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Transformation of the intended direction of movement during continuous motor trajectories

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CHRONOMETRIC and neurophysiological studies have demonstrated that mentally transforming the intended direction of a pointing movement is a time-consuming process, the duration of which increases with the angle of rotation. If the same time-consuming process occurred while tracing a curved trajectory, it would affect the time course of the movement. The data from subjects drawing simple figures match well the predictions made, and support the hypothesis that a time-consuming process of transformation of the intended movement direction operates during the production of continuous trajectories. This biologically inspired hypothesis provides a functional explanation for the relation between speed of the movement and curvature of the path. In addition, it contrasts with the view of continuous movements as essentially oscillatory motions.

Key words: Curvature; Human; Kinematics; Lissajous figures; Mental rotation; Speed

Introduction

When human subjects were asked to point at a specified angle from the direction of a visual stimulus, their response time increased as a linear function of the angle.[1,2] These results suggested that the intended direction of movement undergoes a continuous transformation from the direction of the stimulus towards the direction of the movement. This hypothesis was directly confirmed through the analysis of the activity of an ensemble of motor cortical neurons during a task in which monkeys had to point at an angle from the direction of a visual stimulus.[3,4] The time-varying directional signal coded by an ensemble of motor cortical cells was analyzed using the neuronal population vector method.[5] This analysis revealed an orderly rotation of the directional signal from the direction of the stimulus towards the direction of the movement.[3,4] These results suggest the intriguing hypothesis that when tracing a curved path (e.g. drawing and handwriting) the motor system takes time for the transformation of the intended direction of movement, and that the larger the change in direction the more time is spent. In other words, the same kind of process of transformation of the intended direction of movement disclosed in visuomotor mental rotation tasks[1–4] may also be operating during the production of a continuous trajectory. If this were the case, the ongoing processing of directional information would affect the unfolding of the trajectory in time in a specific way and leave distinctive marks upon the kinematics of the movement. This can be shown in the following way.

Consider a curved path approximated for the sake of the demonstration by successive straight segments Δs (Fig. 1a). The characteristics of directional processing described above suggest that the time Δt spent tracing a segment Δs of the path is composed not only of the duration of translation along the segment, but also in addition of the duration of transforming the direction of movement from the previous direction to the new one. That is, the time Δt is composed of two factors, namely the time Δt_{ROT} taken to transform the intended direction of movement, and the time Δt_{TR} taken to execute the translation along Δs:

$$\Delta t = \Delta t_{ROT} + \Delta t_{TR} \quad (1).$$

The duration Δt_{ROT} corresponds to:

$$\Delta t_{ROT} = \frac{|\Delta\alpha|}{\omega} \quad (2)$$

where $\Delta\alpha$ is the angle of change of direction, and ω is the angular velocity of rotation of the intended direction of movement. The time Δt_{TR} is:

$$\Delta t_{TR} = \frac{|\Delta s|}{V_{TR}} \quad (3)$$

where V_{TR} is the velocity of translation. In addition, we use the definitions of curvature C:

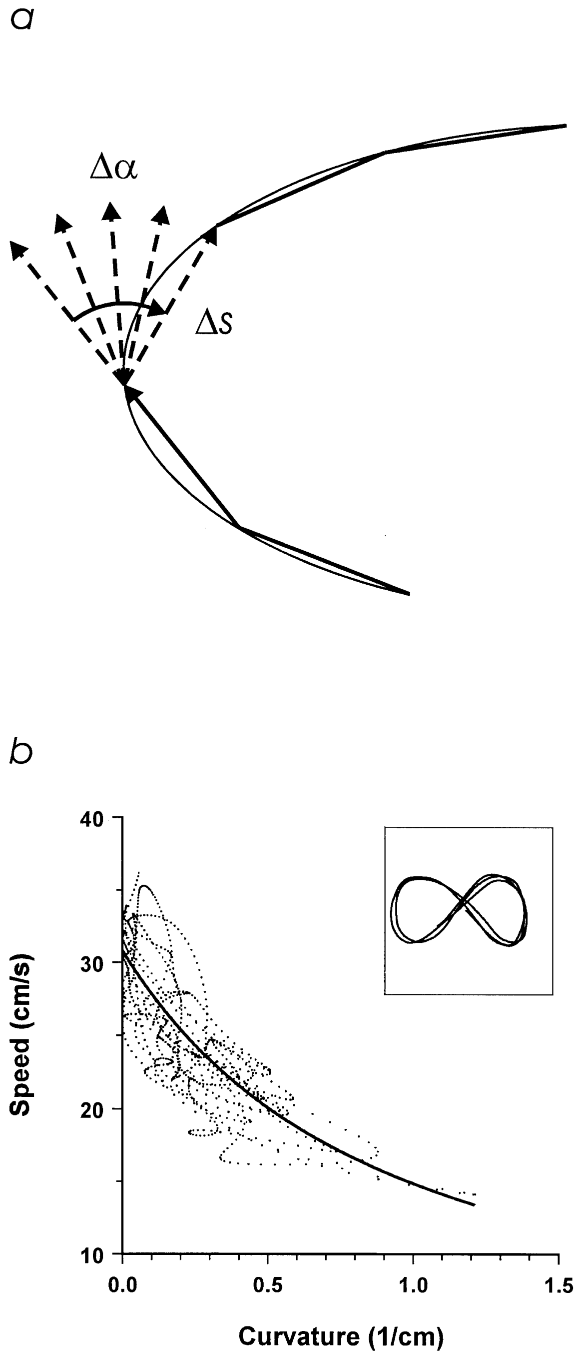

FIG. 1. (a) The intended direction of movement changes continuously during the tracing of a curved path. Mental rotation studies have shown that changing the intended direction of movement is a time-consuming process the duration of which increases with the angle. This suggests that during a continuous movement trajectory time is spent for the transformation of the upcoming direction of movement: by considering an approximation of the path with a series of segments Δs, the time to trace one of the segments is the time taken for the rotation $\Delta\alpha$ in addition to the time spent for the translation along Δs. This is not to suggest that the movement is actually segmented with straight segments, for the argumentation is also valid if Δs is infinitely small. A consequence of this hypothesis is that the speed of the movement is constraint by the curvature of the path. (b) Scattergram of speed and curvature ($n = 980$) for a trial in which a subject drew the figure shown in the inner panel. The fit of equation (6) is superposed on the scattergram (continuous line). The regression coefficients for this trial were: $V_{TR} = 30.8$ cm/s and $\omega = 28.8$ rad/s ($r = 0.909$).

$$C = \left| \frac{\Delta\alpha}{} \right| \quad (4)$$

and speed V:

$$V = \frac{|\Delta\alpha|}{\Delta t} \quad (5)$$

Considering V_{TR} and ω constant within a given segment of trajectory and using the definitions (1) to (4) into (5), one obtains after simplification a function that relates the instantaneous speed $V(t)$ and curvature $C(t)$:

$$V(t) = \frac{V_{TR}\omega}{\omega + V_{TR}\ C(t)} \quad (6)$$

which depends neither on Δs nor on Δt, and defines V along the curve at any instant t.

The parameters V_{TR} and ω can be estimated using a regression procedure on speed $V(t)$ against curvature $C(t)$, both of which can be measured from the trajectory executed. It may be necessary to stress that the parameter ω does not correspond to the angular velocity of the movement but to the velocity of a mental process, namely the process of rotation of the intended direction of movement, which is the same kind of process that was revealed in visuomotor mental rotation tasks.[1–4] The two parameters V_{TR} and ω in equation (6) generalize to continuous movements the distinction between specification of extent and direction that has been introduced for pointing movements.[6–8]

Materials and Methods

To test the validity of this model we examined how well equation (6) fits data. Subjects were asked to draw simple figures that were presented on a screen; they controlled the position of a cursor with a two-dimensional manipulandum. The instructions were to trace continuously the figure at a self-chosen tempo; the emphasis was put on the production of a continuous movement rather than on the accuracy of the copy.

Subjects and procedure: Four subjects (two males and two females, 23–38 years old) participated voluntarily in the experiment. The experimental protocol was approved by the Institutional Review Board. The subjects had normal or corrected to normal vision. The templates displayed on the screen (21 inch Mitsubishi colour monitor) were generated using the following equations: $x(\theta) = a\ \cos(\phi_1\theta)$, and $y(\theta) = b\ \sin(\phi_2\theta)$. Three different templates were created with a = 7.5 cm, and b = 3.75 cm remaining constant, and ϕ_1 and ϕ_2 taking the following values: (1) ϕ_1 =

$\phi_2 = 1$; (2) $\phi_1 = 1$, $\phi_2 = 2$; (3) $\phi_1 = 1$, $\phi_2 = 3$. The order of presentation of the templates was randomized across subjects. Five repetitions were recorded for each subject, giving a total of 15 trials per subject. The screen was in front of the subjects at a distance of approximately 60 cm.

The subjects grasped a torqueable manipulandum with which they controlled the position of a cursor on the screen. The manipulandum was in front of them in the midsagittal plane and at elbow level, the arm along the body. It consisted of a handle mounted on a two axes torqueable platform. The position of the handle about the two axes was sampled at 200 Hz for 5 s. The recording was started a few seconds from the beginning of the trial when the subjects had attained a stable rhythmic movement. Feedback torques were applied on the manipulandum to compensate for its weight. A linear displacement of 5 cm of the top of the handle produced a change of position of the cursor of 13.2 cm. The values of the kinematics given in the text correspond to the movement of the cursor.

Data analysis: The recorded position data were low-pass filtered and differentiated in the frequency domain using a regularization procedure.[9] The filtering procedure uses the information contained in the periodogram of the data to automatically select the optimal (Wiener) filter window. The third time-derivative was used for the regularization process, and the lower order derivatives (i.e. velocity and acceleration) were obtained by analytic integration of the Fourier series. The value of curvature in time was estimated using the vector formula:

$$C(t) = \frac{|\mathrm{V}(t) \times \mathrm{A}(t)|}{|\mathrm{V}(t)|^3} \quad (7)$$

where $\mathrm{V}(t)$ is the velocity vector and $\mathrm{A}(t)$ is the acceleration vector. The first and last 10 data points of each trial were discarded in subsequent analyses because of the greater inaccuracy of the estimates of the derivatives at the end points. This gave a total of 980 data points per trial.

The best fit by equation (6) of the data was estimated by computing a weighted least squares non linear regression using the modified Levenberg–Marquardt algorithm (SPSS, Chicago IL). The initial values of the parameters V_{TR} and ω were obtained from the linearized equation:

$$\frac{1}{V(t)} = \frac{1}{V_{TR}} + \frac{C(t)}{\omega} \quad (8)$$

using an ordinary least squares linear regression.

The variance of speed was markedly non constant in relation to curvature. Therefore, each data point was weighted with the inverse of the estimated variance of the dependent variable.[10] The variance of speed versus curvature was estimated in the following way. The data were grouped in 98 curvature bins each of 10 data points and the variance of speed was calculated within each bin. A cubic polynomial function was fitted on the logarithm of the variance of speed *vs* the logarithm of the mid-point of the curvature bins. This fitted function was then used to estimate the variance of speed at any value of curvature.

Results and Discussion

An example of drawing by a subject and the corresponding plot of speed *vs* curvature are illustrated in Fig. 1b. The continuous line represents the fit of equation (6) to the data using a weighted least squares non-linear regression. In all cases, equation (6) provided a good description of the data: the median correlation coefficient over all trials ($n = 60$) was $r = 0.885$ (the 25th and 75th percentiles were 0.839 and 0.932, respectively). The average velocity of translation V_{TR} across subjects was 33.2 ± 4.6 cm/s ($n = 4$), whereas the average (± s.e.) angular velocity of rotation ω of the intended direction of movement was 29.9 ± 2.5 rad/s ($n = 4$).

These analyses indicate that the relation between speed and curvature modeled by equation (6) fits the data well, and therefore support the hypothesis that the motor system spends time changing the intended direction of movement during the production of a continuous motor trajectory. This hypothesis provides a functional explanation for the existence of the relation between local geometry and kinematics of the movement that has been documented in many different studies for over a century.[11] The results of several studies have suggested that this relation originates from central constraints. First, it is not a consequence of the biomechanical constraints of arm motion, for the relation between speed and curvature is also present when there is no arm displacement and the trajectory is defined in isometric force space.[12] Second, the analysis of the activity of motor cortical neurons using the time-varying neuronal population vector[5] revealed the same kind of relationship between speed and curvature in the neural trajectory as in the actual movement trajectory.[13] Third, the constraint between speed and curvature is not limited to the motor domain: it influences visual perception of two-dimensional stimulus motion.[14,15] The central constraint suggested in this paper is that the transformation of the directional signal is a time-consuming process.

The velocity of rotation estimated here is higher than the average velocity estimated in visuomotor mental rotation experiments,[1,2] but it is within the range that was observed.[2] This difference is not unexpected, since the velocity of mental rotation varies greatly among subjects,[2,16] and in relation to the stimulus and experimental conditions.[2,16,17]

The relationship between speed and curvature has been empirically described previously with the so-called one-third power law,[18,19] the latest formulation of which is:

$$V(t) = K\left(\frac{1}{C(t) + \alpha}\right)^{\beta} \qquad (9)$$

where K is a gain constant, β is the power exponent, and α is an arbitrary constant correction factor. It is interesting that, although the power law (9) and equation (6) which describes a hyperbola are formally different, both equations are qualitatively similar to the extent that they describe a decelerating decrease of speed with increase in curvature. Accordingly, we found that both relations fit the data well. We applied the same weighted non-linear regression procedure described above to test how well the power law fit the data. We chose the correction value $\alpha = 0.05$ that was used in recent work,[19] rather than $\alpha = 0$ as in earlier work. The initial values of the parameters K and β were estimated using an ordinary least squares linear regression analysis with:

$$Log\ (V(t)) = Log\ (K) + \beta Log\left(\frac{1}{C(t) + \alpha}\right)^{\beta} \qquad (10)$$

In most studies, data near points of inflection have been removed from the analyses to fit the power relation.[18,19] Here we kept all the data, so that the exact same set of data points was used to fit equations (6) and (9). The median correlation coefficient for the power law was $r = 0.870$ (the 25th and 75th percentiles were 0.809 and 0.920, respectively). In addition, the average (± s.e.) power coefficient β across subjects was 0.277 ± 0.009 ($n = 4$), which is close to the values reported in other studies.[18,19]

Even though the correlation coefficient for the hyperbola was generally higher than for the power function (in 80% of the trials), it would be futile argumentation to favour one of the descriptions over the other on this basis only. The important point is that whereas the power law was empirically chosen to fit the data, without any hypothesis on why the relation should have that particular form, the model defined by equation (6) was deduced from properties of neural directional processing and the data support it. In other words, the power law is the result of a descriptive curve fitting, whereas equation (6) represents a biologically inspired explanatory hypothesis.

It is also interesting to notice that equation (9) is equivalent to equation (6) if $\beta = 1$, $K = \omega$, and $\alpha = \omega / V_{TR}$. We repeated the weighted non-linear regression analyses of equation (9) leaving this time all three parameters K, β, and α free to vary. We found that, unlike in the previous analyses, the convergence to a solution was very slow and unstable. One reason for this was that the parameters α and β were highly correlated. This is an indication of an overparameterized model.[10] The examination of sum of squares contours[10] in the parameter space $<\alpha,\beta>$ showed large domains of values with nearly as good a fit. These analyses indicate that the models (6) and (9) with two free parameters were sufficient to describe these data.

A corollary of the model defined by equation (6) is that it does not support the common view of drawing and handwriting movements as essentially oscillatory motions.[20,21] In this last perspective, segments of continuous movement trajectories have been often modeled using two orthogonal harmonic oscillators. It was shown that this is consistent with mechanical models of the arm as a mass-spring system.[20,22] However the use of sinusoids is mostly based on mathematical convenience, rather than on physiological justification.[20]

The simple figures used as templates in the present experiment (see Materials and Methods) could be reproduced by coupling two orthogonal harmonic oscillators (i.e. Lissajous figures), but the kinematics modeled from equation (6) necessarily digress from that. The extent to which the components of the movement deviate from sinusoids varies according to the value of V_{TR}, ω and the type of figure. An example of simulated drawing is presented in Fig. 2a, with one cycle of the corresponding velocity components, V_X and V_Y, plotted in Fig. 2b. In this example, the deviation from harmonic oscillations is particularly noticeable on the horizontal component V_X. An example of one cycle of the figure drawn by a subject is illustrated in Fig. 2c with its corresponding velocity components plotted in Fig. 2d. It is noticeable that, in addition to the obvious imperfections of the drawing, the kinematics of the actual movement present similar deviations from harmonic oscillations to those in the simulated case. In particular, as in the simulation, the horizontal component of velocity V_X is less smooth than the vertical component of velocity V_Y. This indicates that the drawing movement digresses in a systematic way from a description in terms of harmonic oscillations, which is not solely attributable to the imprecision of the traced path.

This example shows that the effect of the process of transformation of the intended direction of movement on the kinematics can be quite complex even for the simple figures used in this experiment. Models more complex than harmonic oscillators have

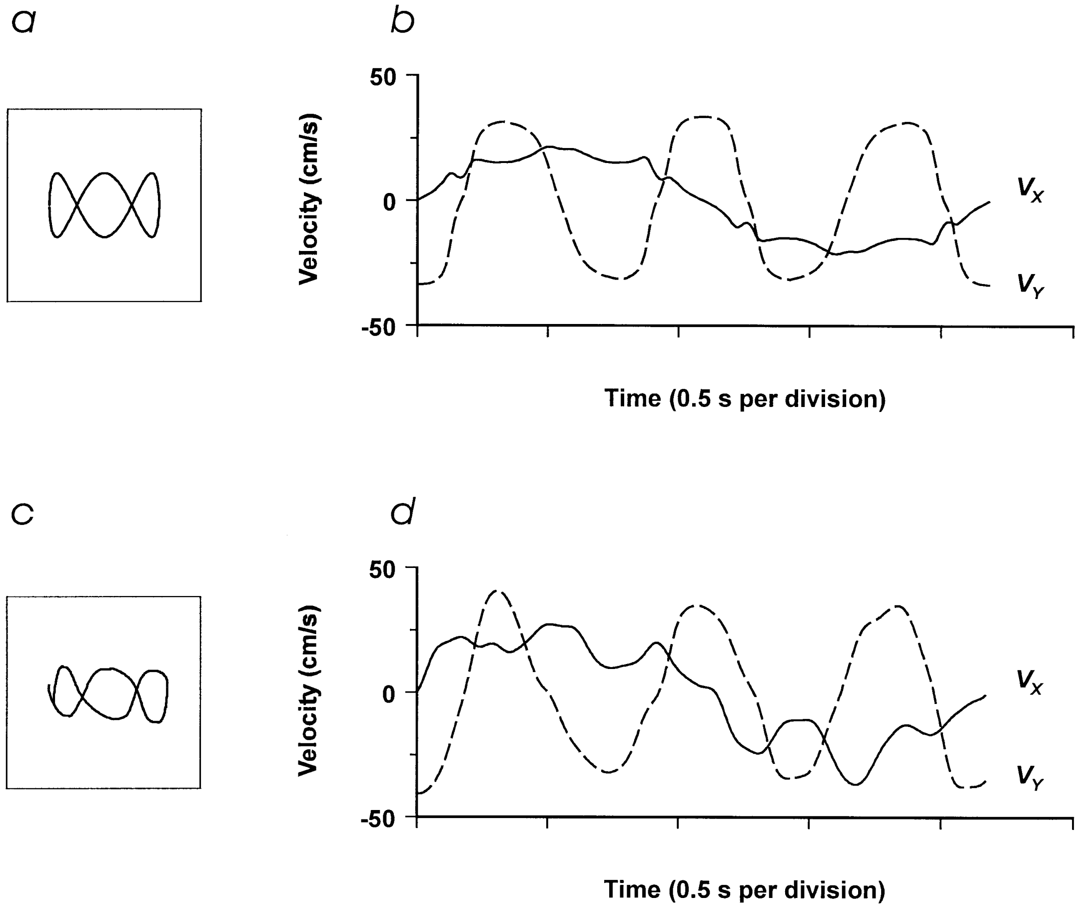

FIG. 2. (a) One of the templates used in the experiment. This figure could be reproduced using harmonic oscillations, but the model described in the text necessarily deviates from such kinematics. (b) The time-varying velocity components V_X and V_Y for a simulated drawing of the figure at left according to the model described by equation (6). The deviation from a sinusoid is more obvious for the horizontal component V_X. (c) Example of one cycle of actual drawing. (d) Velocity components V_X and V_Y of the movement trace represented at left. The kinematics of the actual movement present similar deviations from harmonic oscillations to those in the simulated case. It is noticeable that like in the simulations the horizontal component seems to deviate more from a smooth shape than the one for the vertical components. This indicates that the drawing movement digresses in a systematic way from a description in terms of harmonic oscillations, which is not solely attributable to the imprecision of the traced path.

been used to describe the kinematics of drawing and handwriting movements,[23] but their physiological underpinning is not always clear. In contrast, the hypothesis presented in this study was based on known properties of the specification of the direction of movement that were revealed by independent behavioral and neurophysiological experiments.[1–4] This obviously does not preclude that additional factors, such as, for example, the dynamic properties of the arm, the muscle properties,[22] sensory based corrections may also play a role in shaping the kinematics of drawing movements.

Conclusion

It has been suggested in previous studies that the coupling between speed and curvature emerges from properties of the neural processes leading to the production of a motor output.[12,13,19] This hypothesis received further support by showing that the velocity vector of drawing movements is related to the activity of an ensemble of motor cortical neurons, and that consequently the coupling between speed and curvature is observable at the level of the neural representation of the trajectory.[13] The present work suggests that this coupling is an effect of the constraints on directional processing as revealed by visuomotor mental rotation tasks,[1–4] that is, that transforming the intended direction of movement is a time-consuming process the duration of which increases with the angle. Therefore, the results obtained in this study support the hypothesis that the process of transformation of the intended direction of movement revealed in visuomotor mental rotation tasks is also operating while steering the trajectory in drawing and handwriting movements.

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