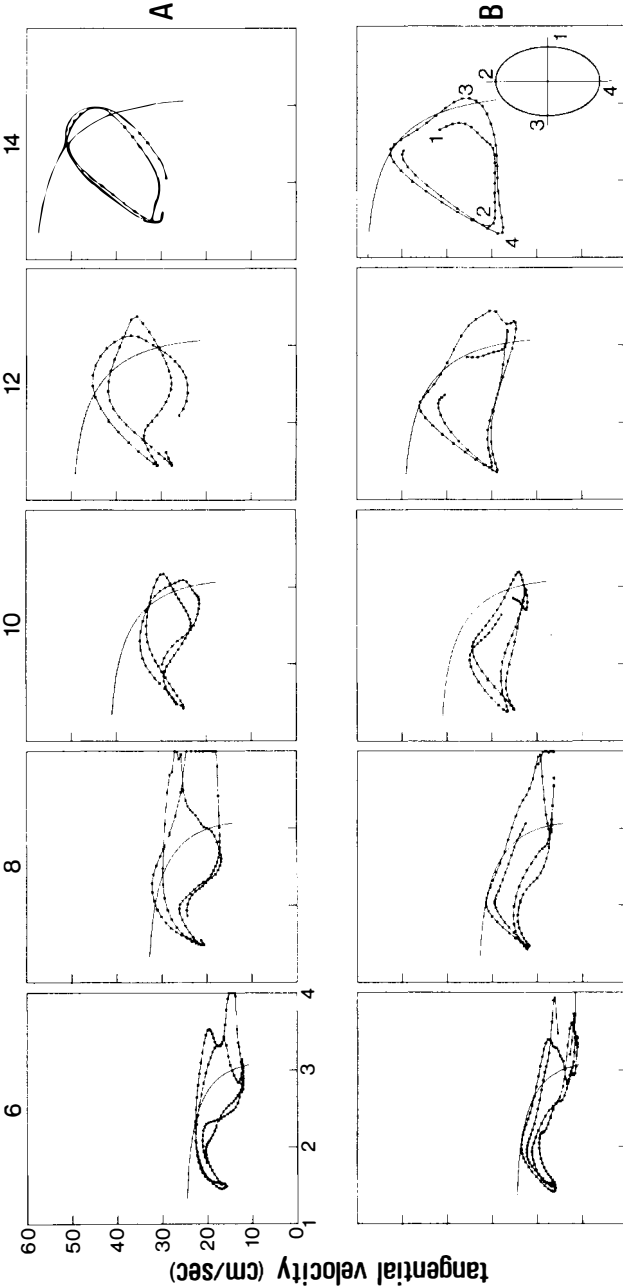


Figure 5. Covariation between form and kinematics in condition L. A. Covariation of the instantaneous tangential velocity with the radius of curvature of the pursuit trajectory for the indicated rhythms (H-type ellipses). B. Analogous data for V-type ellipses. The results shown are averages over all cycles within a trial, all trials for the same condition, and all subjects. Each cluster of points in this plots describes the four alternations between minimum and maximum values of the radius of curvature in one cycle of movement. Thin straight lines that interpolate the data points represent the theoretical predictions in the case of a perfect pursuit (cf. Figure 1). The results demonstrate that, in condition L, the pursuit movement exhibits the same covariation between form and kinematics that is normally observed in spontaneous movements.



radius of curvature power one-third (cm)

Figure 6. Covariation between form and kinematics: condition T. Each pair of panels (A, H-type targets; B, V-type targets) shows the covariation of the tangential velocity with the radius of curvature of the pursuit trajectory for one complete cycle of movement. The data points are averages over all subjects, all cycles within a trial, and all trials recorded at the rhythm indicated above (plots for the two slowest tempos are too noisy to be shown at this scale). The continuous curves superimposed on the data points are the theoretical predictions in the case of a perfect pursuit (cf. Figure 1). The results demonstrate the complete failure of the subjects to reproduce the desired relation between form and kinematics. Notice the large hysteresis effect and the fact that, over a large portion of the cycle, subjects tend to fall back into the mode of covariation that is characteristic of spontaneous movements (cf. Figure 5).

TABLE 1
Analysis of the Effects of the Experimental Factors on Various Performance Parameters

	<i>df</i>	δ	Σ	<i>P</i>	θ	<i>D</i>
A	(1, 9)	45.09*	21.00*	33.52*	56.20*	24.57*
B	(1, 9)	20.32*	3.62 ^a	2.66 ^a	31.87*	3.50 ^a
C	(6, 54)	7.01*	21.00*	8.85*	10.39*	14.37*
A × B	(1, 9)	1.55 ^a	0.21 ^a	0.01 ^a	0.12 ^a	2.90 ^a
A × C	(6, 54)	9.17*	20.68*	21.81*	7.93*	3.27**
B × C	(6, 54)	0.69 ^a	6.75*	1.21 ^a	6.06*	1.67 ^a
A × B × C	(6, 54)	1.69 ^a	1.59 ^a	2.09 ^a	2.07 ^a	0.59 ^a

Note. ANOVA results (*F* values). Columns, parameters of the performance: δ , average delay; Σ , eccentricity; *P*, perimeter; θ , rotation; *D*, distortion. Rows, main effects and interactions of the experimental factors: A, kinematic condition (Lissajous vs. transformed); B, orientation of the major axis (horizontal vs. vertical); C, rhythm.

* $p \leq .001$; ** $p \leq .01$; ^a = nonsignificant.

averages. As already observed in the case of unpredictable targets (Viviani et al., 1987), the average delay varied as much as 100% between subjects. Moreover, the effect of the rhythm was somewhat different among subjects. Those subjects who had long delays also tended to increase them at the highest rhythms; this was particularly obvious in condition T. Other subjects maintained the delay fairly constantly throughout the entire range of rhythms. The significance of these differences is dramatized by the striking similarity between the individual results for the horizontal and vertical orientation of the major axis.

Figure 8 summarizes the quantitative results for all the other descriptive parameters of the performance. Each plot compares the averages across all subjects for the indicated quantity. As in Figure 7, the results for the two orientations are compared within the same plot. Left and right panels refer to conditions L and T, respectively. The most dramatic difference between the two kinematic conditions is revealed by the perimeter data, which, in condition T, show a large decrease in the size of the pursuit movement. The global measure of distortion, *D*, also confirms a qualitative difference between L- and T-type targets. It fails, however, to resolve the different types of distortions documented in Figure 4. Within both kinematic conditions, a significant difference existed between the amount of rotation for the two orientations of the major axis. As a general rule, the effect of the rhythm on all measures of performance was greater in condition T than in condition L. The rhythm interacted with the orientation of the axes only for the purely geometric parameters (eccentricity and rotation). Finally, no significant interaction emerged between orientation and kinematics.

Modeling the Tracking Performance

Definition of the Model

In the previous article on pursuit tracking of random targets (Viviani et al., 1987), we presented a simple formal scheme that accounts with reasonable accuracy for both the general and the idiosyncratic features of the tracking performance. Briefly, the scheme proposed earlier was based on the following ideas. Let $T(t)$ and $P(t)$ be two vectors, representing the instantaneous position of the target and of the pursuit, respectively. Moreover, let $\Delta S = T(t) - P(t)$ and $\Delta V = \dot{T}(t) - \dot{P}(t)$ be the displacement and velocity error vectors. The basic intuition, which we tested using random targets, is that time changes of $P(t)$ are driven uniquely by the differences, ΔS and ΔV . By analogy with the behavior of a mass coupled to a displacement generator via a viscoelastic link, the acceleration of $P(t)$ is supposed to be a linear combination of ΔS and ΔV . We also hypothesized that the processing of the error signals

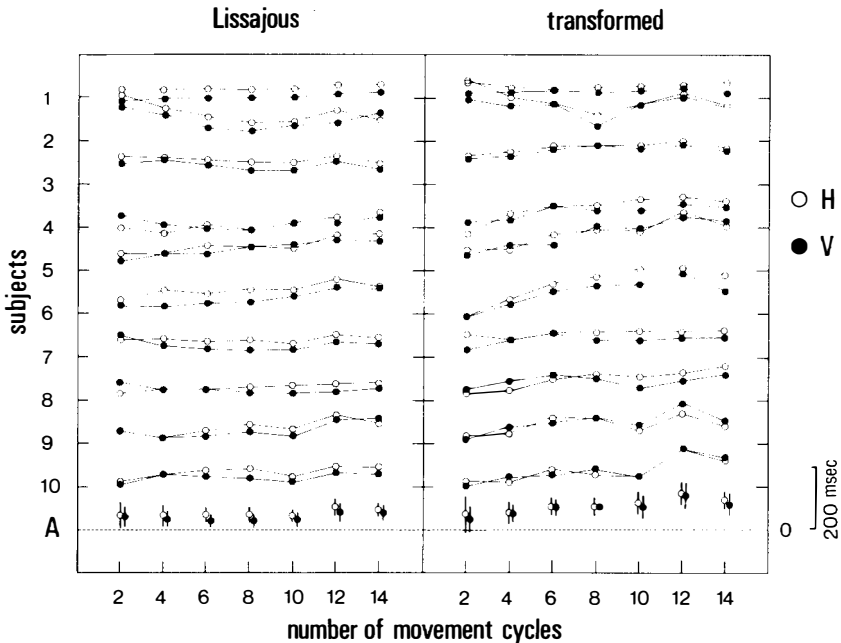


Figure 7. Average delays. Data points (○ for horizontal, ● for vertical ellipses) represent the average over all movement cycles of the instantaneous delay between target and pursuit. Tics on the horizontal axis identify the baseline for the corresponding subject. Averages and standard deviations across subjects are displayed at the bottom and refer to the indicated baseline. In condition L, no clear trend emerges in the relation between the delay and the rhythm. In condition T, the delay increases significantly with the rhythm. Large differences exist among individual performances, however.

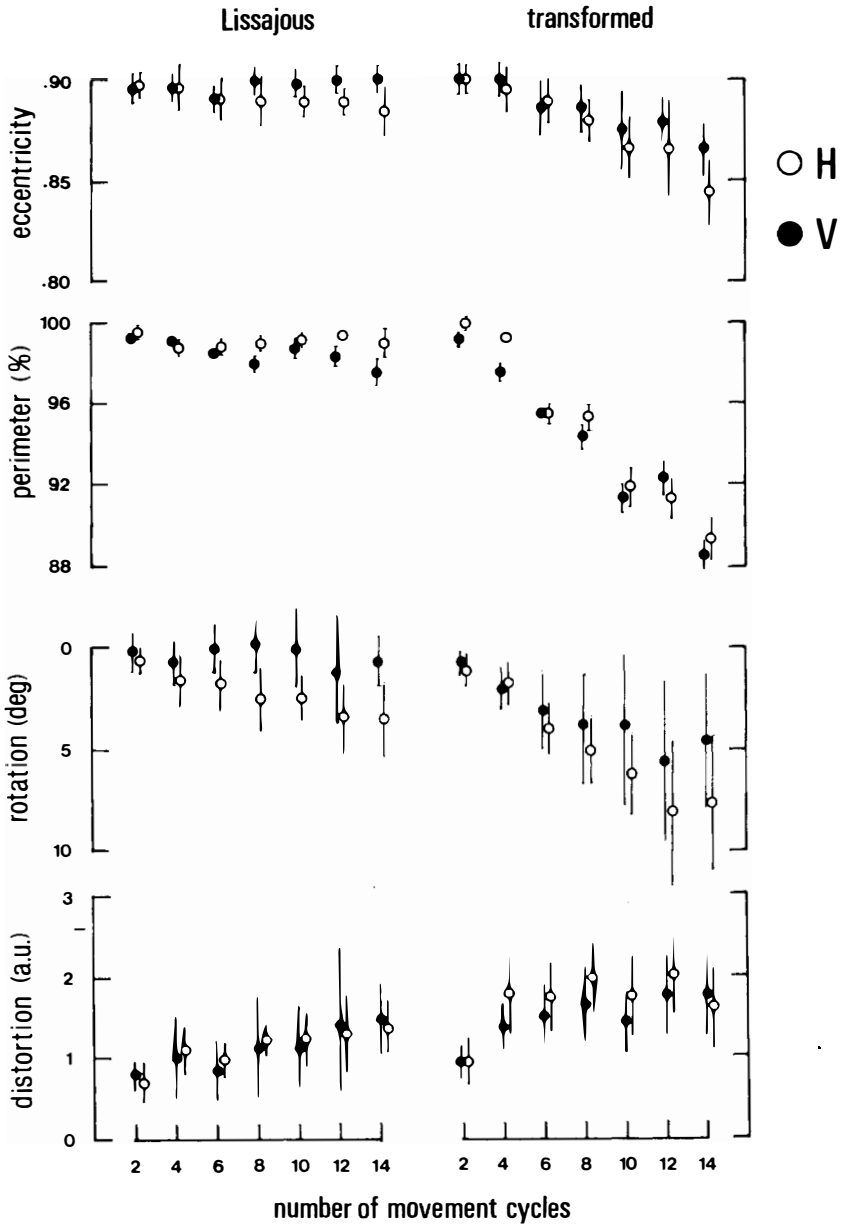


Figure 8. Descriptive parameters of the performance. Each panel displays the average and standard deviations, across all subjects, of the indicated parameters for all rhythms and both kinematic conditions. Empty and filled symbols are relative to H- and V-type targets, respectively. All parameters are more influenced by the rhythm in condition T than in condition L.

is not instantaneous, as it is in a real mechanical system, but takes instead a time, t_c , that may depend on the subject.

To encompass within the same scheme also the case of periodic targets, we now generalize the model in two directions. First, given the predictable nature of the stimuli, we must take into account the possibility that subjects anticipate the future course of the target. Specifically, we assume that the relevant error vectors, $\Delta\mathbf{S}$ and $\Delta\mathbf{V}$, are computed between the actual position and velocity of the pursuit (time t) and the position and velocity of the target at some point in the future (time $t + t_i$). Second, the experiments have shown that the orientation of the major axis of elongation of the pursuit trace undergoes a rotation in the direction of the target movement, the amplitude of which depends on the tempo (see Figure 3). Thus, we must allow for the possibility of cross-coupling between the Cartesian components of the error vectors and those of the pursuit movement (Todosiev, 1967): The error signals $\Delta\mathbf{S}$ and $\Delta\mathbf{T}$ are linearly combined by matrices with non-zero off-diagonal terms. Formally, the pursuit movement is then described by the differential vector equation as follows:

$$\ddot{\mathbf{P}}(t + t_c) = \boldsymbol{\alpha}[\mathbf{T}(t + t_i) - \mathbf{P}(t)] + \boldsymbol{\beta}[\dot{\mathbf{T}}(t + t_i) - \dot{\mathbf{P}}(t)], \quad (1)$$

where

$$\mathbf{P}(t) \equiv \{x_p(t), y_p(t)\},$$

$$\mathbf{T}(t) \equiv \{x_T(t), y_T(t)\},$$

$$\boldsymbol{\alpha} \equiv \begin{vmatrix} \alpha_{xx} & \alpha_{xy} \\ \alpha_{yx} & \alpha_{yy} \end{vmatrix} \quad \boldsymbol{\beta} \equiv \begin{vmatrix} \beta_{xx} & \beta_{xy} \\ \beta_{yx} & \beta_{yy} \end{vmatrix}.$$

Within the spirit of the model, the transformation matrices $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ can be conceptualized as a virtual stiffness and a virtual viscosity tensor, respectively (all the components of $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ are normalized to the unspecified mass of the system). If the link between the target and the pursuit behaves as a spring/dashpot system, it follows that the two tensors must be skew-symmetric ($\alpha_{xy} = \alpha_{yx}$; $\beta_{xy} = \beta_{yx}$) (cf. Hogan, 1985). The components of the stiffness tensor include the contribution of central and peripheral effects. Although it is known (Mussa-Ivaldi, Hogan, & Bizzi, 1985) that the latter are dependent on end-point position within the workspace (at least in isometric conditions), we cannot evaluate the relative weight of the two contributions. Thus, we will make the simplifying assumption that the workspace is isotropic, which implies the further constraints $\alpha_{xx} = \alpha_{yy}$ and $\beta_{xx} = \beta_{yy}$.

By definition, the "look-ahead" parameter, t_i , should be independent of the rhythm of the movement, whereas, of course, the corresponding spatial look-ahead is proportional to the instantaneous velocity. By contrast, not only is there no reason, a priori, to assume independence of the central processing time t_c , but, as we shall see later, the results

even suggest a decrease of t_c with target velocity. Likewise, several studies have shown that both stiffness and viscosity of actual muscles scale with speed. Nevertheless, we estimated that allowing for a modulation of the model parameters by the rhythm of the target would have increased the degrees of freedom of the model too much. Consequently, we assumed that all parameters depend only on the subject and on the compatibility condition.

Because the model is linear, its behavior is best analyzed in the frequency domain. Applying the Laplace transform and rearranging one obtains

$$\begin{aligned} s^2 e^{st_c} \cdot \mathbf{P} &= (\boldsymbol{\alpha} + s\boldsymbol{\beta}) \cdot (e^{st_i} \cdot \mathbf{T} - \mathbf{P}), \\ [s^2 e^{st_c} \cdot \mathbf{I} + (\boldsymbol{\alpha} + s\boldsymbol{\beta})] \cdot \mathbf{P} &= e^{st_i} \cdot (\boldsymbol{\alpha} + s\boldsymbol{\beta}) \cdot \mathbf{T}, \\ \mathbf{P} &= e^{st_i} \cdot [s^2 e^{st_c} \cdot \mathbf{I} + (\boldsymbol{\alpha} + s\boldsymbol{\beta})]^{-1} \cdot (\boldsymbol{\alpha} + s\boldsymbol{\beta}) \cdot \mathbf{T}. \end{aligned}$$

The complex matrix

$$\begin{aligned} \boldsymbol{\Gamma} &= e^{st_i} \cdot [s^2 e^{st_c} \cdot \mathbf{I} + (\boldsymbol{\alpha} + s\boldsymbol{\beta})]^{-1} \cdot (\boldsymbol{\alpha} + s\boldsymbol{\beta}) = \begin{vmatrix} \boldsymbol{\Gamma}_{xx} & \boldsymbol{\Gamma}_{xy} \\ \boldsymbol{\Gamma}_{yx} & \boldsymbol{\Gamma}_{yy} \end{vmatrix}, \\ (\boldsymbol{\Gamma}_{xx} &= \boldsymbol{\Gamma}_{yy}; \boldsymbol{\Gamma}_{xy} = \boldsymbol{\Gamma}_{yx}), \end{aligned}$$

represents globally the visuomanual transformation tensor. Both the diagonal and off-diagonal components of $\boldsymbol{\Gamma}$ can be described by the corresponding amplitude (A) and phase (ϕ) characteristics. Explicit formulas for $A(\boldsymbol{\Gamma}_{xx})$, $\phi(\boldsymbol{\Gamma}_{xx})$, $A(\boldsymbol{\Gamma}_{xy})$, and $\phi(\boldsymbol{\Gamma}_{xy})$ are derived in Appendix B.

Validation of the Model

The model has six parameters; α_{xx} , α_{xy} , β_{xx} , β_{xy} , t_c , and t_i , which are supposed to be independent of the rhythm of the movement. Thus, for any choice of values for the parameters, the model yields a full set of predictions about the effects of the rhythm on the motor performances. For the purpose of validating the model, however, we concentrate only on four quantitative aspects of the pursuit track: the perimeter, P ; the eccentricity, Σ ; the rotation of the major axis, Θ ; and the average delay, δ , between target and pursuit (see Figures 7 and 8). Specifically, we searched the parameter space for the values that simultaneously minimize the mean square error between the predicted and observed values of P , Σ , ϕ , and δ at all tested rhythms. The validity of the model is then gauged jointly by the size of the residual error and by the discrepancy between model and data for other qualitative aspects of the performance that were not taken into account in the search process (see later). It should be stressed that, although the temporal parameters, t_c and t_i , seem to have opposite effects on the pursuit acceleration, in fact, no appreciable trade-off can exist between their least squares estimates.

Because of the considerable individual differences, it would be inappropriate to fit the model to the average results shown in Figures 7 and 8. To demonstrate the range of applicability of the model, it is sufficient instead to consider two of the most dissimilar individual performances. Specifically, we singled out the two subjects who demonstrated the largest and the smallest interactions between the kinematic condition factor (L vs. T) and the rhythm of the movement, SS and SM, respectively. Moreover, because the differences between the results for the two orientations of the templates were not a main point of concern in this context, only the trials with horizontal ellipses were subjected to analysis. For the purpose of testing the validity of the model, the performances of the two selected subjects were characterized by a relatively small subset of the available data: namely, the variations with the rhythm of the gain, the rotation, the eccentricity, and the average delay (28 data points). For both subjects and both kinematic conditions, a simplex algorithm was used to determine the values of the six parameters that minimized the sum of the squared relative deviations from these 28 observed values. The results of the fit-to-horizontal T-type trials for the two subjects are shown in Figures 9 and 10, respectively. In the left (A) panels of the figures, the predictions concerning the quantitative parameters are grouped, together with the actual data. In the right (B) panels of the figures, the polar representation already adopted in Figure 4 is used to compare the observed time course of the instantaneous delay for four selected rhythms with the predictions of the model corresponding to the best-fitting parameters. Notice that, although the delay data were not used for the fitting, the model captures the qualitative changes of the plots as the rhythm increases. Figures 11 and 12 illustrate the results of the fitting for horizontal L-type targets. Because the instantaneous delays for these targets are almost constant (see Figure 4), as are the predictions of the model, the graphic comparison of actual and predicted delay plots was omitted in this case.

The best-fitting values of the model parameters for the two subjects in both conditions are reported in Table 1. Notice that in all four cases, the value of parameter t_c was found to be very small. This point will be dealt with in the discussion. Finally, Figure 13 illustrates, with the help of a few representative examples, the fact that the model also predicts some systematic distortion of the trajectories that are observed in the T condition at the slowest rhythms.

Considering that the degrees of freedom of the model are far less than the imposed constraints, the close approximation of the model to the experimental results can be taken to be satisfactory. In particular, we would like to stress again the fact that the dynamic aspects of the performances—summarized by the instantaneous time delay—and the distortions of the trajectory are reproduced quite accurately by the model, even though they were not taken into account in the fitting procedure. Some systematic discrepancies do exist, however. They show up mostly in the values of the eccentricity and of the perimeter, which

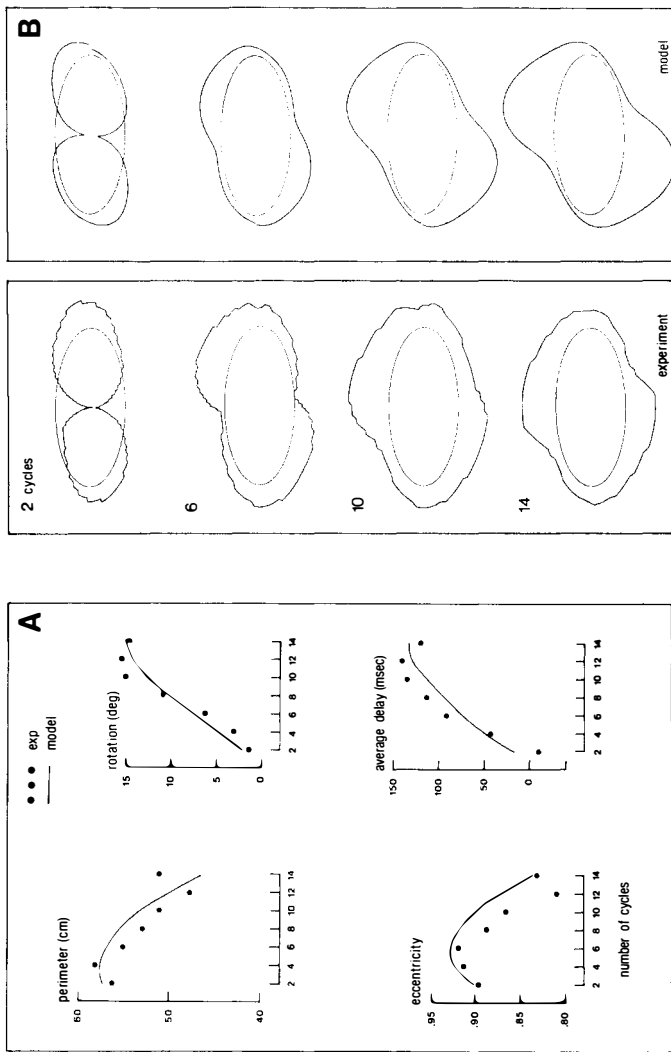


Figure 9. Fitting the model to an individual performance. Data from subject SS for T-type targets (condition H). In A, each of the four panels compares the values of the indicated parameter (data points ●) with the corresponding predictions of the model (continuous lines). In B, the four polar plots on the left show the instantaneous delay across a complete cycle of movement for the indicated rhythms. On the right are the corresponding predictions of the model. The slight asymmetry in the theoretical plots is due to rounding errors in the numerical computation of the model predictions.

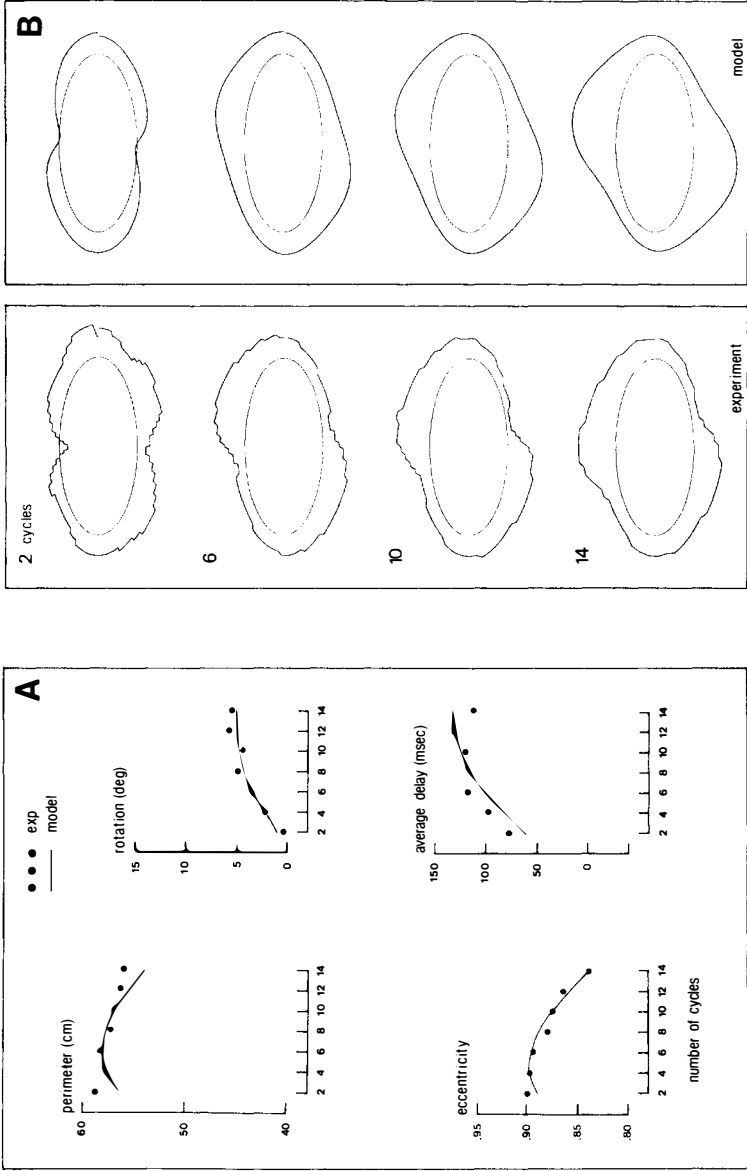


Figure 10. Fitting the model to an individual performance. Data from Subject SM for T-type targets (condition H). Same conventions as in Figure 9.

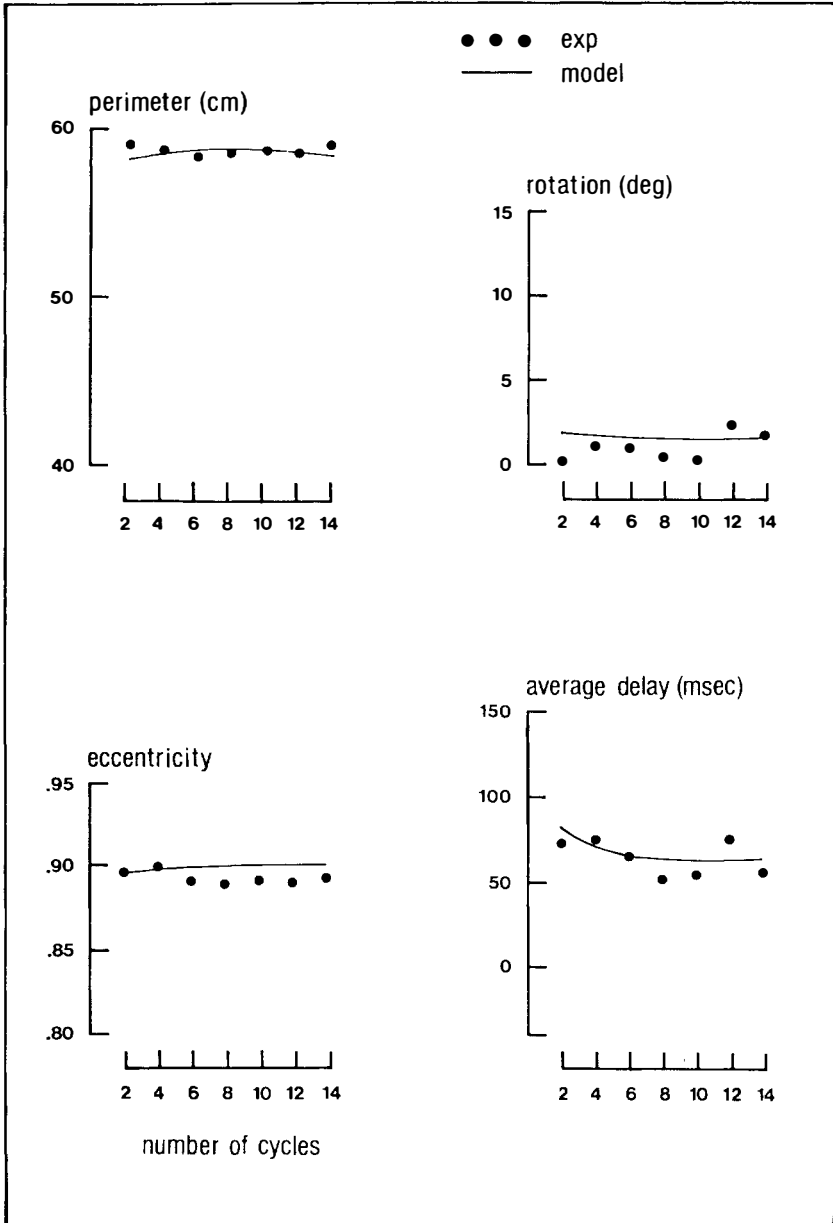


Figure 11. Fitting the model to an individual performance. Data from Subject SS for L-type targets. Because the results for H- and V-type targets are very similar, data points in each of the four plots are averages of the results measured in each condition.

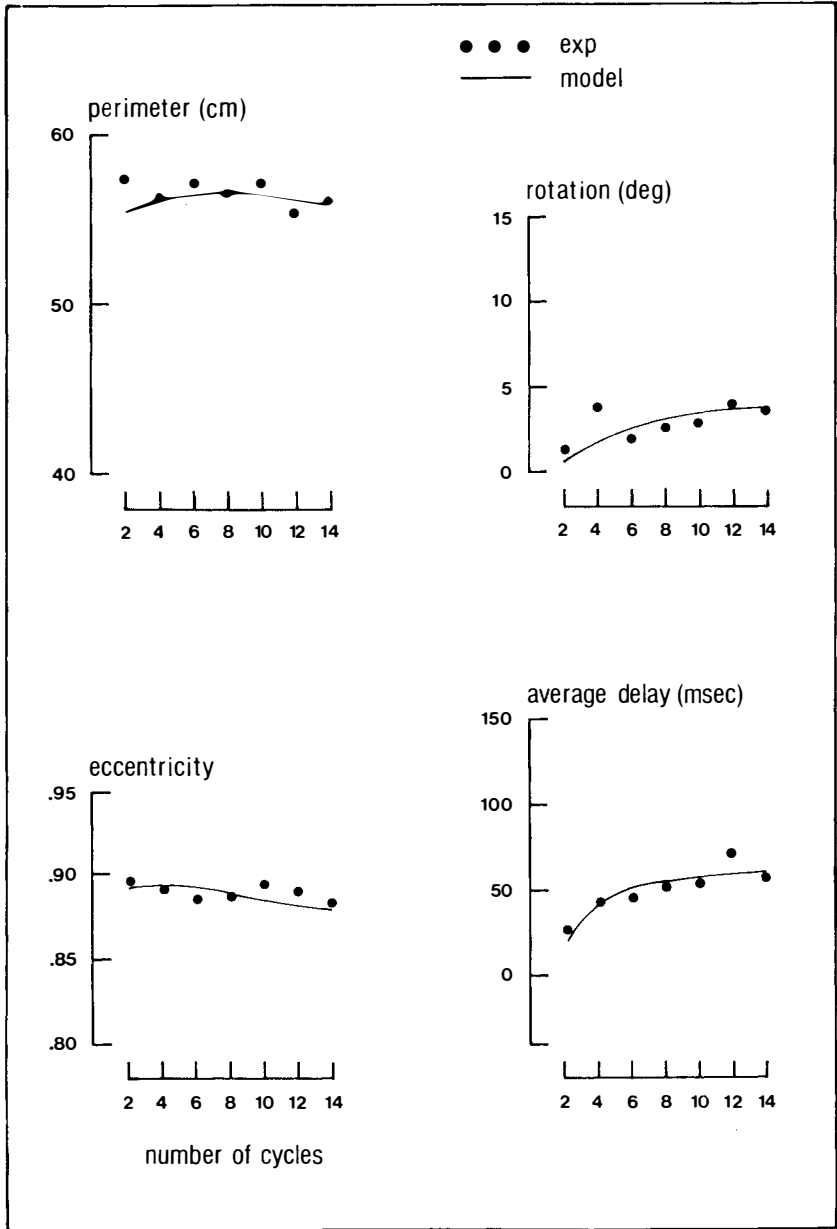


Figure 12. Fitting the model to an individual performance. Data from Subject SM for L-type targets. Same conventions as in Figure 11.

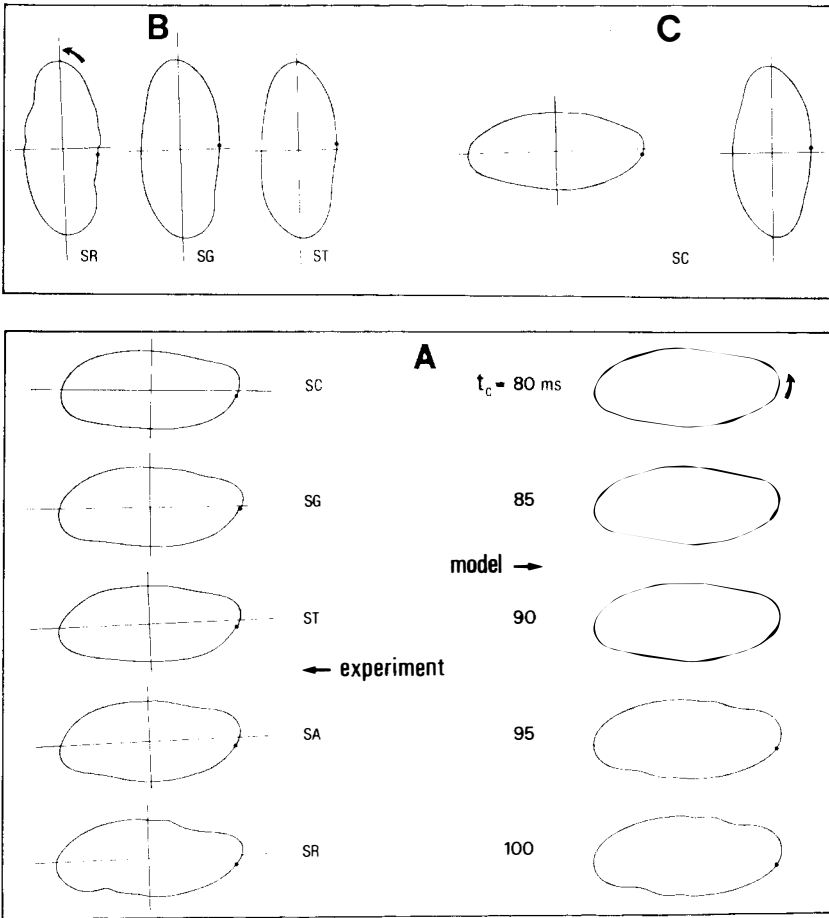


Figure 13. Systematic distortions of the trajectories. In condition T, at the lowest rhythms severe distortions occurred in the pursuit trajectories. A. On the left are examples of 5 subjects (H-type targets, number of cycles = 4), ranked from top to bottom in order of increasing distortion. On the right are predictions of the model corresponding to the values of the following parameters: $\alpha_{xx} = \alpha_{yy} = 16 (1/s^2)$, $\alpha_{xy} = \alpha_{yx} = 8 (1/s^2)$, $\beta_{xx} = \beta_{yy} = 10 (1/s)$, $\beta_{xy} = \beta_{yx} = 0 (1/s)$, $t_f = 0$ ms, and for the indicated values of t_c . B. Examples in 3 of the subjects shown in A (V-type targets: number of cycles = 4). C. Comparison for 1 subject of the distortion for an H- and V-type target (number of cycles = 2).

are overestimated by the model (see Figure 9). Moreover, the sudden decrease of the delay that always occurs in condition T when the target slows down in the flattest portions of the trajectory is somewhat anticipated and smoothed out by the model. An analysis of the model suggests that these discrepancies could be greatly reduced by relaxing the condition that the virtual stiffness and viscosity are constant at

TABLE 2
Best-Fitting Parameters of the Model

Modality	Subject SM		Subject SS	
	L	T	L	T
α_{xx} (1/s ²)	2.1	14.1	9.8	8.0
α_{xy} (1/s ²)	6.5	7.0	15.3	5.9
β_{xx} (1/s)	17.5	8.6	11.7	5.4
β_{xy} (1/s)	0.0	0.0	0.0	0.5
t_c (ms)	10.0	10.0	10.0	10.0
t_f (ms)	20.0	0.0	0.0	130.0

Note. Best-fitting estimates of the model parameters corresponding to the predictions shown in Figures 9–12. The temporal parameters are multiples of one integration step (4.82 ms), rounded to the nearest 0.1 ms.

all rhythms. As mentioned before, however, our aim was not to produce the most accurate possible fitting of the data points but to demonstrate the general adequacy of the model.

Discussion

Compatibility: Implications for Motor Control Theory

We have shown that the motor control system is limited in its tracking performance by the same constraints that apply to the generation of voluntary movements. If the target movement violates the relation between form and kinematics that exists in all natural movements, the response cannot be a faithful reproduction of the input. The degradation of the performance is all the more obvious in that the violation of the natural constraints is severe. In the previous study of two-dimensional pursuit (Viviani et al., 1987) we considered the case in which the velocity is independent of the curvature. The effects of this mild departure from the natural velocity profile were only conspicuous in the $V(t) - R(t)$ relation and in the parameters that describe the tracking strategy. The violation realized in the elliptic targets is more severe, in that the natural $V(t) - R(t)$ relation is actually inverted. As a consequence, a deterioration of the performance becomes evident in all measurable aspects of the motor response: (a) The average delay is longer and much more variable, (b) the eccentricity becomes rhythm-dependent, (c) the gain of the response is increasingly reduced with the rhythm, (d) the rotation of the figure in the workspace is larger, and (e) large distortions appear in the trajectory.

The findings suggest a specific connection between the processes involved in the reproduction of external templates and some recent

developments of the *equilibrium position hypothesis* for the generation of voluntary movements (Asatryan & Feldman, 1965; Bizzi, Polit, & Morasso, 1976; Feldman, 1966a, 1966b; Kelso & Holt, 1980; Polit & Bizzi, 1979). In its original formulation, the hypothesis postulated that movements are produced by abrupt shifts in the viscoelastic equilibrium point between agonist and antagonist joint torques. The refined version of the theory (*equilibrium trajectory hypothesis*, Birkenblit, Feldman, & Fukson, 1986; Feldman, 1974, 1980, 1986; Flash, 1987; Hogan, 1985) holds, instead, that the change of the equilibrium point is in fact a gradual process. The time course of this change can then be construed as a virtual trajectory that is taken to be the true output of the motor planning stage. The actual trajectory would simply be the result of applying to this internal template an appropriate operator that represents the viscoelastic properties of the biomechanical system (we neglect for the moment the fact that the virtual trajectory can be specified in a principled manner [Hogan, 1985; Nelson, 1983]). As we see it, this amounts to the postulate that the generation of voluntary movements is but a special case of the pursuit-tracking action, which only differs from conventional tracking in the nature of the target; in one case the target is an internal template, and in the other it is a template supplied from without.

The analogy between the two cases extends also to the proposed descriptions of the operator that translates the template into overt action. In its simplest form, the equilibrium trajectory hypothesis assumes a linear second-order differential operator, acting independently on each cartesian component of the template (we are not considering here the so-called lambda-model [Birkenblit, Feldman, & Fukson, 1986; Feldman, 1986], which cannot be framed in terms of operators). The model expressed by Equation 1 is more complex, because it allows for cross-component interaction and includes a velocity feedback term. The general flavor of the two schemes is similar, however. In both cases, the nature of the operator (technically, its eigenfunctions) defines the range of compatibility for input-output pairs: For some inputs the operator will be, so to speak, more transparent than for others. For voluntary movements, of course, compatibility poses no problem, because the virtual trajectory can be specified according to the required movement. By contrast, in a real tracking task, compatibility is not to be taken for granted. A final comment on the relation between the equilibrium trajectory hypothesis and pursuit tracking: The virtual trajectory is supposed to be compatible with the condition that the corresponding actual trajectory satisfies a minimum-jerk constraint (Flash, 1987; Hogan, 1984, 1985). We will not provide here a detailed analysis of the congruence between the consequences of the minimum-jerk hypothesis and the observed regularities of natural trajectories. As pointed out by Flash and Hogan (1985), however, some of these regularities can be predicted qualitatively from the imposed constraint. Thus, it is not surprising that natural movements supplied as targets in a tracking task are minimally distorted.

Predictability and Input-Output Delays

Targets that move—periodically or aperiodically—according to some perceptually identifiable rule offer to the subject the possibility of predicting their future course. Generally, subjects take advantage of this possibility, even when this is not implied by the assignment. In one-dimensional pursuit tracking, predictability generally entails a reduction of the average delay between target and pursuit. Indeed, the most typical evidence of predictive behavior is the occurrence of negative delays, moments in which the response of the subject actually precedes the target. Our results with two-dimensional targets do not completely confirm this general picture. There is, indeed, a reduction of the average delay: The means across all subjects, all velocities, and both conditions are smaller in both conditions L (46 ms) and T (73 ms) than the corresponding results observed with unpredictable stimuli (104 and 107 ms, respectively; see Table 2 in Viviani et al., 1987). No subject in condition L ever ran ahead of the target, however. As for condition T, negative delays did occur for almost all subjects at the slowest velocities, but they cannot be interpreted as the result of an anticipatory action. Despite the fact that T-type targets are just as predictable as L-type ones, the running ahead of the response in the flattest portions of the trajectory (see Figures 4, 9, and 10) is rather the consequence of the inability of the subject to slow down there, as the law of motion of the target would require.

To conclude on this point, we discuss the implications of the fact that, in our two-dimensional targets, both the kinematics and the trajectory are entirely predictable and provide a further (possibly independent) basis for anticipatory actions. The simplest form that such an action could take would be intentional shortcuts with respect to the target trajectory. Isolated instances of such behavior were indeed observed in some of the fastest pursuit trajectories, but, as a rule, subjects respected the experimental assignment, which stressed spatial proximity between pursuit and target. Instead, rather common in condition T were those instances in which subjects continued more than the required high-curvature, high-velocity movements at the extremities of the ellipse (see upper right quadrant of Figures 4 and 13). It is difficult, however, to construe this tendency as the manifestation of an anticipatory action. There could be other reasons (Mussa-Ivaldi et al., 1985) to credit these distortions to specific properties of the motor and biomechanical systems (e.g., arm stiffness, inertial couplings) quite independent of the central representation of the intended movement. It is known, for instance (Abend, Bizzi, & Morasso, 1982), that subjects fail to follow accurately a constant-curvature path. Two reasons can be cited, however, for not placing too much emphasis on peripheral factors in this case. The first is that, although the two target orientations require different postural settings, the distortions are quite similar (compare panels A and B in Figure 13). The second and more important reason is that inertial coupling effects should increase with the

rhythm, whereas the distortions are only conspicuous at low frequency. An alternative explanation is suggested by the model. We know that the motor control system has difficulty in negotiating a simultaneous increase of curvature and velocity (cf. Figure 6). One manifestation of such a difficulty could be the increase of the central processing delay, t_c , which, in its turn, reduces the effectiveness of the anticipation and makes the system more resonant (cf. Figure 11 in Viviani et al., 1987). These two consequences of increasing t_c would ultimately be the cause of the observed prolongation of the high-curvature segments. The simulations in Figure 13A lend some support to this interpretation, inasmuch as they show that a progressive increase of parameter t_c brings about the same type of distortion observed experimentally.

The control factors that are held responsible for the fact that sometimes voluntary movements deviate from the intended trajectory (Soechting et al, 1986; Soechting & Terzuolo, 1986) could also be invoked to explain the rotation of the pursuit tracks. Even in this case, however, the hypothesis is not completely convincing. First of all, rotation effects have never been documented in the spontaneous drawing of ellipses. Second, if the rotation were the result of internal constraints on the covariation of joint angles, its direction should be independent of both the rhythm and the direction of the movement. In fact, the distortions that can be credited to such constraints relate only to the orientation of the limb segments in a body-centered system of reference. Finally, contrary to experimental evidence, the rotation amplitude should also be independent of the specific law of motion. The involvement of biomechanical factors and, in particular, of the inertial couplings among the body segments, is suggested by the strong dependence of the rotation from the rhythm. Furthermore, the significant difference between the average rotation for vertical and horizontal targets (cf. Figure 8) is indeed likely to be the reflection of an intrinsic anisotropy of the motor workspace. The very surprising fact that such large rotations went totally unnoticed by the subjects, however, may also suggest an involvement of the perceptual system. Indeed, an old experiment by Benussi (1915) demonstrated that a rectangular array of visual stimuli, lit in temporal sequence, produces the phenomenal impression of an ellipse tilted in the direction of the sequence. Moreover, Viviani and Stucchi (1989) have recently reported deformations in the perceived geometry of dynamic stimuli, which are specifically related to a manipulation of the law of motion similar to the one considered here.

Modeling: Scope and Limitations

As a general preliminary remark, we would like to emphasize again a point that was made already in our discussion of the results with unpredictable targets. The model is far too simple to represent anything but a streamlined functional description of the relation between the input stimuli and the motor response. We take comfort, however,

from the fact that the major descriptors of the performance throughout the entire range of rhythms is adequately predicted by Equation 1, even though we chose not to incorporate the possibility that the model parameters depend on the rhythm. The motor responses to visual inputs are modulated by a number of central processes, most of which are poorly understood. The model acknowledges explicitly only two well-documented sources of modulation. The first one is the possibility discussed above, of forecasting the future course of the input. Such a possibility was embodied in the generalized version of the model through parameter t_i , in order to account for the changes in behavior that are normally observed with periodic stimuli. The second source of modulation is the process whereby visual information is transcoded in terms of motor commands. The necessity of postulating a central delay, t_c , associated with this process was suggested by the results with random inputs.

The fact that the simultaneous presence of the parameters t_c and t_i makes the model capable of predicting satisfactorily both predictable and unpredictable targets should not obscure the fact that the nature of the processes that these parameters purport to represent remains largely a matter of speculation. Anticipatory actions are likely to result from higher cognitive processes distinct from those involved in pursuit (cf. Poulton, 1974). As a conscious effort to outsmart the target, these response components appear to be superimposed upon those under direct visual control and organized at a different hierarchical level. Indeed, the qualitative analysis of response tracks supports this distinction, especially in the case of ramp- and step-tracking experiments, in which the pursuit track shows sudden accelerations that bring it ahead of the target and even responses that precede the stimulus (cf. Stark, 1972). Unfortunately, it seems difficult at the moment to provide an independent analysis of these higher processes, let alone to formalize their coordination with the sensorimotor loop. As a consequence, in this and other formal descriptions of pursuit tracking the processes responsible for anticipatory actions are construed as an integral part of the sensorimotor loop, which can be influenced both by idiosyncratic biases and environmental contingencies.

Temporal Parameters

Sensitivity analysis of the model shows that the anticipation parameter, t_i , reduces the delay by an amount that is almost independent of the rhythm, while leaving the gain curve almost unaffected. Within the context of the "viscoelastic" analogy expressed by Equation 1, a high roll-off rate of the gain characteristics (as in the upper left plot of Figure 9A) indicates slack coupling between target and pursuit. In a system without anticipation, this would necessarily imply large delays. Thus, adjusting t_i was instrumental in reconciling the gain and delay characteristics in individual performances. The values of t_i in Table 2 are precisely those that, in both conditions, make the gain data compatible

with the delay data by reducing the delay that would otherwise correspond to the observed gain. In summary: (a) The modeling analysis confirms that temporal anticipation may exist also in two-dimensional pursuit tracking, and (b) the proposed model interprets this anticipation as an action for compensating—whenever necessary—the slackness of the sensorimotor coupling.

As for the central delay, we begin by noting that the estimates of t_c in Table 2 are negligibly small. Thus, the instantaneous delay between target and pursuit is accounted for basically by the balance between the forecasting parameter, t_f , and second-order dynamics of the visuomanual transformation tensor. This seems to contradict the fact that some systematic deformations of the trajectory have been interpreted as the result of a substantial computational load (see Figure 13A). The explanation is that nonnegligible values of t_c are required only for modeling some of the performances at the lowest rhythms at which most of the distortions are concentrated. In all other cases, no central delay is required to fit the data. Because the estimates in Table 1 are those that optimize the fit over the entire range of rhythms, they cannot reflect adequately the vanishing influence of this factor. The fact that evidence of a central delay exists only at the lowest velocity is in keeping with our interpretation of t_c as the minimum time necessary for modifying the ongoing movement on the basis of visual information. Early estimates of this minimum time (250 ms, Vince, 1948; Woodworth, 1899) have been revised downward in more recent experiments and are now set in the 120- to 200-ms range (for a complete review, see Jeannerod, 1988). Changes in direction that must take place in less time are not likely to be under visual monitoring. Given the range of velocities covered in our experiments, this suggests that only the slowest targets can be monitored continuously. As the average velocity increases, it becomes increasingly difficult (and/or irrelevant) to maintain such a continuous visual control. Therefore, faster targets would have to be pursued on the basis of occasional sampling of the visual input. Such a transition from a closed-loop to a sort of piece-by-piece open-loop control mode implies a drastic reduction of the computational load associated with visual processing and may explain why the average estimates of t_c are so low. It might also explain why, in contrast with the results of Table 2, the estimates of t_c obtained with unpredictable inputs (about 120 ms) are comparable with the values reported by Jeannerod. In fact, the range of velocities covered in those experiments overlaps the range in which distortions of the elliptic trajectories are more likely to occur. Moreover, and perhaps more important, the transition to an open-loop control mode is not viable if the targets are not predictable.

A final remark on the central processing time. The notion that predictable targets can be monitored only occasionally does not contradict the fact that the model postulates a continuous availability of velocity and position error signals. In fact, as emphasized by the presence of a forecasting parameter, the only essential requirement of

the model is the availability of a central representation of these signals, irrespective of the specific mechanisms used to arrive at this representation. From this point of view, the conception that we defend here is rather different from the so-called intermittent feedback control theory proposed both for hand (Craig, 1947) and eye (Young & Stark, 1963) tracking movements. This theory, in fact, assumes a periodic sampling of the visual input and a truly discontinuous mode of operation that should manifest itself as discontinuities in the actual movement. We never found evidence of such discontinuities in our pursuit trajectories.

Coupling Parameters

As mentioned above, the look-ahead parameter, t_p , is instrumental in ensuring the compatibility of gain and delay characteristics. One can then surmise that this parameter is adjusted by each subject on the basis of the "viscoelastic" coupling established between target and pursuit. In the previous report, we inferred from the data that direct coupling is dominated by the "viscous" component (i.e., by the velocity feedback) and that the strength of this component drops in the transition from a natural to a constant velocity profile. Subject SM (Table 2), who exhibited some of the highest gains and shortest delays fitted this scheme. The more extreme transformation of the velocity profile realized in the present experiments entailed a clear reversal in the relative importance of velocity and position feedbacks, however. Subject SS, who showed some of the lowest gains and longest delays, also reduced the direct "viscous" component of the coupling when tracking transformed targets. The direct "elastic" component remained almost unchanged, however. Were it not for the intervention of a substantial amount of forecasting, the resulting slackening of the coupling would have produced a much larger instantaneous delay than the one actually measured.

Cross-component interaction was significantly present in both subjects and both conditions and was instrumental in reproducing the rotation of the pursuit trajectory. As in the case of the temporal parameters t_c and t_p , great caution must be exerted in attempting to relate the interaction terms in Equation 1 to the mechanisms underlying the rotation effects. Two remarks seem to be warranted, however. First, although velocity error signals play a major role in direct coupling, cross-coupling is basically elastic (i.e., transverse forces depend mostly on position errors). Thus, direct and interaction forces may result from independent processes. Second and more important, the very presence of the rotation effect and its interpretation as a cross-component interaction reemphasize the essential difference between classical pursuit tasks and the more general two-dimensional condition investigated here. Over and above the effects specifically related to the interaction between geometry and kinematics, the fact remains that the two-dimensional task cannot be fully described by combining concep-

tually and mathematically the results obtained in one dimension. From this point of view, the presence of interaction terms in Equation 1 represents a significant new finding with respect to the previous study.

APPENDIX A

Let G and D be two ellipses with the same perimeter, which we call geometric and dynamic ellipse, respectively. In general, both the eccentricity and the orientation of the major axis of G and D are different. We present the analytical procedure to solve the following problem. Compute the parametric equations of a target such that the following conditions are met:

Condition 1. The trajectory of the target is the geometric ellipse.

Condition 2. The tangential velocity of the target at any time, t , is equal to that of the unique movement that traces the dynamic ellipse by orthogonal composition of two harmonic functions (Lissajous movement).

We introduce the following notation:

A_{xg}, A_{yg} = semiaxes of the geometric ellipse, G

A_{xd}, A_{yd} = semiaxes of the dynamic ellipse, D.

Σ_g, Σ_d = eccentricities of geometric and dynamic ellipses.

$E(\Sigma, \phi)$ = incomplete elliptic integral of the second kind (Σ , modulus; ϕ , phase).

Ω = rhythm of the movement.

$\Phi(t)$ = law of motion of the target.

$V(t)$ = tangential velocity of the target.

P = common perimeter of both geometric and dynamic ellipse.

Four cases must be distinguished.

1. $A_{xg} \geq A_{yg}, A_{xd} \geq A_{yd}$
2. $A_{xg} \geq A_{yg}, A_{xd} \leq A_{yd}$
3. $A_{xg} \leq A_{yg}, A_{xd} \geq A_{yd}$
4. $A_{xg} \leq A_{yg}, A_{xd} \leq A_{yd}$

For simplicity, we will only develop in detail Case 2, which is directly relevant to the experiment described in this article. All the others can be worked out in a similar manner. In order to comply with Condition 1 above, the parametric equation of the geometric ellipse must have the general form

$$\begin{aligned} x_g(t) &= A_{xg} \cdot \sin \Phi(t), \\ y_g(t) &= A_{yg} \cdot \cos \Phi(t), \end{aligned} \tag{A-1}$$

$$0 \leq t \leq 2\pi/\Omega; d\Phi(t)/dt \geq 0; \Phi(0) = 0, \Phi(2\pi/\Omega) = 2\pi/\Omega,$$

where $\Phi(t)$ must be so chosen as to satisfy Condition 2.

The tangential velocity of the target can then be expressed as

$$V(t) = A_{xg} \cdot d\Phi(t)/dt \cdot [1 - \Sigma_g^2 \cdot \sin^2 \Phi(t)]^{1/2}. \tag{A-2}$$

The Lissajous parametric equation for the dynamic ellipse is

$$\begin{aligned} x_d(t) &= A_{xd} \cdot \sin \Omega t, \\ y_d(t) &= A_{yd} \cdot \cos \Omega t, \end{aligned} \tag{A-3}$$

Thus, in order for the law of motion to satisfy the required condition on the tangential velocity, one must also have, for any t :

$$V(t) = \Omega \cdot A_{yd} \cdot (1 - \Sigma_d^2 \cdot \cos^2 t)^{1/2} \tag{A-4}$$

Eliminating $V(t)$ between Equations A-2 and A-4, and remembering that the geometric and dynamic ellipses have the same perimeter:

$$P = 2 \cdot A_{xg} \cdot E(\Sigma_g, \pi) = 2 \cdot A_{yd} \cdot E(\Sigma_d, \pi).$$

One obtains the following nonlinear differential equation:

$$d\Phi(t)/dt = \Omega \cdot \frac{E(\Sigma_g, \pi)}{E(\Sigma_d, \pi)} \cdot \left[\frac{1 - \Sigma_d^2 \cdot \cos^2 t}{1 - \Sigma_g^2 \cdot \sin^2 \Phi(t)} \right]^{1/2}$$

The equation is separable and can be integrated:

$$\begin{aligned} E(\Sigma_d, \pi) \int_0^t [1 - \Sigma_g^2 \cdot \sin^2 \Phi(t)]^{1/2} d\Phi = \\ \Omega \cdot E(\Sigma_g, \pi) \int_0^t [1 - \Sigma_d^2 \cdot \cos^2 t]^{1/2} dt. \end{aligned}$$

Noting that, by simple changes of variables, both integrals in this equation can be expressed as incomplete elliptic integrals of the second kind, one obtains

$$E(\Sigma_d, \pi) \cdot E[\Sigma_g, \Phi(t)] = \Omega \cdot E(\Sigma_g, \pi) [E(\Sigma_d, \pi/2) - E(\Sigma_d, \pi/2 - t)].$$

This nonlinear implicit equation can finally be solved for the desired law of motion, Φ , with the help of the well-known Landen's expansion of the elliptic integral (Abramowitz & Stegun, 1972, p. 598). T-type targets for the experiments described in this article have been created by applying this procedure in the special case, $\Sigma_g = \Sigma_d$, and using the general parametric representation (A-1).

APPENDIX B

The model represents the characteristics of the visuomanual transformation by the second-order symmetric tensor, Γ .

$$\Gamma = \begin{vmatrix} \Gamma_{xx} & \Gamma_{xy} \\ \Gamma_{yx} & \Gamma_{yy} \end{vmatrix} \quad (\Gamma_{xx} = \Gamma_{yy}; \Gamma_{xy} = \Gamma_{yx})$$

Standard calculations permit one to derive explicit formulas for the amplitude, A , and phase, ϕ , of the diagonal and off-diagonal components of Γ in the frequency domain. Let

$$\begin{aligned} \sigma_r = w^4 \cos(2wt_c) + 2w^3 \beta_{xx} \sin(wt_c) - w^2[\beta_{xx}^2 \\ - \beta_{xy}^2 + 2\alpha_{xx} \cos(wt_c)] + \alpha_{xx}^2 - \alpha_{xy}^2, \end{aligned}$$

$$\sigma_i = w^4 \sin(2wt_c) - 2w^3 \beta_{xx} \cos(wt_c) - 2w^2 \alpha_{xx} \sin(wt_c) + 2w(\alpha_{xx}\beta_{xx} - \alpha_{xy}\beta_{xy}),$$

$$\mu_{xxr} = w^3 \beta_{xx} \sin(wt_c) - w^2[\beta_{xx}^2 - \beta_{xy}^2 - \alpha_{xx} \cos(wt_c)] + \alpha_{xx}^2 - \alpha_{xy}^2,$$

$$\mu_{xxi} = -w^3 \beta_{xx} \cos(wt_c) - w^2 \alpha_{xx} \sin(wt_c) + 2w(\alpha_{xx}\beta_{xx} - \alpha_{xy}\beta_{xy}),$$

$$\mu_{xyr} = w^3 \beta_{xy} \sin(wt_c) - w^2 \alpha_{xy} \cos(wt_c),$$

$$\mu_{xyi} = -w^3 \beta_{xy} \cos(wt_c) - w^2 \alpha_{xy} \sin(wt_c),$$

where w is the pulsation ($w = 2\pi f$). Then

$$A(\Gamma_{xx}) = \left[\frac{\mu_{xxr}^2 + \mu_{xxi}^2}{\sigma_r^2 + \sigma_i^2} \right],$$

$$A(\Gamma_{xy}) = \left[\frac{\mu_{xyr}^2 + \mu_{xyi}^2}{\sigma_r^2 + \sigma_i^2} \right],$$

$$\phi(\Gamma_{xx}) = wt_i + tg^{-1} \left[\frac{\sigma_r \mu_{xxi} - \sigma_i \mu_{xxr}}{\sigma_r \mu_{xxr} + \sigma_i \mu_{xxi}} \right],$$

$$\phi(\Gamma_{xy}) = wt_i + tg^{-1} \left[\frac{\sigma_r \mu_{xyi} - \sigma_i \mu_{xyr}}{\sigma_r \mu_{xyr} + \sigma_i \mu_{xyi}} \right].$$

REFERENCES

- Abend, W., Bizzi, E., & Morasso, P. (1982). Human arm trajectory formation. *Brain*, 105, 331–348.
- Abramowitz, M., & Stegun, I. A. (Eds.). (1972). *Handbook of mathematical functions*. New York: Dover.
- Asatryan, D., & Feldman, A. (1965). Functional tuning of the nervous system during control of movement or maintenance of a steady posture. I. Mechanographic analysis of the work of the joint on execution of a postural task. *Biophysics*, 10, 925–935.
- Benussi, V. (1915). Über Scheinbewegungskombination. *Archiv für des Gesamte Psychologie*, 37, 232–282.
- Birkenblit, M. B., Feldman, A. G., & Fukson, O. I. (1986). Adaptability of innate motor patterns and motor control mechanisms. *Behavioral and Brain Sciences*, 9, 585–638.
- Bizzi, E., Accornero, N., Chapple, W., & Hogan, N. (1984). Posture control and trajectory formation during arm movement. *Journal of Neuroscience*, 4, 2738–2745.
- Bizzi, E., Polit, A., & Morasso, P. (1976). Mechanisms underlying achievement of final head position. *Journal of Neurophysiology*, 39, 435–443.
- Craik, K. J. W. (1947). Theory of the human operator in control systems. I. The operator as an engineering system. *British Journal of Psychology*, 38, 56–61.
- Feldman, A. G. (1966a). Functional tuning of the nervous system during control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics*, 11, 565–578.
- Feldman, A. G. (1966b). Functional tuning of the nervous system during control of movement or maintenance of a steady posture. III. Mechanographic analysis of execution by man of the simplest motor task. *Biophysics*, 11, 766–775.
- Feldman, A. G. (1974). Change of muscle length as a consequence of a shift in an equilibrium of muscle-load system. *Biophysics*, 19, 544–548.
- Feldman, A. G. (1980). Superposition of motor programs. I. Rhythmic forearm movements in man. *Neuroscience*, 5, 81–90.
- Feldman, A. G. (1986). Once more on the equilibrium-point hypothesis (lambda-model) for motor control. *Journal of Motor Behavior*, 18, 17–54.

- Flash, T. (1987). The control of hand equilibrium trajectories in multi-joint arm movements. *Biological Cybernetics*, 57, 257–274.
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *Journal of Neuroscience*, 7, 1688–1703.
- Hogan, N. (1984). An organizing principle for a class of voluntary movements. *Journal of Neuroscience*, 4, 2745–2754.
- Hogan, N. (1985). The mechanics of multi-joint posture and movement. *Biological Cybernetics*, 52, 315–331.
- Hollerbach, J. M., & Atkeson, C. G. (1986). Characterization of joint-interpolated arm movements. In H. Hauer & C. Fromm (Eds.), *Generation and modulation of action patterns* (pp. 41–54). Berlin: Springer Verlag.
- Jagacinski, R. J., & Hah, S. (1988). Progression-regression effects in tracking repeated patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 14, 77–88.
- Jeanerod, M. (1988). *The neural and behavioral organization of goal-directed movements*. Oxford: Clarendon Press.
- Kelso, J. A. S., & Holt, K. G. (1980). Exploring a vibratory system analysis of human movement production. *Journal of Neurophysiology*, 34, 908–919.
- Lacquaniti, F., Terzuolo, C. A., & Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*, 54, 115–130.
- Miller, R. A., Jagacinski, R. A., Navalade, R. B., & Johnson, W. W. (1982). A finite-state description of coordination in two-handed target acquisition task. *IEEE Transaction on System, Man, and Cybernetics*, SMC-12, 529–538.
- Mussa-Ivaldi, F. A., Hogan, N., & Bizzi, E. (1985). Neural, mechanical and geometric factors subserving arm posture in humans. *Journal of Neuroscience*, 5, 2732–2743.
- Nelson, W. (1983). Physical principles for economies of skilled movements. *Biological Cybernetics*, 46, 135–147.
- Polit, A., & Bizzi, E. (1979). Characteristics of the motor programs underlying arm movements in monkeys. *Journal of Neurophysiology*, 42, 183–194.
- Poulton, E. C. (1974). *Tracking skill and manual control*. London: Academic Press.
- Soechting, J. E., Lacquaniti, F., & Terzuolo, C. A. (1986). Coordination of arm movement in three-dimensional space. Sensorimotor mapping during drawing movements. *Neuroscience*, 17, 295–311.
- Soechting, J. F., & Terzuolo, C. A. (1986). An algorithm for the generation of curvilinear wrist motion in an arbitrary plane in three-dimensional space. *Neuroscience*, 19, 1393–1405.
- Stark, L. (1972). *Neurologic control systems*. New York: Plenum Press.
- Todosiev, E. P. (1967). Human performance in a cross-coupled tracking system. *IEEE Transaction on Human Factors in Electronics*, HFE-8, 210–217.
- Vince, M. A. (1948). Corrective movements in a pursuit task. *Quarterly Journal of Experimental Psychology*, 1, 85–106.
- Viviani, P., Campadelli, P., & Mounoud, P. (1987). Visuo-manual pursuit tracking of human two-dimensional movements. *Journal of Experimental Psychology: Human Perception and Performance*, 13, 62–78.
- Viviani, P., & Cenzato, M. (1985). Segmentation and coupling in complex movements. *Journal of Experimental Psychology: Human Perception and Performance*, 11, 828–845.
- Viviani, P., & Schneider, R. (in press). A developmental study of the relation between geometry and kinematics in drawing movements. *Journal of Experimental Psychology: Human Perception and Performance*.
- Viviani, P., & Stucchi, N. (1989). The effect of movement velocity on form perception: Geometric illusions in dynamic displays. *Perception & Psychophysics*, 46, 266–274.
- Viviani, P., & Terzuolo, C. A. (1982). Trajectory determines movement dynamics. *Neuroscience*, 7, 431–437.
- Wann, J., Nimmo-Smith, I., & Wing, A. M. (1988). Relation between velocity and curvature in movement: Equivalence and divergence between a power law and a minimum-jerk model. *Journal of Experimental Psychology: Human Perception and Performance*, 14, 622–637.

- Wickens, C. D. (1986). The effects of tracking dynamics on manual control. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (Vol. 2, pp. 39:1–39:60). Wiley & Sons.
- Woodworth, R. S. (1899). The accuracy of voluntary movements. *Psychological Review Monograph* (Supp. 3).
- Young, L. R., & Stark, L. (1963). Variable feedback experiments testing a sampled data model for eye tracking movements. *IEEE Transactions on Human Factors in Electronics*, *HFE-4*, 38–51.

Submitted March 21, 1989
Revised September 7, 1989
Second revision December 14, 1989