

N. Dounskaia · A.W.A. Van Gemmert · G.E. Stelmach

## Interjoint coordination during handwriting-like movements

Received: 11 February 2000 / Accepted: 27 May 2000 / Published online: 1 August 2000  
© Springer-Verlag 2000

**Abstract** The present study investigates intrinsic preferences and tendencies in coordination of the wrist and finger movements during handwriting-like tasks. Movement of the inkless pen tip in nine right-handed subjects was registered with a digitizer. One circle-drawing task and four line-drawing tasks were included in the experiment. The line-drawing task included: (1) drawing with the wrist only, (2) drawing with the fingers only, (3) an equivalent pattern consisting of the simultaneous flexion/extension of the wrist and fingers, and (4) a non-equivalent pattern in which wrist flexion was accompanied by finger extension and wrist extension was accompanied by finger flexion. Both the line and circle drawing were performed repetitively at four speed levels, ranging from slow to “as fast as possible” movements. The analysis of the line drawing revealed differential variability and temporal characteristics across the four movement patterns. While the equivalent pattern had characteristics of performance similar to those observed in the wrist-only and fingers-only pattern, the nonequivalent pattern was more variable and was executed slower when as fast as possible movement was required, compared to the other three patterns. The circle-drawing task also revealed intrinsic tendencies in coordination of the wrist and fingers. These tendencies were manifested by a spontaneous transition of the circular path of the pen tip to a tilted oval with increases in movement speed. The transition to the oval shape was accompanied by decreases in relative phase between the wrist and finger movements, whereas amplitudes of these movements were not affected by movement speed manipulations. The results suggest that subjects did not display a tendency to decrease the number of joints involved when executing the patterns that required simultaneous wrist and finger movements. Instead, there were preferences during these

patterns to integrate wrist and finger movements with low relative phase. The findings are interpreted in terms of biomechanical constraints imposed on the wrist-finger linkage. This interpretation was further examined by testing two left-handed subjects. The data obtained showed symmetrical preferences in joint coordination. Collectively, the findings support a supposition that the shape of cursive letters may have been adjusted to the biomechanical structure of the hand to facilitate the motor act of handwriting.

**Key words** Multijoint movements · Handwriting · Relative phase · Coordination · Drawing · Joint interactions

### Introduction

One of the most intriguing motor acts critically involving hand movements is handwriting. It requires a delicate manipulation of the pen to draw various geometric forms of specific orientation and size on a specifically oriented writing surface. Although the elbow, shoulder and trunk also participate in this complex motor act, providing horizontal relocation of the pen tip along the line, transfer to the new line and posture maintenance (Lacquaniti et al. 1987; Van Emmerik and Newell 1988, 1990; Schillings et al. 1996), the wrist and fingers are primarily responsible for the variety of graphical output (Teulings et al. 1988). This makes the study of hand movements involved in handwriting of particular interest.

Although the hand-finger biomechanical system has at least 10 degrees of freedom, the actual number of degrees of freedom during handwriting is reduced to 2 (Teulings 1996). One degree of freedom arises from simultaneous flexion/extension of all finger joints and results in the pen-tip movement to and from the hand palm. The other degree of freedom is rotation of the entire hand about the wrist as a combination of palmar flexion/extension and radial abduction/dorsal flexion and

N. Dounskaia (✉) · A.W.A. Van Gemmert · G.E. Stelmach  
Motor Control Laboratory, ESPE Department,  
Arizona State University, PO Box 870404, Tempe,  
AZ 85287-0404, USA  
e-mail: natalia.dounskaia@asu.edu  
Tel.: +1 480 965 9081, Fax: +1 480 965 8108

ulnar abduction, depending upon the level of supination/pronation of the forearm (Teulings et al. 1988). A wide variety of forms of the cursive handwriting that might be produced with these two biomechanical degrees of freedom suggest that the wrist and finger movements are the main components of handwriting. These components have been addressed as *main (principal, natural) axes* and their influence on handwriting output has been extensively studied (Dooijes 1983; Maarse et al. 1986; Muelenbroek et al. 1998; Plamondon and Lamarche 1986; Schomaker and Plamondon 1990; Teulings et al. 1988). Evidence has been obtained that variability and duration of strokes produced in different directions depends on the main axes (Langolf et al. 1976; Teulings et al. 1988). However, movements along the main axes could not account for some other handwriting features, such as pen pressure, the average slant, direction of the baseline or the direction of the most frequent movements in handwriting, which were found to not coincide or correlate with any of the main axes (Maarse et al. 1986; Maarse and Thomassen 1983; Schomaker and Plamondon 1990; Teulings et al. 1988).

This observation, together with the high degree of invariance of letter forms and writing slant when writing tasks are performed with different effectors (Bernstein 1967; Lacquaniti 1989), led to a conclusion that graphic targets of handwriting are represented in an effector-independent form at higher levels of the control system (Teulings 1996; Wright 1990). According to this scheme, the handwriting apparatus serves as a slave to these control structures, implementing the preplanned graphical targets, whatever geometric shape they would have (Van Galen 1991; Meulenbroek et al. 1996). The question of exactly how the implementation of the graphical plan is executed has been approached from different perspectives. According to one approach, motor programs for each graphical element are retrieved from a motor buffer (Van Galen 1991; Teulings and Schomaker 1993; Wright 1990). Another approach suggests that letter shapes are implemented by modulation of parameters of a system of two coupled oscillators (Hollerbach 1981; Singer and Tishby 1994). A number of studies argue that handwriting is a process of coming through a sequence of via-points with the submovements between each pair of the via-points being attributed to a certain model (Meulenbroek et al. 1996; Wada and Kawato 1995).

In spite of these varying approaches, the starting supposition (although sometimes not explicitly stated) in the majority of them is that the target graphic forms are preplanned independently of biomechanical properties of the hand. The task of the research has therefore been viewed as revealing the control mechanisms that allow the hand to implement the graphic output created at the higher levels of the control system (Van Galen and Morasso 1998).

When the theoretical approaches do not consider biomechanical properties of the effector they are in conflict with studies that have found that the multijoint mechanical structure of the limbs can play an important role in

coordination of multijoint movements. Bernstein was the first who suggested that the CNS uses mechanical interactions among limb segments in its control strategies (Bernstein 1967). Recently, this issue has attracted particular interest (for instance, Abend et al. 1982; Almeida et al. 1995; Gordon et al. 1994; Hasan 1991; Hollerbach and Flash 1982; Kaminski and Gentile 1986, 1989; Karst and Hasan 1991a, 1991b; Sainburg et al. 1999; Schneider et al. 1990; Ulrich et al. 1994; Virji-Babul and Cooke 1995; Zernicke and Schneider 1993). The mechanical interactions among the limb segments are manifested by interactive torques generated by movement of each segment at all other joints of the limb. The effect of the interactive torques has to be taken into account during control of limb movements. For instance, during single-joint movements when only one joint of the limb is actively rotated, a specific muscle effort is necessary to prevent motion caused by the interactive torques at the other joints (Almeida et al. 1995; Latash et al. 1995). During multijoint movements, the effect of interactive torques can result in different complexity of movements, depending on the coordination pattern. Namely, performance of a pattern can be facilitated by interactive torques if they act in the desired direction. Also, the mechanical factor can produce the opposite effect and make movement more difficult if it requires joint rotations against the effect of the interactive torques (Gribble and Ostry 1999). This has been demonstrated by Dounskaia et al. (1998), who examined different coordination patterns of elbow and wrist movements. The results have suggested that the multijoint movements that require minimal suppression of the interactive torques are easier to perform and can be maintained at higher speed levels than the patterns that require substantial muscular interference with the interactive torques.

Whereas interactive torques seem to be the dominant biomechanical factor responsible for differential complexity of arm movements, movement of the hand holding the pen might be additionally influenced by other biomechanical factors arising from the complexity of the structure of this effector. For instance, elastic forces caused by physical limits of joint displacements can be very influential (Dounskaia et al. 1998). Although the biomechanical factors influencing the wrist and finger movements might be various, they are expected to facilitate or restrain hand movements in a way similar to that observed in the arm movements. In this study we examine the hypotheses that: (1) similar to other joint linkages, finger and wrist coordination patterns also have differential complexity, (2) simultaneous wrist and finger movements, when integrated in a way that aids movement, are preferred patterns (as explained in the next paragraph), and (3) graphical output of the preferred patterns has a slant similar to that which has been observed in the graphical output of handwriting.

Any two-dimensional graphical form can be reproduced by the wrist and fingers during slow movements, as it can be reproduced by any effector whose number of degrees of freedom is more than one. However, when

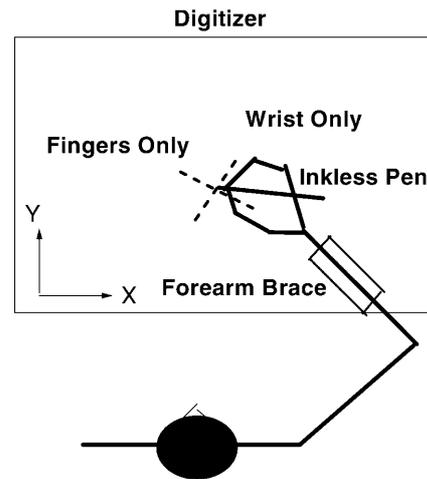
movement speed is increased, the constraints imposed by the mechanical structure of the effector become more pronounced. This occurs because the interaction torques are proportional to joint accelerations and square of joint velocities (Hollerbach and Flash 1982). Presumably, these torques become difficult to manage and require much larger muscle effort to be successfully suppressed during fast movements (Topka et al. 1998). In addition, coping with interaction torques may require processing of afferent information, which is also more difficult during fast compared to slow movements due to processing limitations (Dounskaia et al. 1998; Hoy et al. 1985). Therefore, preferences in joint coordination caused by the biomechanical structure of the limb are expected to be more explicit during fast movements. Based on these considerations, we tested repetitive performance of different combinations of wrist and finger movements when cycling frequency was modulated in a wide range. It has been recognized that preferences in joint coordination may manifest themselves by lower variability of movement characteristics, higher movement speed at which the pattern is preserved and transitions from the less preferred patterns to the more preferred patterns when movement speed increases (for instance, Franz and Ramachandran 1998; Kelso 1984; Scholz and Kelso 1990; Swinnen et al. 1995; Turvey 1990). We expected that with increasing movement speed the preferences in wrist and finger coordination would manifest themselves in three ways. First, at all speed levels the preferred movements would be characterized by lower variability than the other movements. Second, when movements are performed as fast as possible, the highest velocities would be reached during the preferred coordination patterns. Third, increases in movement speed may cause deviation from the kinematic task requirements during less preferred coordination patterns and cause trends in joint coordination towards the more preferred patterns. Revealing these three features of coordination preferences was the primary focus of the data analysis.

The experiment involved right-handed subjects. However, it was expected that if the biomechanical constraints underlie the preferences in wrist and finger coordination patterns, then left-handers, who have the same handwriting skills but a symmetrical biomechanical structure of the effector, would demonstrate symmetrical tendencies in wrist and finger coordination, being presented the same task. To investigate if this is the case, two left-handed subjects were additionally tested.

## Materials and methods

### Subjects

Nine right-handed students (five males and four females) were recruited from the Arizona State University campus to participate. The subjects ranged between 20 and 29 years of age. All volunteers received a brief explanation of the experiment before they signed an informed consent in accordance with human subject policies. Their participation, which took an average of an hour, fulfilled class experimentation requirements.

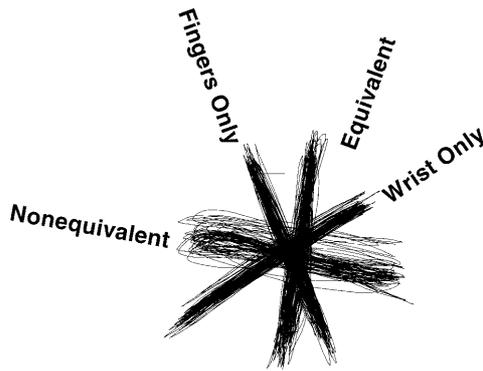


**Fig. 1** Schematic representation of the experimental setup. *Dashed lines* show the orientation of the pen-tip path during the wrist-only and finger-only movements

### Procedure

A computer-controlled digitizer (WACOM Intuos 12×18) and an inkless pen (WACOM Intuos) were used to record hand movements. The digitizer was positioned on a height-adjustable table in front of the subject. Kinematic data were acquired from the digitizer with respect to the X- and Y-axis component at a sampling frequency of 200 Hz. The X-axis was parallel to the transverse plane. The Y-axis was parallel to the sagittal plane and perpendicular to the X-axis. The spatial accuracy of registration was 0.1 mm. Subjects were comfortably seated with both forearms positioned on the table. They were asked to adopt the most comfortable writing posture. The right forearm was immobilized at the angle of 130° relative to the transverse axis by an arm rest attached to the table (see Fig. 1). Subjects performed repetitive drawing movements that involved flexion/extension at the wrist and flexion/extension of the fingers holding the pen. Five drawing tasks were included in the experiment: circle drawing and four types of line drawing. Initially, the circle drawing was performed. During this task a sample circle of 2.5 cm diameter was presented to subjects out of the field of drawing, and they were instructed to repetitively draw circles of approximately the same size in the counterclockwise direction one on top of each other. After this task was completed, subjects performed the four line-drawing tasks. The sample circle was located at the place on the digitizer surface where the subject previously drew the circles. Subjects were instructed to draw the lines back and forth within the sample circle. The trial duration in line and circle drawing was 15 s. Although the size of the drawn lines and the circle was defined by the diameter of the sample circle, the accuracy of size production was deemphasized, and the subject's attention was focused on joint coordination and temporal characteristics of movements, as explained next.

No instructions about the orientation of the lines on the digitizer surface were provided. Instead, the tasks were formulated in terms of coordination of the wrist and finger movements. The orientation of the lines resulted from coordination patterns between wrist and finger movements. Two patterns were 1-degree-of-freedom (1-*df*) movements, and the other two were 2-degrees-of-freedom (2-*df*). During the first 1-*df* pattern, subjects were instructed to perform flexions/extensions at the wrist. To help subjects to detect involuntary finger movements, a light thin bar was attached to the thumb (the "wrist-only" pattern). The second 1-*df* pattern was flexion/extension of the fingers (the "fingers-only" pattern). Similar to the wrist-only movement, a light thin bar was attached to the wrist during finger-only movements that did



**Fig. 2** An example of line drawing in the four coordination patterns during the fast condition performed by a right-handed subject

not significantly restrain movement of the wrist but helped subjects to detect possible wrist motion. Thus, the wrist-only and fingers-only patterns were performed voluntarily without passive damping of the other degree of freedom (the fingers or wrist, respectively).<sup>1</sup> The lines that emerged from the 1-*df* movements are schematically shown in Fig. 1. The 2-*df* patterns included movement of both the wrist and fingers. During the “equivalent” pattern, subjects were instructed to flex and extend the wrist and fingers simultaneously. The “nonequivalent” pattern combined flexion of the fingers with extension at the wrist, and, vice versa, extension of the fingers with flexion at the wrist. Prior to recording movements of each particular pattern, subjects practiced coordinating the wrist and fingers in the required way. An example of individual traces of the end-point movement in the four coordination patterns is given in Fig. 2. All types of movements were performed at four speed levels: *slow* movements performed at a cycling frequency of 1 Hz, *self-paced* movements, *fast* movements performed at a cycling frequency of 3 Hz, and *fastest* movements performed “as fast as possible.” The slow and fast movements were paced with computer-generated short auditory signals. In this case, subjects were asked to draw a complete circle or a line back and forth with each pulse of the computer-generated sound. Both the accuracy of the required pattern and the required speed level were emphasized during slow and self-paced movements. With respect to the fast and fastest condition, subjects were instructed to concentrate on producing the required movement speed (defined by the auditory signals in the fast condition and the utmost movement speed in the fastest condition) and to continue movement in spite of possible deterioration of performance.

#### Data analysis

The *X*- and *Y*-digitizer data were smoothed with a Butterworth low-pass filter with a 15-Hz frequency cut-off. The purpose of the analysis was to assess the level of complexity associated with each coordination pattern and to reveal intrinsic preferences in the patterns. The displacement of the pen tip was divided into separate lines within each line-drawing trial and into circles within each circle-drawing trial. The lines were defined through the coordi-

<sup>1</sup> Although the wrist only and the fingers only were involved in the 1-*df* patterns, these movements can be viewed as multijoint as far as their control is considered. This is supported by multiple evidence that unconstrained single-joint movements require suppression of motion at the adjacent joints caused by mechanical interactions among the linked body segments, and, therefore, can be considered as a specific case of multijoint movements (Almeida et al. 1995; Latash et al. 1995). This consideration allows us to refer to the 1-*df* movements as coordination patterns between the wrist and fingers.

nates of their extreme points. The extreme points were detected as those characterized by local minimum or maximum of the *Y*-coordinate during the finger-only and equivalent movement, and as those characterized by local minimum or maximum of the *X*-coordinate during the wrist-only and nonequivalent pattern. Maximal values of the *Y*-coordinate were used to divide circle-drawing trials into separate circles.

In assessing preferences in coordination patterns during line drawing we took as a basis the consideration that performance of less preferred patterns would be, first, more variable and, second, characterized by lower velocity during “as fast as possible” movements. Therefore, two groups of movement characteristics were used in the analysis of line drawing. First, line variability was assessed with standard deviation (SD) of line orientation and with line spread. The orientation of each line was computed as the angle to the *X*-axis. The spread of the lines characterized the degree of parallel shift of the lines from each other. It was assessed as mean distance to the lines from the averaged line within each trial. Peak velocity of the pen tip and cycle duration comprised the second group of characteristics of line drawing.

During circle drawing, preferences in wrist and finger coordination could be manifested by systematic distortions in the circular path when movement speed is increased. To study the trend in these distortions, the orientation of the maximal diameter of the path contour within each cycle and the ratio between the maximal diameter and the perpendicular diameter were computed and averaged across cycles for each trial. The maximal diameter was found with running over all pairs of path points within each cycle and computing the distances between them.

To reveal the possible trend in joint motion during circle drawing, the coordinates  $x'$  and  $y'$  in the oblique coordinate system  $X'Y'$  associated with the wrist and finger movements were calculated for each subject with the formulas:

$$x' = x \cos \theta_w + y \sin \theta_f$$

$$y' = x \cos \theta_f + y \sin \theta_w$$

where  $\theta_w$  and  $\theta_f$  are the angular orientations of the lines emerging from the wrist-only and fingers-only coordination patterns, respectively, during self-paced movement. The oblique wrist-finger coordinate system was used to calculate displacements of the wrist and fingers and relative phase between them during the circle-drawing task. Relative phase was computed using the formula proposed by Schmidt et al. (1992).

To investigate the effect of increases in movement speed across the four levels, a one-way ANOVA was applied to line orientation for each coordination pattern, the circle diameter ratio, wrist and finger amplitudes and relative phase between wrist and finger movements. A one-way ANOVA designed for four levels of coordination pattern (wrist-only, fingers-only, equivalent and nonequivalent) was applied to the scores of cycle duration and peak velocity of the pen tip obtained at the fastest speed. Line orientation SD and line spread were analyzed with use of a 4×4 (Speed × Pattern) repeated measures ANOVA, where Speed referred to the four movement speed levels and Pattern referred to the four coordination patterns between the wrist and fingers. When ANOVA indicated significance, the Bonferroni post hoc test was applied with the significance level cut-off set at 0.05.

## Results

### Line drawing

Averaged orientations and lengths of the four line types as well as their SDs are given in Table 1. The average scores of cycle duration and SDs at the four frequency levels are shown in the first column of Table 2. Figure 2 gives an example of individual performance of the four

**Table 1** Mean (and SD) of line orientation and length

Line type	Orientation (°)	Length (cm)
Wrist-only	36 (6.7)	2.98 (0.87)
Fingers-only	107 (15)	2.91 (0.65)
Equivalent	64 (12)	3.20 (0.83)
Nonequivalent	165 (15)	2.72 (0.46)

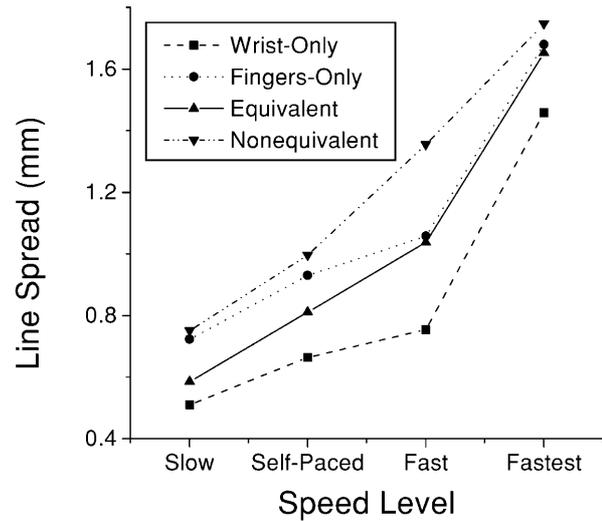
**Table 2** Mean (and SD) of cycle duration (ms)

	Line	Circle
Slow	910 (60)	950 (71)
Self-paced	550 (210)	700 (330)
Fast	310 (26)	320 (40)
Fastest	190 (21)	190 (34)

coordination patterns during fast movement. The main goal of the analysis of the line-drawing movements was to reveal the preferences in the coordination patterns. The lower line variability at all frequency levels and higher pen velocity during the fastest condition was considered as being indicative of the preferred coordination patterns. To assess these characteristics, the line orientation SD, line spread, cycle duration and peak velocity of the pen tip were computed.

#### Line orientation SD

For each coordination pattern, line orientation was, on average, the same at all four speed levels, as indicated by a one-way ANOVA applied separately to each coordination pattern data ( $P > 0.05$ ). However, SD of line orientation was affected by both experimental manipulations of frequency levels and coordination patterns. The average SD of line orientation obtained for each coordination pattern is plotted in Fig. 3 against the speed levels. A  $4 \times 4$  (Speed  $\times$  Pattern) repeated measures ANOVA was applied to the orientation SD data. Speed referred to the four speed levels and Pattern referred to the four coordination patterns. Both the main effects and the interaction were significant. The increases in movement speed caused significant increases in line orientation SD,  $F(3,24) = 36.2$ ,  $P < 0.001$ . The significant main effect of pattern indicated that performance of different patterns was characterized by different levels of line orientation variability,  $F(3,24) = 13.5$ ,  $P < 0.001$ . The post hoc test revealed that the orientation SD of the “nonequivalent” line was significantly higher than the orientation SD of the “wrist-only” line, although no significant differences were found between the lines obtained in the wrist-only and the fingers-only patterns as well as between the lines obtained in the equivalent and fingers-only patterns. The significant interaction [ $F(9,72) = 5.05$ ,  $P < 0.05$ ] can be attributed to the fact that orientation SD substantially increased at the fastest condition in all the coordination patterns, except for the fingers-only pattern, as observed



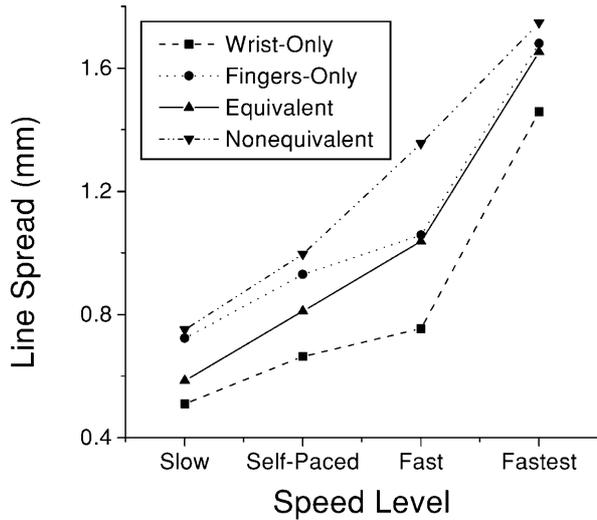
**Fig. 3** Mean SD of line orientation in the four coordination patterns at the four movement speed levels. The nonequivalent pattern had a higher orientation SD than the other patterns at all speed levels

in Fig. 3. The decreases in the orientation SD in the equivalent pattern from slow to self-paced to fast movements might also contribute to the interaction.

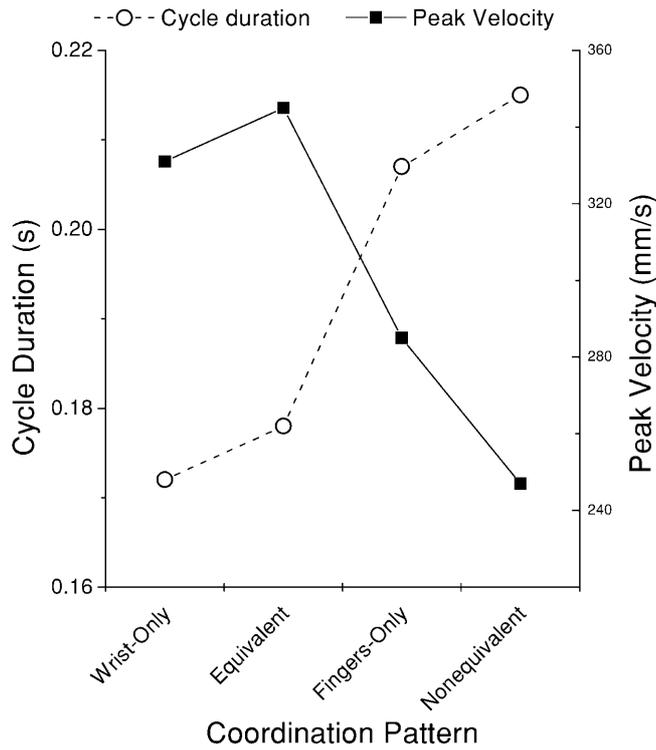
#### Line spread

A  $4 \times 4$  (Speed  $\times$  Pattern) repeated measures ANOVA was applied to the line spread data. Both main effects were significant [ $F(3,24) = 29.6$ ,  $P < 0.001$  and  $F(3,24) = 6.3$ ,  $P < 0.01$  for the speed and pattern effect, respectively], whereas the interaction was not significant ( $P > 0.05$ ). The increases in line spread with increases in movement speed and across the coordination patterns are illustrated in Fig. 4, showing the averaged line spread during the four coordination patterns at the four speed levels. The post hoc analysis was applied to the pattern effect. It revealed that line spread was significantly higher during the nonequivalent pattern than during the wrist-only pattern, whereas no significant differences in this characteristic were found among the other patterns.

In addition to line variability, preferences in wrist and finger coordination were expected to manifest themselves in the temporal characteristics of movement, allowing faster movements during the coordination patterns of lower complexity. To reveal the differences in temporal characteristics among the patterns, we analyzed cycle duration as the duration of the back-and-forth movement and peak velocity of the pen tip during drawing each line. This analysis was applied only to the fastest condition when subjects had to move “as fast as possible.”



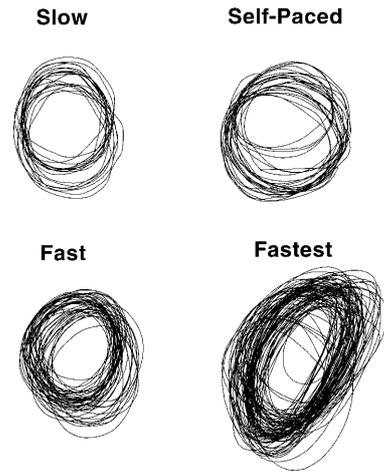
**Fig. 4** Mean line spread in the four coordination patterns at the four movement speed levels. The lines produced during the non-equivalent pattern were more variable than the lines produced during the other patterns



**Fig. 5** Mean cycle duration (left Y-axis) and peak pen-tip velocity (right Y-axis) reached during the fastest condition in the four coordination patterns of line drawing

*Cycle duration at the fastest condition*

Averaged cycle duration scores in the four coordination patterns are shown in Fig. 5 together with maximal pen-tip velocity, which will be discussed next. A one-way ANOVA applied to the data revealed a significant effect



**Fig. 6** An example of circle drawing by a right-handed subject at the four levels of movement speed. A transition to drawing a tilted oval is observed at the fastest speed level

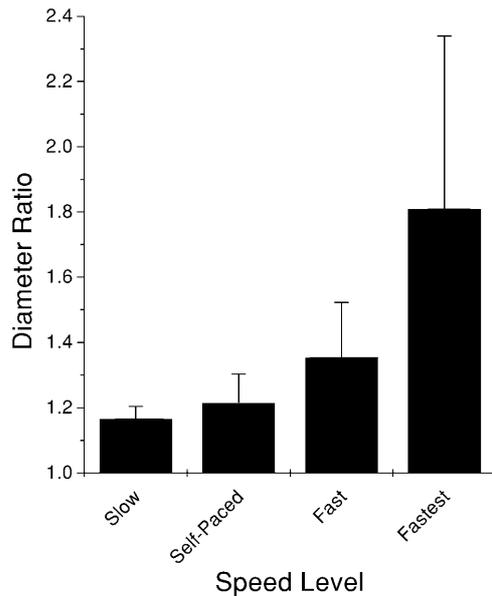
of coordination pattern,  $F(3,24)=5.4, P<0.005$ . The post hoc analysis demonstrated that cycle duration was significantly shorter during the wrist-only and equivalent patterns than during the nonequivalent pattern. The difference between the wrist-only and fingers-only pattern was found to be marginally significant ( $P=0.061$ ).

*Peak velocity of the pen tip at the fastest condition*

This characteristic is shown in Fig. 5 with the Y-axis depicted on the right side of the plot. As was demonstrated by means of a one-way ANOVA, coordination pattern produced a significant effect on the pen-tip velocity,  $F(3,24)=2.9, P<0.05$ . The post hoc test revealed that peak velocity was higher during the equivalent than non-equivalent pattern, although the difference was marginally significant ( $P=0.076$ ). Thus, the results of the analyses of cycle duration and peak velocity were in agreement with each other, demonstrating that subjects were able to perform faster movements during the 1-*df* patterns and the equivalent pattern than during the nonequivalent pattern.

*Circle drawing*

The averaged scores of cycle duration and its SDs documented during circle drawing are given in the second column of Table 2. A representative example of individual circle drawing is shown in Fig. 6. This figure demonstrates a common tendency to transform the circle into an oval at higher speed levels. To describe this tendency quantitatively, we found the diameter of maximal length within each cycle of circle drawing and computed a ratio of the maximal diameter to the perpendicular diameter. This ratio is equal to one for a perfect circle and accepts higher values for ovals. The trend of this characteristic to

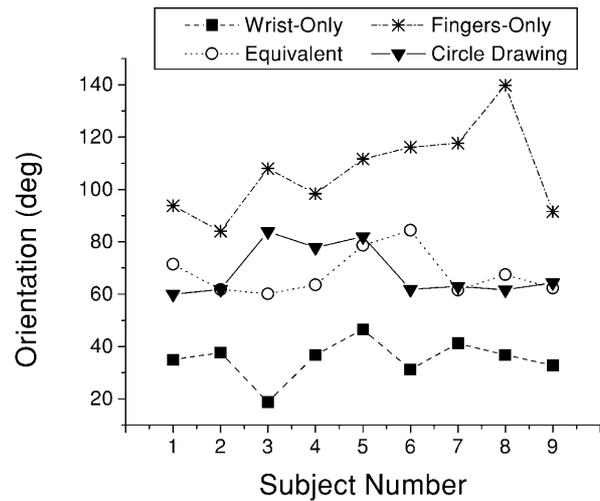


**Fig. 7** Mean ratio of the maximal circle diameter to the perpendicular diameter obtained at the four levels of movement speed. Values are given in arbitrary units. Values close to 1.0 characterize drawing of a regular circle. Values higher than 1.0 indicate a distortion of the circular shape and transition to an oval

increase with increases in movement speed is observed in Fig. 7. A one-way ANOVA supported this observation, revealing a significant effect of movement speed on the diameter ratio,  $F(3,24)=9.54$ ,  $P<0.001$ .

It is observed from Fig. 6 that the oval emerging at the fastest speed level was tilted to the right. This tilt was consistent across subjects. This is demonstrated in Fig. 8, which includes individual data of the orientation of the maximal diameter documented at the fastest speed level as well as orientation of the lines produced in the wrist-only, fingers-only and equivalent pattern at the self-paced speed level.<sup>2</sup> The mean value of the oval orientation was  $68^\circ$  ( $SD=10^\circ$ ). The comparison of this value with the orientations of the lines given in Table 1 and the data shown in Fig. 8 demonstrate that the oval orientation was close to the orientation of the line produced during equivalent movements and different from those produced during both the 1-*df* movements. This observation was supported by a one-way ANOVA applied to the orientation scores in Fig. 8. The difference among the data groups was found significant,  $F(3,24)=59.8$ ,  $P<0.001$ . According to the post hoc test, the orientation of the “equivalent” line and of the oval diameter were found significantly different from the orientation of the “wrist-only” and “fingers-only” line, which, in their turn, were found significantly different from each other ( $P<0.05$ ). No difference was found between the orientation of the “equivalent” line and the orientation of the oval diameter ( $P>0.05$ ).

<sup>2</sup> The orientation of the lines in the nonequivalent pattern was not included in the plot, because it was much higher than the oval tilt and any similarity between them was out of the question.

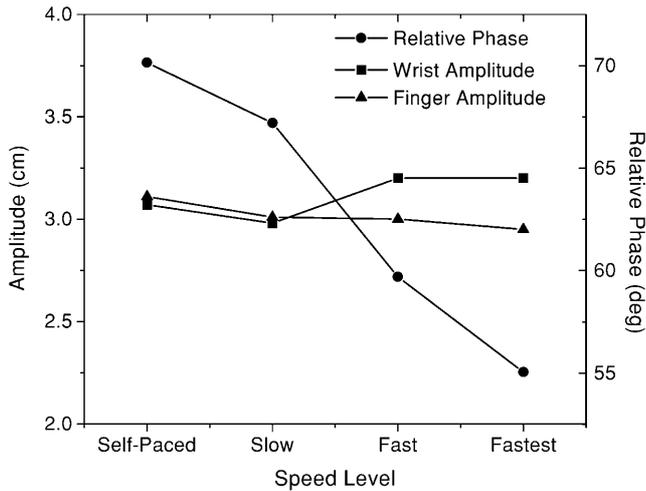


**Fig. 8** Mean orientation of the lines produced in the wrist-only, fingers-only and equivalent pattern during self-paced movement, and mean orientation of the maximal diameter during circle drawing at the fastest speed level. Data obtained from each right-handed subject are shown

The above analysis demonstrates that the orientation of the oval spontaneously adopted at the fastest speed level was similar to the orientation of the line in the equivalent pattern (when both the wrist and fingers participated in the movement) and distinct from the orientation of the lines in the 1-*df* patterns. This suggests that the trend observed during circle drawing was not associated with a tendency to decrease the number of degrees of freedom. To verify this supposition, the analysis of the wrist and finger amplitudes and relative phase was performed. Changes in either amplitudes or relative phase or both would result in deformation of the circular shape. If there were a tendency to decrease the number of degrees of freedom, this tendency would be manifested by decreases in amplitude of the wrist or finger movements. Changes in relative phase would indicate changes in the coordination pattern between the wrist and finger movements. The purpose of the analysis of the wrist and finger movements was to reveal to what degree each of the two factors contributed to deformation of the circular path.

#### Wrist and finger movements

To analyze movements of the wrist and fingers, the pen-tip path represented by the orthogonal *X*- and *Y*-components was decomposed into wrist and finger displacements, as described in the “Data analysis” section. The time series of the wrist and finger displacements were then used to compute amplitudes of the wrist and finger movements as well as relative phase between these movements. The mean values of these three characteristics are presented in Fig. 9 with use of separate scales for the amplitude and relative phase data. It is observed from this figure that both the wrist and finger am-



**Fig. 9** Mean amplitude of wrist and finger movements (the left Y-axis) and relative phase between them (the right Y-axis) in circle drawing as a function of movement speed levels. Amplitude of both the wrist and fingers was not affected by speed manipulations, whereas deviations from the self-paced condition caused decreases in relative phase

plitudes did not change across the speed levels. This was supported by one-way ANOVAs applied separately to the wrist and finger amplitudes at the four speed levels. Neither the wrist nor finger amplitudes were found significantly influenced by the speed manipulations ( $P > 0.05$ ). Thus, no tendency to decrease or increase involvement of any of the 2 degrees of freedom in movement production was found when movement speed increased and the circular shape was transformed into the tilted oval.

Contrary to the consistency of the amplitudes, relative phase between the wrist and finger movements demonstrated a pronounced trend to decrease at higher levels of movement speed, as observed in Fig. 9. Notice that while drawing a perfect circle in the orthogonal coordinates would require  $90^\circ$  relative phase between the X- and Y-displacements, drawing a circle in nonorthogonal coordinates requires relative phase equal to the angle between the coordinate axes. In the case of drawing a perfect circle with the wrist and fingers, the required relative phase is equal to the angle between the orientations of the “wrist-only” and the “fingers-only” lines (*wrist-fingers angle*). On average, the wrist-fingers angle reconstructed from line drawing by each subject was  $71.58^\circ$  (compare with  $70^\circ$  reported by Dooijes 1983). Averaged actual relative phase between the wrist and finger movements in the self-paced condition was  $70.15^\circ$ . This demonstrates that, on average, subjects were able to adhere to a correct circular shape in this speed condition, as prescribed by the task. However, any constraint imposed on the movement speed caused decreases in relative phase that were most pronounced during fast and fastest movements, as suggested by the data shown in Fig. 9.

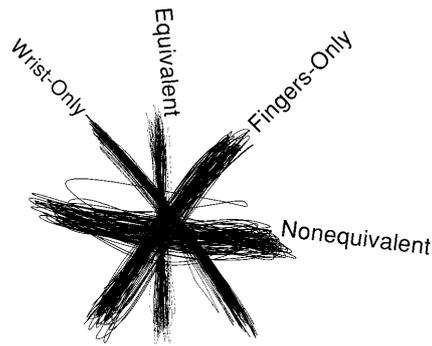
Since there was a significant variability in the individual wrist-finger angles ( $M = 71.58^\circ$ ,  $SD = 18.05^\circ$ ), relative

phase data were normalized prior to application of statistical analysis to them. The reason for the normalization of relative phase was that the purpose of the analysis was to reveal if relative phase significantly decreased across speed levels *with respect to the value required for ideal circle drawing* (i.e., with respect to the individual wrist-finger angle). For this purpose, the relative phase scores were normalized by the individual wrist-fingers angle. In this normalization, relative phase equal to 1 is required to draw a perfect circle. The mean and SD values of the normalized relative phase were: 0.93 (0.11), 0.98 (0.07), 0.83 (0.1) and 0.73 (0.13) for slow, self-paced, fast and fastest condition, respectively. Application of a one-way ANOVA to these data revealed a significant effect of movement speed,  $F(3,32) = 10.05$ ,  $P < 0.001$ . As was demonstrated by the post hoc test, normalized relative phase was significantly higher during self-paced movements than during fast and fastest movements ( $P < 0.05$ ).

#### Preferences in the wrist-finger coordination and geometry of the hand

The above analysis demonstrated consistent preferences and constraints in the wrist and finger coordination. Were the observed effects caused by the biomechanical structure of the hand or they were the result of habits acquired during handwriting? To address this question, two left-handed subjects were additionally tested based on the following reasons: if left-handers (who developed the same skills in handwriting with the use of the left hand as right-handers with the use of the right hand) demonstrate symmetrical tendencies in the wrist and finger coordination, this would be supportive for the conclusion that the geometry and biomechanics of the hand are the crucial factors underlying the observed preferences. The experimental procedure applied to the two left-handed subjects (two male students, both using the left hand for handwriting) was similar to that applied to right-handed subjects. The left forearm was immobilized in a symmetrical position compared to that used for the right-handed subjects, namely, at the angle of  $50^\circ$  relative to the transverse axis. Left-handed subjects performed the same tasks as right-handed subjects, i.e., drawing a circle in the counterclockwise direction and drawing four types of lines that came out of the wrist-only, fingers-only, equivalent and nonequivalent coordination patterns. However, drawing the circle in the counterclockwise direction with the left hand required a coordination pattern between the wrist and fingers different from that employed by right-handers. Therefore, left-handed subjects were presented an additional task of drawing a circle in the clockwise direction. This task was performed after the completion of the counterclockwise circle drawing.

The purpose of the analysis of the left-hander data was to demonstrate that spatial characteristics of left hander performance had symmetrical properties, compared to right handers. Therefore, the analysis of the left-

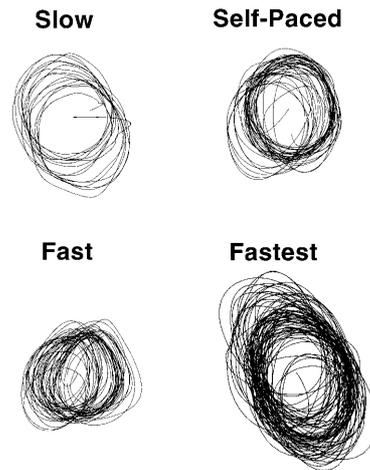


**Fig. 10** An example of line drawing in the four coordination patterns during the fast condition performed by a left-handed subject

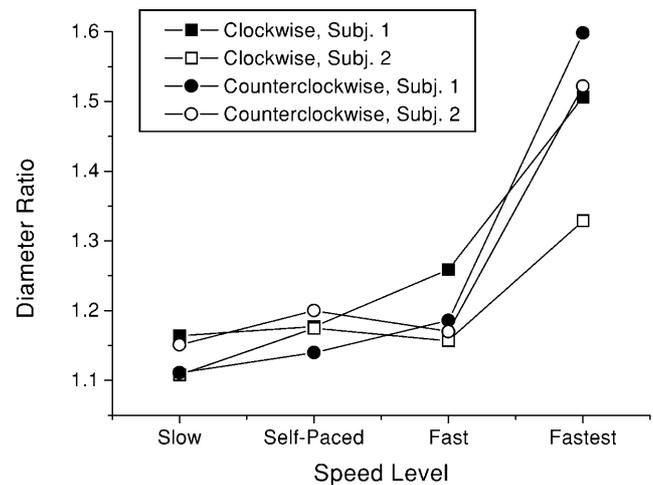
hander data was limited to computations of the orientation of the lines during line drawing and of the ratio between the maximal diameter and the perpendicular diameter as well as the orientation of the maximal diameter during circle drawing. Since a statistical analysis was not applicable to the data obtained from two subjects, individual scores were examined.

It was expected that the biomechanical structure of the left hand would cause the mirror-symmetrical orientation of the four lines produced by left-handed subjects, compared to that produced by right-handed subjects. However, both the left-handed subjects “hooked” the wrist, which was probably a consequence of the habit acquired during handwriting. The “hooked” wrist resulted in a slight clockwise rotation of all lines, but did not affect the preferences in coordination of the wrist and fingers. An individual performance of line drawing by a left-handed subject at the self-paced speed level is shown in Fig. 10. The clockwise rotation of the lines presented in this figure with respect to the mirror image of the lines produced by right-handed subjects is obvious from the comparison of the lines in Fig. 10 with the lines in Fig. 2 (the latter includes an example of individual line drawing by a right-handed subject).

An individual performance of circle drawing in the counterclockwise direction is shown in Fig. 11. The tendency to transform the circle into a tilted oval similar to that observed in right-hander performance is obvious in this figure. It is also represented by Fig. 12, which includes the average scores of the diameter ratio obtained for each subject during circle drawing in both the clockwise and counterclockwise directions. Similar to the right-handed performance, transitions of the circular path into the oval shape in left-handed subjects were accompanied by decreases in the absolute value of relative phase, as observed from Fig. 13, whereas both the wrist and fingers were equally involved in movement at all speed levels. The latter was demonstrated by computing the ratio between the wrist and finger amplitudes. Its mean value computed for the two subjects across all conditions was 1.01 (SD=0.076). However, while the ovals emerging during the right-hander circle drawing were tilted right, the ovals produced by left-handers were tilt-

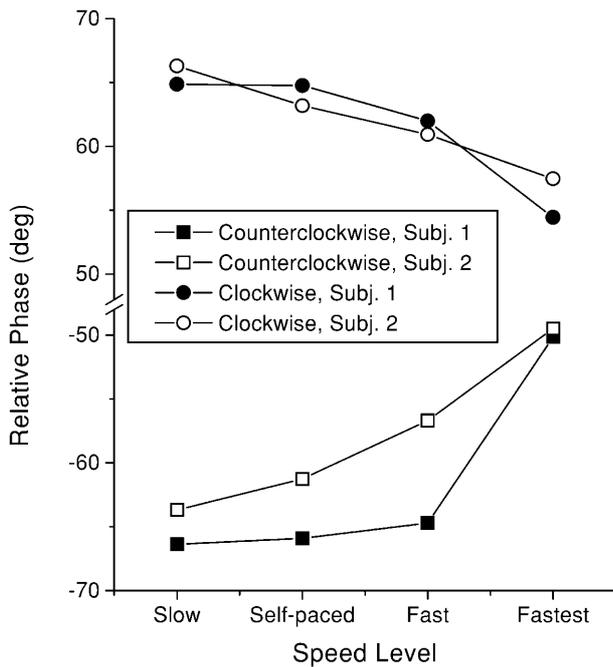


**Fig. 11** An example of circle drawing by a left-handed subject at the four levels of movement speed. A transition to drawing an oval tilted left is observed at the fastest speed level



**Fig. 12** The diameter ratio obtained at the four levels of movement speed during drawing circles in the clockwise and counterclockwise directions by two left-handed subjects. The values are given in arbitrary units

ed left (see Fig. 11). Additionally, the oval orientation in both circle-drawing tasks was close to the orientation of the line produced in the equivalent pattern and different from the orientation of the lines produced in the other coordination. For instance, at the self-paced speed level, the oval orientation in the two subjects was 85° and 89° during the clockwise movements and 103° and 107° during the counterclockwise movements, the orientation of the “equivalent” line was 92° and 101°, the orientation of the “wrist-only” line was 123° and 129°, the orientation of the “fingers-only” line was 52° and 62°, and the orientation of the “nonequivalent” line was 154° and 175°. Thus, as was predicted based on the biomechanical considerations, the features characterizing coordination of the wrist and fingers in left-handers were symmetrical to those documented in the right-handers.



**Fig. 13** Individual scores of relative phase between the wrist and finger movements during left-hander circle drawing

## Discussion

Preferences in wrist-finger coordination and their interpretation in terms of biomechanical constraints

Movement speed manipulations have proven to be a powerful tool for revealing intrinsic tendencies in human motor performance (Atkeson and Hollerbach 1985; Corcos et al. 1989; Flash 1987; Soechting and Lacquaniti 1981). Multilimb movement studies have extensively used this experimental paradigm to invoke spontaneous changes in movement patterns, indicating preferences and constraints in limb coordination (Baldissera et al. 1982; Beek et al. 1995; Kelso 1984; Turvey 1990; Scholz and Kelso 1990). In previous work, we used movement speed manipulations to reveal tendencies in coordination between the elbow and wrist (Dounskaia et al. 1998). Subjects performed repetitive movements of three coordination patterns. Two of them were similar to the equivalent and nonequivalent patterns studied in the present work. The first included simultaneous flexion and extension of the elbow and wrist (the unidirectional pattern) and the second consisted of the combinations of elbow flexion with wrist extension and elbow extension with wrist flexion (the bidirectional pattern). The third pattern was rhythmic flexion/extension at the elbow with the wrist relaxed (the free-wrist pattern). It was demonstrated in that study that passive torques arising from the mechanical structure of the elbow-wrist linkage played an important role in control of all three movement types and that wrist muscle activity intervened with these torques to provide the different coordination patterns.

When movement speed increased, the relative contribution of the interaction torque in wrist control became more pronounced (due to a dependence of the interaction torque on angular velocities and accelerations), making muscular counteraction with it increasingly difficult. This imposed constraints on possible coordination patterns between the two joints at high speed levels, which was manifested by gradual deterioration of the unidirectional and bidirectional patterns and their convergence to the free-wrist pattern with increases in movement speed.

The influence of increases in speed on performance of both the circle-drawing and line-drawing tasks observed in the present study suggests that some speed-dependent constraints are also imposed on coordination of the wrist and finger movements, when holding a pen. During circle drawing, these constraints were manifested by the transformation of the circular pen-tip path into the oval shape at high levels of movement speed. The ability of subjects to produce an almost perfect circular shape at the lower speed levels indicates that these constraints can be overcome during slow and moderate movements. However, they appeared to be too influential during fast movements to be successfully integrated. As a result, spontaneous decreases in relative phase between the wrist and finger movements were observed at the high levels of speed that caused the transformation of the circular pen-tip path into the oval path. The influence of these constraints on the line-drawing performance was indicated by differential levels of variability in the four coordination patterns as well as by differences in temporal characteristics of performance across the patterns during “as fast as possible” movements, as was demonstrated for right-handed subjects.

Interpretation that the constraints imposed on the wrist and finger coordination are caused by the biomechanical factors provides a logical explanation for the changes in performance observed in this study. Indeed, the existence of biomechanical constraints imposed on the wrist-finger coordination implies that different patterns might be characterized by differential complexity (Gribble and Ostry 1999; Sainburg et al. 1995). Simultaneous wrist and finger movements can be integrated in such a way that mechanical interactions between them assist motion at each degree of freedom. Such a coordination pattern is likely to be characterized by higher consistency and higher possible movement speed than a pattern in which interactions hinder movement at any of the degrees of freedom. The results of the present study of right-hander performance indicate that the examined wrist-finger coordination patterns were characterized by differential complexity. Among the four coordination patterns of the line drawing, the nonequivalent pattern obviously was the most difficult to perform; this pattern was characterized by the largest variability in terms of both the line spread and the SD of line orientation. Also, the analyses of cycle duration and peak velocity of the pen tip revealed that subjects were unable to move as fast during the nonequivalent pattern as during the other three coordination patterns. The other three coordination

patterns were not statistically distinguishable from each other in terms of movement variability and temporal characteristics. However, the cycle duration analysis at the fastest condition revealed marginally significant decreases in this characteristic during the fingers-only pattern, compared to the wrist-only pattern. Although the other differences were not found to be statistically significant, all examined characteristics of line drawing, on average, indicated lower levels of performance during the fingers-only pattern than during the wrist-only and equivalent pattern (see Fig. 3, 4, 5). The lower speed and accuracy of finger movements compared to wrist movements is also reported by Teulings et al. (1988). This is suggestive for higher complexity of the fingers-only pattern in comparison with the wrist-only and equivalent pattern.

The circle-drawing task provided additional evidence for differential complexity of the wrist and finger coordination patterns. At high levels of movement speed, the spontaneous transitions of the circular shape of the pen-tip path to the oval shape indicate that the circle-drawing task was not a preferred movement pattern. The analysis of finger and wrist movements during circle drawing in right-handed subjects revealed that the preferences were related to temporal coordination between the wrist and finger movements and not to the number of joints involved in movement production. This follows from the observation that relative phase between the wrist and finger movements decreased with increases in movement speed, whereas the wrist and finger amplitudes were not affected by the speed manipulations. The transformations of the circular shape into the tilted oval suggest that the coordination pattern that consisted of the same movements of the wrist and fingers when they were integrated with lower relative phase decreased complexity of the movement compared to the circle drawing. The preference for low levels of relative phase between the wrist and finger movements are supported by the fact that the equivalent pattern (consisting of simultaneous wrist and finger movements with zero relative phase) was one of the preferred patterns in line drawing, whereas the non-equivalent pattern (characterized by relative phase of  $180^\circ$ ) was the least preferred pattern.

The tendency to integrate joint movements in a coordination pattern with low relative phase is in agreement with the biomechanical interpretation of the constraints imposed on the wrist-finger linkage. A similar tendency to coordinate joints with low relative phase (although not zero) when movement speed increased was observed by Kelso et al. (1991) during elbow-wrist movements. It was demonstrated by Dounskaia et al. (1998) that this tendency was caused by the biomechanical constraints imposed on the coordination between the elbow and wrist. The mechanical influence between the wrist and fingers might be less powerful than that between the elbow and wrist. This might account for a wider range of preferred values of relative phase (a region around zero) during wrist and finger movements than during elbow and wrist movements in which relative phase tended to

acquire some particular value. Although the elbow-wrist linkage and the wrist-finger linkage have different mechanical properties, and, therefore, the preferred values of relative phase could be different for them, nevertheless, in both cases the observed trends in relative phase were most probably caused by the biomechanical constraints.

The observation that amplitudes of the wrist and finger movements were not affected by changes in movement speed provides additional evidence in favor of the idea of biomechanical constraints underlying the preferences in wrist and finger coordination. Although from the point of view of processing complexity, one could expect that movements involving fewer degrees of freedom are easier to perform, mechanical interactions among joints imply that to reduce the number of joints involved in the motion, an additional muscle effort is required to counteract motion-dependent torque (Almeida et al. 1995; Latash et al. 1995). The combined results of the circle and line drawing in right-handed subjects demonstrate that it was not the number of degrees of freedom that provided differential complexity of the wrist-finger movements. No tendency to decrease the number of degrees of freedom as movement frequency increased was observed during circle drawing. Similarly, during line drawing one of the 2-*df* patterns, namely, the equivalent pattern, was characterized by as low variability and high temporal characteristics as the 1-*df* patterns, sometimes even displaying better movement characteristics than the fingers-only pattern. Instead of a tendency to decrease the number of degrees of freedom, the results rather suggest that there was a tendency to adopt a coordination pattern characterized by low relative phase between the wrist and finger movements, which probably violates the constraints imposed on wrist-finger movements to a lesser extent than the patterns with high relative phase.

Additional support for the biomechanical interpretation of the reasons underlying the preferences in wrist and finger coordination comes from a comparison between the performance of right-handed and left-handed subjects. Similarly to right-handed subjects, left-handers also deviated from the circular path and adopted an oval shape with increases in movement speed. However, the ovals produced by left-handers at the fastest speed level were tilted left contrary to the right-tilted ovals produced by right-handed subjects in the same condition. Since both left-handed subjects used the left hand for writing, the left tilt of the ovals cannot be accounted for with the influence of the handwriting skill that requires the right tilt. Additionally, it was found that, first, the transformation of the circular path into the oval shape was caused by decreases in the absolute value of relative phase, whereas the wrist or fingers were equally involved in motion at all speed levels, and, second, tilt of the ovals drawn in both the clockwise and counterclockwise directions was close to the orientation of the line produced during the equivalent pattern. This indicates that the oval shape was not caused by limited involvement of one of the degrees of freedom, but, similar to the right-handed

performance, resulted from changes in the coordination pattern between the wrist and fingers. Altogether, the data obtained from left-handed subjects suggest that the symmetrical structure of the left hand was responsible for the preferences in mirror tilt of the ovals in left-handed subjects in comparison with the preferences displayed by right-handed subjects. This conclusion is in agreement with the biomechanical nature of the constraints giving rise to systematic errors at the kinematic level when movement speed is high.

The tendency to transform a circular path into an oval at higher speed levels has also been documented by Z. Hasan and colleagues (personal communication<sup>3</sup>) when shoulder and elbow motions were used for circle drawing. The distortion observed by the authors was such that there was more motion in the direction of least inertia, and less motion in the direction of larger inertia of the arm. The existence of systematic errors during reaching and their relation to the mechanical structure of the arm was pointed out by Gordon et al. (1994) in a human study and by Turner et al. (1995) in monkeys. Similarly, Massaquoi and Hallet (1996) observed increasing curvature in point-to-point movements of normals and patients with cerebellar ataxia in the increasing speed conditions in spite of the direct instruction to produce a straight path. Although the effector was different, these studies converge with the present work in the interpretation of the observed kinematic aberrations as a tendency to pursue a simplified kinetic design for the movement.

#### Implications of the present findings for handwriting

Although movements studied in this work were not exactly handwriting movements, they consisted of wrist and finger coordination patterns that are involved in production of cursive letters, and, therefore, our findings allow drawing of some indirect conclusions with respect to handwriting.

For instance, the ability of subjects to produce various wrist-finger coordination patterns at low and moderate speed levels and deterioration of performance of some coordination patterns when high movement speed was required broadens our understanding of an observation often referred to in handwriting studies as motor equivalence. Namely, it has been repeatedly pointed out that participation of different joints or even different limbs in a drawing task can result in graphical output of striking resemblance (see, for instance, Bernstein 1967; Castiello and Stelmach 1993; Keele et al. 1990; Lacquaniti 1989; Stelmach and Teulings 1983; Wright 1990). However, any effector that has two or more degrees of freedom can

<sup>3</sup> Subjects performed circle drawing with an inkless stylus attached to the hand. The shoulder and elbow motions were confined to the horizontal plane, while the wrist was immobilized. It was found that the circular shape was maintained at moderate speed levels. However, it was distorted and transformed into an oval shape with increases in movement speed. Based on the kinetic analysis, the authors interpret the results in essentially biomechanical terms

theoretically produce any geometrical form on a planar surface. This observation was postulated in the models of handwriting as an output of two coupled oscillations, although orthogonal oscillations have usually been considered (Hollerbach 1981; Singer and Tishbi 1994). Our findings of differential complexity of the wrist-finger coordination patterns propose that even the biomechanical structure of the hand is not equally adjusted to various handwriting-like movements. This implies that although any graphical shape can be produced in a moderate speed, some of the shapes would deteriorate when drawn rapidly. When other effectors are used, they also can produce any required geometric forms, although slow and highly variable movements would be expected. The dependence of performance of a graphical task on the biomechanical structure of the effector revealed in the present work suggests that the geometrical forms easily produced by the hand might be distorted when they are produced with another effector at high speed. This implies that the principle of motor equivalence has substantial limitations and would be violated at high speed levels.

A related point, which is generally accepted in the handwriting literature and which is not supported by our findings, is the concept of planning of handwriting graphical output independently of the biomechanical structure of the hand. Ignoring constraints imposed on wrist and finger movements would decrease efficiency of the hand structure as a handwriting tool and result in some awkward movements. The present study provided some indirect evidence for adjustment of handwriting graphics to the preferred coordination patterns between the wrist and finger movements. Remarkably, both the preferred *2-df* coordination patterns, the equivalent line-drawing pattern and the oval drawing emerging during the fastest speed condition were characterized by the same orientation (about 70°) of their graphical output (see Fig. 8). A similar slant in handwriting is reported in the literature. For instance, Maarse et al. (1986) presented the slant of a handwriting output registered during five different levels of rotation of the wrist ranging from adduction to abduction. Averaging the data presented in this work results in the slant of 72.15°. Teulings et al. (1988) registered pen-tip movements during handwriting and drawing small lines back and forth in 32 directions. The mean orientation of the most frequent movement during handwriting was 78°. The shortest stroke duration and lowest spatial variability during line drawing were registered in lines oriented on average 73° and 63°, respectively. These data together with the results of our study are supportive for the conclusion that handwriting slant largely coincides with the orientation of the pen-tip path in the most preferred *2-df* hand movements. An additional item of evidence for the shape of cursive letters being adjusted to the preferred coordination patterns among the hand joints is the observation that shape of the pen-tip path in handwriting is invariant across changes in writing time (Wright 1993). Indeed, the constraints imposed on joint coordination would otherwise cause systematic changes in the letter shape with increases in

movement speed, as suggested by the results of the present study. Altogether, these observations contradict the hypothesis that graphical output of handwriting is pre-planned independently of the biomechanics of the hand. Conversely, it rather suggests that shape of cursive letters is adjusted to the biomechanical structure of the hand, which facilitates execution of handwriting.

Whereas many previous studies on handwriting concentrated on revealing the role of the wrist-only and the fingers-only movements along “main axes,” and their contribution to handwriting has been extensively investigated (for instance, Maarse et al. 1986; Meulenbroek et al. 1998; Teulings et al. 1988), our findings demonstrate that not these movements themselves but rather combinations of them characterized by low relative phase might play an important role in production of handwriting. This opens new perspectives for the development of the approach that views handwriting as an output of a system of two coupled oscillators. The studies that introduced this approach (Hollerbach 1981; Singer and Tishby 1994) used the notion of orthogonal oscillators and implied that all combinations of their movements were equally possible. Considering non-orthogonal oscillators corresponding to the oblique angle between the wrist and finger movements, and taking into account the present finding that the constraints imposed on wrist-finger movements make coordination patterns with low relative phase more preferential than the others, is a promising direction in elucidating how the complicated motor act of handwriting is organized.

In conclusion, different combinations of wrist and finger movements when the hand holds a pen were studied. Manipulations with movement speed revealed that there are differential preferences in wrist and finger coordination. The 1-*df* movements and the coordination patterns characterized by low relative phase were the preferred movements. During line drawing, the preferences were demonstrated by lower variability of performance and higher possible velocity levels. During circle drawing, increases in movement speed caused gradual deviation from the prescribed kinematics to a coordination pattern characterized by lower relative phase. The findings are interpreted in terms of biomechanical constraints imposed on possible combinations of wrist and finger movements. These constraints can be overcome during slow and moderate movements, but they are too influential at high movement speed to be successfully integrated. These findings are in agreement with the idea that the biomechanical structure of the human limbs is an important factor in control and coordination of multijoint movements and that everyday human movements are largely adjusted to this factor.

**Acknowledgements** This work was supported by NS33173 grant from the National Institute of Neurological Diseases and Strokes.

## References

- Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. *Brain* 105:331–348
- Almeida GL, Hong DA, Corcos D, Gottlieb GL (1995) Organizing principles for voluntary movement: extending single-joint rules. *J Neurophysiol* 74:1374–1381
- Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained vertical arm movements. *J Neurosci* 5:2318–2329
- Baldissera F, Cavallari P, Civaschi P (1982) Preferential coupling between voluntary movements of ipsilateral limbs. *Neurosci Lett* 34:95–100
- Beek PJ, Peper CE, Stegeman DF (1995) Dynamical models of movement coordination. *Hum Mov Sci* 14:573–608
- Bernstein N (1967) *The co-ordination and regulation of movements*. Pergamon Press, Oxford, UK
- Castiello U, Stelmach GE (1993) Generalized representation of handwriting: evidence of effector independence. *Acta Psychol* 82:53–68
- Corcos DM, Gottlieb GL, Agarwal GC (1989) Organizing principles for single-joint movements. II. A speed-sensitive strategy. *J Neurophysiol* 62:358–368
- Dooijes EH (1983) Analysis of handwriting movements. *Acta Psychol* 54:99–114
- Dounskaia NV, Swinnen SP, Walter CB, Spaepen AJ, Verschueren SMP (1998) Hierarchical control of different elbow-wrist coordination patterns. *Exp Brain Res* 121:239–254
- Flash T (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biol Cybern* 57:257–274
- Franz EA, Ramachandran VS (1998) Bimanual coupling in amputees with phantom limbs. *Nature Neurosci* 6:443–444
- Gordon J, Ghilardi MF, Cooper SE, Ghez C (1994) Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy. *Exp Brain Res* 99:112–130
- Gribble PL, Ostry DJ (1999) Compensation for interaction torques during single- and multijoint limb movement. *J Neurophysiol* 82:2310–2326
- Hasan Z (1991) Biomechanics and study of multijoint movements. In: Humphrey DR, Freund HJ (eds) *Motor control: concepts and issues*, pp 75–84
- Hollerbach JM (1981) An oscillation theory of handwriting. *Biol Cybern* 39:139–156
- Hollerbach JM, Flash T (1982) Dynamic interactions between limb segments during planar arm movement. *Biol Cybern* 44:67–77
- Hoy MG, Zernicke RF, Smith JL (1985) Contrasting roles of inertial and muscle moments at knee and ankle during paw-shake response. *J Neurophysiol* 54:1282–1294
- Kaminski T, Gentile AM (1986) Joint control strategies and hand trajectories in multijoint pointing movements. *J Mot Behav* 18:261–278
- Kaminski T, Gentile AM (1989) A kinematic comparison of single and multijoint movements. *Exp Brain Res* 78:547–556
- Karst GM, Hasan Z (1991a) Initiation rules for planar, two-joint arm movements: agonist selection for movements throughout the work space. *J Neurophysiol* 66:1579–1593
- Karst GM, Hasan Z (1991b) Timing and magnitude of electromyographic activity for two-joint arm movements in different directions. *J Neurophysiol* 66:1594–1604
- Keele SW, Cohen A, Ivry R (1990) Motor programs: concepts and issues. In: Jennerod M (ed) *Attention and performance, vol XIII, motor representation and control*. Erlbaum, Hillsdale, NJ, pp 77–111
- Kelso JAS (1984) Phase transitions and critical behavior in human bimanual coordination. *Am J Physiol Regul Integr Comp Physiol* 15:R1000–R1004
- Kelso JAS, Buchanan JJ, Wallace SA (1991) Order parameters for the neural organization of single, multijoint limb movement patterns. *Exp Brain Res* 85:432–444
- Lacquaniti F (1989) Central representations of human limb movement as revealed by studies of drawing and handwriting. *Trends Neurosci* 12:287–291

- Lacquaniti F, Ferrigno G, Pedotti A, Soechting JF, Terzuolo C (1987) Changes in spatial scale in drawing and handwriting: kinematic contributions by proximal and distal joints. *J Neurosci* 7:819–828
- Langolf GD, Chaffin DB, Foulke JA (1976) An investigation of Fitts' law using a wide range of movement amplitudes. *J Mot Behav* 8:113–128
- Latash ML, Aruin AS, Shapiro MB (1995) The relation between posture and movement: study of a simple synergy in a two-joint task. *Hum Mov Sci* 14:79–107
- Maarse FJ, Thomassen AJWM (1983) Produced and perceived writing slant: difference between up and down strokes. *Acta Psychol* 54:131–147
- Maarse FJ, Schomaker LRB, Thomassen AJWM (1986) The influence of changes in the effector coordinate system on handwriting movements. In: Kao HSR, Van Galen GP, Hoosain R (eds) *Graphonomics: contemporary research in handwriting*. Elsevier (North-Holland), Amsterdam, pp 31–46
- Massaquoi S, Hallet M (1996) Kinematics of initiating a two-joint arm movement in patients with cerebellar ataxia. *Can J Neurol Sci* 23:3–14
- Meulenbroek RGJ, Rosenbaum DA, Thomassen AJWM, Loukopoulos LD, Vaughan J (1996) Adaptation of a reaching model to handwriting: how different effectors can produce the same written output, and other results. *Psychol Res* 59:64–74
- Meulenbroek RGJ, Thomassen AJWM, Van Lieshout PHHM, Swinnen SP (1998) The stability of pen-joint and interjoint coordination in loop writing. *Acta Psychol* 1000:55–70
- Plamondon R, Lamarche F (1986) Modelization of handwriting: a system approach. In: Kao HSR, Van Galen GP, Hoosain R (eds) *Graphonomics: contemporary research in handwriting*. Elsevier, Amsterdam, pp 169–183
- Sainburg RL, Ghilardi MF, Poizner H, Ghez C (1995) Control of limb dynamics in normal subjects and patients without proprioception. *J Neurophysiol* 73:820–835
- Sainburg RL, Ghez C, Kalakanis D (1999) Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. *J Neurophysiol* 81:1045–1056
- Schillings JJ, Meulenbroek RGJ, Thomassen AJWM (1996) Limb segment recruitments as a function of movement direction, amplitude and speed. *J Mot Behav* 28:241–254
- Schmidt RC, Treffner PJ, Shaw BK, Turvey MT (1992) Dynamical aspects of learning an interlimb rhythmic movement pattern. *J Mot Behav* 24:67–84
- Schneider K, Zernicke RF, Ulrich BD, Jensen JL, Thelen E (1990) Understanding movement control in infants through the analysis of limb intersegmental dynamics. *J Mot Behav* 22:521–535
- Scholz JP, Kelso JAS (1990) Intentional switching between patterns of bimanual coordination depends on the intrinsic dynamics of the patterns. *J Mot Behav* 22:98–124
- Schomaker LRB, Plamondon R (1990) The relation between pen force and pen-point kinematics in handwriting. *Biol Cybern* 63:277–289
- Singer NY, Tishby N (1994) Dynamical encoding of cursive handwriting. *Biol Cybern* 71:227–237
- Soechting JF, Lacquaniti F (1981) Invariant characteristics of a pointing movement in man. *J Neurosci* 1:710–720
- Stelmach GE, Teulings H-L (1983) Response characteristics of prepared and restructured handwriting. *Acta Psychol* 54:51–67
- Swinnen SP, Dounskaia N, Verschueren S, Serrien DJ, Daelman A (1995) Relative phase destabilization during interlimb coordination: the disruptive role of kinesthetic afferences induced by passive movement. *Exp Brain Res* 105:439–454
- Teulings HL (1996) Handwriting movement control. In: Keele SW, Heuer H (eds) *Handbook of perception and action*, vol 2. Motor skills. Academic Press, London, pp 561–613
- Teulings H-L, Schomaker LRB (1993) Invariant properties between stroke features in handwriting. *Acta Psychol* 82:69–88
- Teulings H-L, Thomassen AJWM, Maarse FJ (1988) A description of handwriting in terms of main axes. In: Plamondon R, Suen CY, Simner M (eds) *Computer and human recognition of handwriting*. World Scientific Publishing, Singapore, pp 69–82
- Topka H, Konczak J, Schneider K, Boose A, Dichgans J (1998) Multijoint arm movements in cerebellar ataxia: abnormal control of movement dynamics. *Exp Brain Res* 119:493–503
- Turner RS, Owens JWM, Anderson ME (1995) Directional variation of spatial and temporal characteristics of limb movements made by monkeys in a two-dimensional work space. *J Neurophysiol* 74:684–697
- Turvey MT (1990) Coordination. *Am Psychol* 45:938–953
- Ulrich BD, Jensen JL, Thelen E, Schneider K, Zernicke RF (1994) Adaptive dynamics of the leg movement patterns of human infants: II. Treadmill stepping in infants and adults. *J Mot Behav* 26:313–324
- Van Emmerik REA, Newell KM (1988) The relationship between pen-point and joint-kinematics in handwriting and drawing. In: Plamondon R, Suen CY, Simner M (eds) *Computer and human recognition of handwriting*. World Scientific Publishing, Singapore, pp 231–248
- Van Emmerik REA, Newell KM (1990) The influence of task and organismic constraints on intralimb and pen-point kinematics in a drawing task. *Acta Psychol* 73:171–190
- Van Galen GP (1991) Handwriting: issues for a psychomotor theory. *Human Mov Sci* 10:165–191
- Van Galen GP, Morasso PG (1998) Neuromotor control in handwriting and drawing: introduction and overview. *Acta Psychol* 100:1–7
- Virji-Babul N, Cooke JD (1995) Influence of joint interactional effects on the coordination of planar two-joint arm movements. *Exp Brain Res* 103:451–459
- Wada Y, Kawato M (1995) A theory for cursive handwriting based on the minimization principle. *Biol Cybern* 73:3–13
- Wright CE (1990) Generalized motor programs: reexamining claims of effector independence in writing. In: Jeannerod M (ed) *Attention and performance*, vol XIII. Erlbaum, Hillsdale, NJ, pp 294–320
- Wright CE (1993) Evaluating the special role of time in the control of handwriting. *Acta Psychol* 82:5–52
- Zernicke RF, Schneider K (1993) Biomechanics and developmental neuromotor control. *Child Dev* 64:982–1004