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Sabine M.P. Verschueren · Stephan P. Swinnen
Paul J. Cordo · Natalia V. Dounskaia

Proprioceptive control of multijoint movement: bimanual circle drawing

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Abstract Proprioception is used by the central nervous system (CNS) in the control of the spatial and temporal characteristics of single joint and multiple joint movement. The present study addressed the role of proprioception in the control of bilateral cyclical movements of the limbs. Normal blindfolded human subjects drew circles simultaneously and symmetrically with the two arms (16 cm diameter, 1 /s) upon two digitizing tablets. In selected trials, vibration (60–70 Hz) was applied to the tendon of the biceps and/or anterior deltoid muscles of the dominant arm to distort the proprioceptive information from muscle spindle afferents. One goal of this study was to identify whether tendon vibration influenced the spatial characteristics of circles drawn by the vibrated, dominant arm and the non-vibrated, non-dominant arm. A second goal was to determine the effect of vibration on the temporal coupling between the two arms during circle drawing. The results revealed that tendon vibration affected the spatial characteristics of circles drawn by the vibrated arm in a manner similar to that previously found for unilateral circle drawing. During bimanual circle drawing, vibration had only a minimal effect on the spatial characteristics of the non-vibrated, non-dominant arm. Temporal interlimb coupling was quantified by the relative phasing between the arms. Without tendon vibration, the dominant arm led the non-dominant arm. Vibration of the dominant arm increased the average phase lead. In a first control experiment, vibration of the non-dominant arm decreased the phase lead of the dominant arm, or even reversed it to a non-dominant arm phase lead. In a second control experiment, the subjects performed the bimanual circle-drawing task with vision of only the vibrated arm, in which case there was no spatial distortion of the circles drawn by the vibrated arm, but the phase relation between the two arms was still shifted as if vision were completely unavailable. It was concluded that, in bimanual movements such as these, the spatial and temporal characteristics of movement are controlled independently. Whereas the spatial characteristics of hand movement seem to be controlled unilaterally, the temporal characteristics of interlimb coupling appear to be controlled by proprioceptive information from both limbs, possibly by a proprioceptive triggering mechanism.

Key words Proprioception · Interlimb coordination · Humans · Tendon vibration · Bimanual coordination

Introduction

In the preceding paper (Verschueren et al. 1998), it was shown that proprioception is used by the CNS to coordinate the proximal joints during a unilateral multijoint movement of the arm. However, the role of proprioception in the coordination of bilateral arm movements is not well understood. The present series of experiments addressed how proprioceptive information influences the control of bimanual circle drawing.

It was hypothesized that proprioceptive input from the two limbs influences both the spatial and temporal aspects of interlimb coordination. Similar to the previous study (Verschueren et al. 1998), circle drawing was chosen because of its readily definable spatial and temporal requirements. To study the role of proprioception in interlimb coordination, vibration was applied to the tendons of two primary muscles of the subject's dominant arm (i.e., biceps brachii and/or anterior deltoid). Vibration is known to distort the perception of movement (Goodwin et al. 1972) by modifying the discharge patterns of muscle spindle afferents, with the primary afferents being most sensitive to this form of stimulation (Brown et al. 1967; Burke et al. 1976). Thus, during performance of the circle-drawing task, some propriocep-

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S.M.P. Verschueren (✉) · S.P. Swinnen · N.V. Dounskaia
Department of Kinesiology, Catholic University of Leuven,
Tervuursevest 101, B-3001 Heverlee (Leuven), Belgium
e-mail: sabine.verschueren@flok.kuleuven.ac.be
Tel.: +32-16329070, Fax: +32-16329197

P.J. Cordo
Robert S. Dow Neurological Sciences Institute,
1120 NW 20th Ave., Portland, OR 97209, USA

tive afferents were presumed to fire exclusively in response to the vibration input; some partly to the vibration and partly to the arm movement and some were presumed to be insensitive to vibration and to respond exclusively in relation to the arm kinematics (Cordo et al. 1995).

Two specific questions were addressed. First, we investigated whether the proprioceptive information of both arms is coupled in the control of the spatial characteristics of this bimanual task by studying how tendon vibration affected the spatial characteristics of the hand movement in both the vibrated and non-vibrated arm. Previous studies have convincingly demonstrated the existence of assimilation effects in bimanual movements such that the amplitude of each hand is influenced by the concurrent amplitude of the other hand movement (Sherwood 1990, 1991, 1994; Spijkers and Heuer 1995; Heuer 1993; Heuer et al. 1998). This interference (coupling or crosstalk between the limbs) becomes particularly evident when different amplitudes have to be generated simultaneously in both limbs.

Whether or not the monitoring of proprioceptive information is involved in this spatial coupling is still debated. Previous work demonstrated that a passive limb motion influenced the amplitude of the contralateral homologous limb during coordination of the ipsilateral arm and leg, suggesting that kinesthetic information of the limb moved passively influenced the spatial characteristics of the contralateral limb (Swinnen et al. 1995). The present study further elaborated on the notion of a spatial coupling between the arms, by distorting the proprioceptive input of one arm with tendon vibration and by studying the corresponding changes in the spatial characteristics of circles drawn by both arms. Spatial coupling between the two limbs would also be suggested if proprioceptive input from the non-vibrated arm were found to modify the ipsilateral effect of vibration, i.e., compared to that observed during unimanual circle drawing (Verschueren et al. 1998). Therefore, it was anticipated that, during bimanual circle drawing, the effect of vibration on circles drawn by the vibrated arm would be different to that previously found for unilateral circle drawing (Verschueren et al. 1998).

Second, we investigated whether proprioceptive information of both arms is used in the temporal control of the task. Previous studies on in-phase and anti-phase coordination patterns in two-limb cyclical movements have shown that proprioceptive input serves to maintain the stability of temporal coupling between ipsilateral limbs (Baldissera et al. 1991; Swinnen et al. 1995). Accordingly, it was anticipated that tendon vibration would increase the mean and variability of the relative phasing between both arms.

Experiments on unperturbed circle drawing have shown that the dominant arm leads the non-dominant arm by about 15–30 ms, depending on the condition (Semjen et al. 1995; Stucchi and Viviani 1993; Swinnen et al. 1996, 1997; Viviani et al. 1998), even though the origin of this asymmetry is controversial. In the present study, tendon vibration was used to determine whether peripheral sensory mechanisms – as opposed to or in addition to central mechanisms proposed by Stucchi and Viviani (1993) – might mediate this asynchrony. If the relative phasing between the arms during bimanual circle drawing changed as a result of vibration, this would indicate that the temporal coupling of the two arms is proprioceptively controlled.

Materials and methods

Design

The general methods for the experiment described in this paper have been described in detail previously (Verschueren et al. 1998) and will only be briefly reviewed in this section.

Subjects

Nine undergraduate students with no known neuromuscular deficits participated in the main experiment. Each subject provided written consent for participation. The subjects were naive about the purpose of the experiment and were not paid for their services.

Apparatus and task

The subjects sat in front of two digitizing tablets (Terminal Display Systems LC20-TDS), and they were instructed to draw a target circle (16 cm diameter) upon the surface of the digitizing tablet with each hand. During each 15-s trial, the subjects were instructed to draw circles continuously with the two arms, a complete circle for each beat of the metronome, which paced at 1 Hz. The movements were performed according to the in-phase or symmetrical coordination pattern between the arms and without any direct visual information. A computer screen in front of the subject provided knowledge of results (KR) after completion of each trial, consisting of two plots of the actual circular movements produced by the subject, superimposed on the target circle. The pen trajectories on the digitizers were recorded for both hands (accuracy 0.25 mm, sampling frequency 150 Hz), and the coordination between the two arm movements was determined.

Procedure

Before the start of the recording session, subjects practiced the task to internalize the spatial characteristics of the target circles. Initially, the subjects could see the hands during practice to become familiar with the task parameters, and then they were gradually weaned from using vision.

Subjects produced the circle-drawing movements under four different proprioceptive conditions: (1) no vibration (control trial), (2) biceps brachii vibration (60–70 Hz, 1 mm peak-to-peak), (3) anterior deltoid vibration, and (4) simultaneous vibration of both muscles. The main protocol consisted of a total of 34 trials, 4 trials per vibration condition interspersed with 11 control trials and 11 recalibration trials, which were performed with intermittent vision of the hands. Each vibration trial was followed by a recalibration trial to minimize the after effects of tendon vibration (Rogers et al. 1985). The entire sequence was randomized with respect to the vibration condition.

Data analysis

The role of the proprioceptive input from the vibrated muscles in this motor task was inferred from the influence of tendon vibration on the subject’s accuracy in producing the circular movements. The data analysis focused on the spatial and temporal features of the drawing movements of the individual arms as well as the coordination between the arms. Intralimb coordination was defined by the diameter and circularity of the movements produced by each limb as well as the drift of the hands across the graphics tablets (for calculation methods see Verschueren et al. 1998). The circularity of the hand movements was based on two measures, namely the SD of curvature and the relative phase between the x-axis and the y-axis components of the pen trajectory.

Interlimb coordination was quantified from the continuous relative phase between the movements of the right and left hands and was based on a measure proposed by Kelso et al. (1986). The within trial SD represented the variability of relative phase.

Statistical analysis

ANOVAs with repeated measures were used to test for differences among the four proprioceptive conditions, i.e., no vibration, vibration of biceps, vibration of anterior deltoid, or vibration of both biceps and anterior deltoid. Significant effects were defined as those at the $P<0.05$ probability level. When significant effects were found, post hoc tests (contrast analyses) were conducted to identify the loci of these effects. The results of the statistical analysis on the spatial and temporal characteristics of movement are presented in Tables 1 and 2. Independent variables used in the ANOVAs include Condition (presence and locus of vibration), Arm (dominant or non-dominant) and Axis (x and y).

Control experiments

Two control experiments were performed. One was designed to determine whether vibration of the non-dominant arm produced the same effect on interlimb coupling as dominant arm vibration. Subjects (N=10) not involved in the main experiment drew circles with both hands. In selected trials, vibration was applied to the biceps tendon of either the dominant or the non-dominant arm. The relative phasing between the limbs was calculated for the control and for two vibration conditions, i.e., vibration of the dominant or non-dominant arm.

The other control experiment was conducted to determine whether eventual changes in relative phase between the limbs as a result of vibration were directly associated with changes in spatial characteristics (such as drift). To test this, subjects (N=10) not involved in any related experiments drew circles with both hands while observing the dominant (vibrated) arm. As vibration does not produce movement illusions when the vibrated limb can be seen by the subject (Lackner and Taublieb 1984), no spatial distortions were expected in the movements of the vibrated arm. Accordingly, it was predicted that the effects of tendon vibration on interlimb coupling could be studied independently of the effects of vibration on spatial characteristics.

Results

As with unilateral circle drawing (Verschueren et al. 1998), tendon vibration during bimanual circle drawing distorted the spatial characteristics of hand movement in the vibrated arm, with minimal effects in the non-vibrated arm. In addition, vibration during bimanual circle drawing distorted the temporal coupling between the two arms. These effects will be discussed in more detail next.

Spatial effects of tendon vibration on hand kinematics

Figure 1 illustrates qualitatively how a representative subject drew circles with both hands, with and without tendon vibration applied to the dominant arm. Movements of the non-dominant and dominant hands on the digitizing tablet are shown in the left and right columns, respectively. In each panel, the y-axis movement of the hand is plotted against the x-axis movement for a single 15-s trial.

Table 1 Statistical results with respect to diameter and drift

	df	Diameter	Diameter (dominant)	Diameter (non-dominant)	Drift
		Mean (*F*)	Mean (*F*)	Mean (*F*)	Mean (*F*)
Condition	3,24	1.25	6.26**	3.57*	33.90**
Arm	1,8	14.09**			10.33*
Axis	1,8	3.85	4.03	1.61	5.56**
Condition × Arm	3,24	22.18**			41.65**
Condition × Axis	3,24	2.40	<1	6.15**	23.51**
Arm × Axis	1,8	<1			29.68**
Condition × Arm × Axis	3,24	5.08			52.30**

*$P<0.05$; **$P<0.01$

Table 2 Statistical results of experiment 1 with respect to SD of curvature and relative phase within a limb and between the limbs

	df	SDcurvature	Relative phase (x–y)	Relative phase (dom.-non-dom.)	
		Mean (*F*)	Mean (*F*)	Mean (*F*)	SD (*F*)
Condition	3,24	12.47**	10.64**	9.66**	14.43**
Arm	1,8	3.91	1.78		
Condition × Arm	3,24	3.63*	36.22**		
Axis	1,8			1.09	56.85**
Condition × Axis	3,24			6.04**	<1

*$P<0.05$; **$P<0.01$

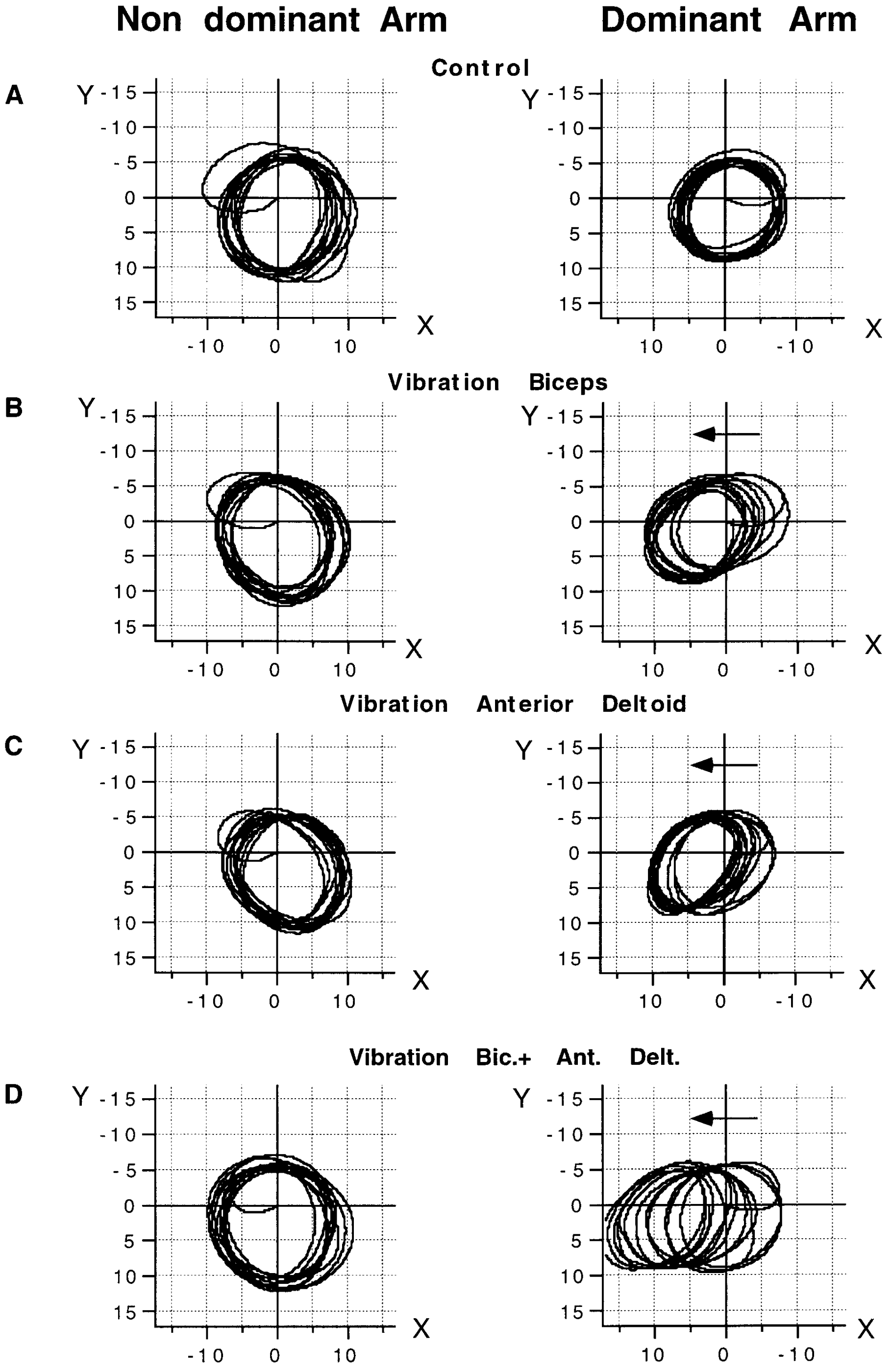

Fig. 1A–D Effect of vibration on movements of both arms. Single trials of hand movement trajectories are shown from a representative subject (**A** control trial; **B** biceps brachii vibration; **C** anterior deltoid vibration; **D** biceps and anterior deltoid vibration). *Each plot* corresponds with a top view of the actual movements performed on the digitizers; the body midline is situated in between the plots of the non-dominant (*left*) and dominant arms (*right*)

Vibration distorted the spatial characteristics of the vibrated arm, whereas the effects of vibration on the non-vibrated arm were small. The control trial (top row) shows that, without vibration, the dominant hand followed a relatively stable circular pattern, whereas the circles drawn by the non-dominant hand were slightly more variable, confirming previous observations (Swinnen et al. 1996, 1997). Vibration of the biceps brachii or the anterior deltoid tendon resulted in an inward drift of the dominant hand (middle two rows). Simultaneous vibration of the biceps brachii and anterior deltoid (bottom row) resulted in a drift of the dominant hand that exceeded the two individual effects. Vibration of the dominant arm had little effect on the spatial characteristics of circles drawn by the non-dominant hand.

Circle diameter

Figure 2 shows the *x*- and *y*-components of the mean diameters of circles drawn by the dominant and non-dominant hands for each vibration condition. In each group of

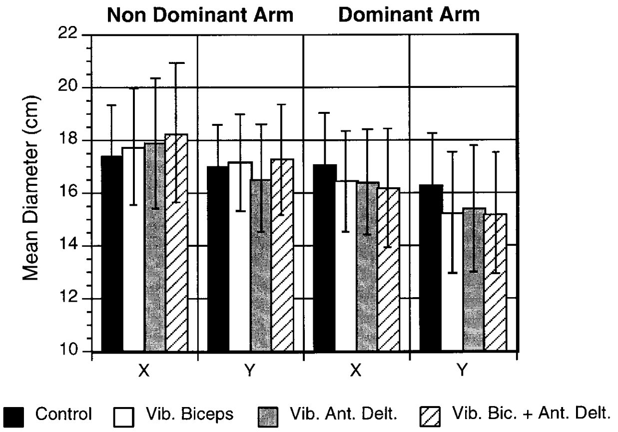

Fig. 2 Effect of vibration on the mean diameter of circles drawn by both limbs. *Each bar* represents the grand mean of nine subjects, and *each group of four bars* represents the *x*- or the *y*-axis diameter. In each group of four bars, *the black bar* represents the control condition; *the white bar*, biceps vibration; *the light gray bar*, anterior deltoid vibration; *the hatched bar*, simultaneous vibration of both muscles

four vertical bars, the bar height represents the mean circle diameter. Tendon vibration decreased the mean diameter of the circles drawn by the dominant hand and increased the mean diameter of the circles drawn by the non-dominant hand.

A $4 \times 2 \times 2$ (Condition × Arm × Axis) ANOVA with repeated measures on all factors was conducted on the circle diameter data (Table 1). Only the main effect for Arm was significant. The left hand produced bigger circles ($M=17.375$ cm) than the right hand ($M=15.99$ cm). A significant interaction arose between the factors Condition and Arm, because the difference in diameter between circles drawn by the two hands increased with vibration due to a decrease in diameter on the dominant side and an increase on the non-dominant side. The interaction among all three factors was also significant. To better understand this interaction, a 4×2 (Condition × Axis) ANOVA with repeated measures on the two factors was performed separately on the data from each hand. In the vibrated, dominant arm, vibration produced a significant decrease in diameter. Post hoc testing revealed that circle diameter in each condition with tendon vibration differed from circle diameter in the control condition ($P<0.05$), but the diameter did not differ among the three conditions with tendon vibration ($P>0.05$). In the non-vibrated, non-dominant arm, vibration of the contralateral arm caused a significant increase in circle diameter. This increase in diameter was bigger for movement along the *x*-axis than along the *y*-axis, resulting in a significant interaction between Condition and Axis. Post hoc testing revealed that only the condition with simultaneous vibration of biceps brachii and anterior deltoid produced a significantly larger circle diameter compared to the control condition ($P<0.05$).

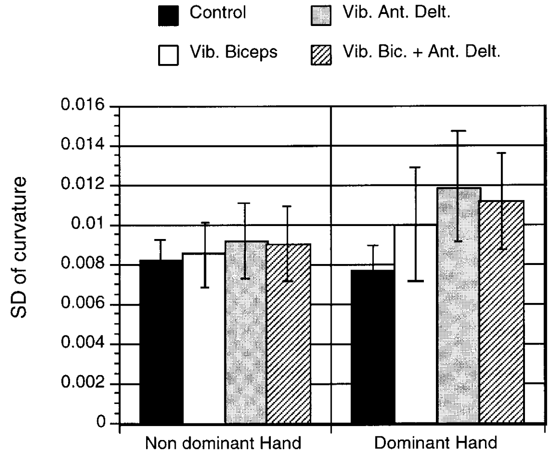

Fig. 3 Effect of vibration on the SD of curvature of both hand movements. *Each bar* represents the grand mean of nine subjects. In each group of four bars, *the black bar* represents the control condition; *the white bar*, biceps vibration; *the light gray bar*, anterior deltoid vibration; *the hatched bar*, simultaneous vibration of both muscles

Standard deviation of curvature

Tendon vibration resulted in an increase in the SD of curvature, a measure of circularity. Figure 3 shows the effect of tendon vibration on the SD of curvature for circles drawn by the non-dominant, non-vibrated arm (left) and the dominant, vibrated arm (right). A 2×4 (Arm × Condition) ANOVA with repeated measures was conducted on the SD of curvature data (Table 2). The significant main effect for condition confirms the observation that vibration increased the SD of curvature. The significant interaction between the factors Arm and Condition adds that the effect of vibration was mainly present in the dominant arm. A one-way ANOVA with repeated measures on the factor Condition was performed separately on the data from each hand. In the vibrated, dominant arm, vibration produced a significant increase in the SD of curvature ($F(3,24)=8.48$, $P<0.001$), but not in the non-vibrated, non-dominant arm, $F(3,24)<1$.

Continuous relative phase between the x- *and* y-*components of hand movements*

Vibration changed the relative phasing between the within limb *x*- and *y*-components of the movement of both hands, although the effect on the non-dominant, non-vibrated arm was small. Circles are characterized by a relative phase of 90°. In Fig. 4, the height of each bar represents the mean relative phase between the *x*-axis and *y*-components of the non-dominant, non-vibrated arm movement (left) and the dominant, vibrated arm movement (right). With the exception of the dominant arm during biceps vibration, the relative phasing (averaged over the 15-s trial) was always <90, that is, the phasing of the *y*-component lagged compared to the ideal timing.

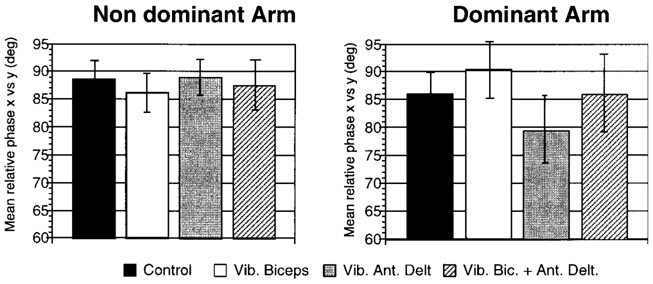

Fig. 4 Effect of vibration on the mean of the relative phase between the *x*- and the *y*-axis components of the movements of both arms. A perfect circle has a mean relative phase of 90°. *Each bar* represents the grand mean of nine subjects. In each group of four bars, *the black bar* represents the control condition; *the white bar*, biceps vibration; *the light gray bar*, anterior deltoid vibration; *the hatched bar*, simultaneous vibration of both muscles

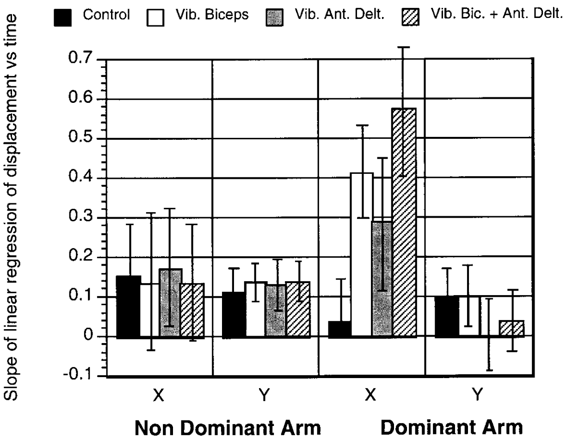

Fig. 5 Effect of vibration on drift of the hand. Drift was defined as the slope of the linear regression of hand displacement over time. Positive slopes for the *x*-component of hand movement represent drift toward the midline, and for the *y*-component, toward the body. *Each bar* represents the grand mean of nine subjects. *Each group of four bars* represents the slope values in the *x*- or *y*-direction. In each group of four bars, *the black bar* represents the control condition; *the white bar*, biceps vibration; *the light gray bar*, anterior deltoid vibration; *the hatched bar*, simultaneous vibration of both muscles

Tendon vibration in the dominant arm appeared to have opposite effects on the dominant and non-dominant arms. In the non-dominant, non-vibrated arm, biceps vibration increased the phase lag of the *y*-axis component of the hand movement, and anterior deltoid vibration reduced the lag (Fig. 4, left). In the dominant, vibrated arm, biceps vibration decreased the lag or eliminated it altogether, and anterior deltoid vibration increased the lag (Fig. 4, right).

A 4×2 (Condition × Arm) ANOVA with repeated measures on both factors revealed a significant main effect for Condition (Table 2) and a significant interaction effect between Condition and Arm. These significant effects indicate that there was a difference in relative phase among the four proprioceptive conditions, but this difference was not the same for both arms. For the dominant vibrated arm, post hoc tests revealed that biceps vibration increased the relative phase ($P<0.01$) relative to the control condition, whereas anterior deltoid vibration decreased the phase ($P<0.01$). Simultaneous vibration of both muscles appeared to cancel out the individual effects, resulting in no difference in relative phase compared to that in the control condition ($P>0.05$). As a result of the opposing effects of vibration of individual muscles, the relative phases in the three conditions with tendon vibration also differed significantly from each other ($P<0.01$). For the non-dominant, non-vibrated limb, however, post hoc tests revealed that vibration of the contralateral biceps significantly decreased relative phase compared to the control condition ($P<0.05$), without a significant difference between the remaining two vibration conditions and the control condition ($P>0.05$).

Drift

Vibration caused the hand of the vibrated arm to drift in the *x*-direction. This drift was quantified by the slope of the linear regression of hand displacement in the *x*- and *y*-direction as a function of time, as shown in Fig. 5. In the vibrated, dominant arm (rightmost two panels), vibration of biceps (white), anterior deltoid (light gray) and both muscles (hatch) increased the slope of the hand displacement in the *x*-direction compared to the control condition (black). Anterior deltoid vibration also produced a small decrease in slope along the *y*-axis (see also Fig. 1). In contrast, the non-vibrated, non-dominant arm did not drift as a result of vibration of the contralateral arm.

A 4×2×2 (Condition × Arm × Axis) ANOVA with repeated measures confirmed this observation. All main effects and interactions were significant. The significant three-factor interaction corresponds to the observed effect of vibration on the slope of hand position, but this slope change was only observed in the vibrated arm and mainly along the *x*-axis. Post hoc tests on the data of the vibrated limb revealed that the slopes of all three vibration conditions were significantly different from the control condition ($P<0.05$). The three vibration conditions also differed amongst each other ($P<0.05$), suggesting that every vibration condition caused a distinctive effect on the drift of the hand.

Temporal effects of tendon vibration on interlimb coordination: relative phase

Vibration of the dominant arm

Vibration had a significant effect on the mean continuous relative phase between the two hand movements. According to the instructions presented to the subjects, the required relative phase between the hands was supposed to approximate 0°, as the circles were to be drawn according to the “in-phase” coordination pattern. A posi-

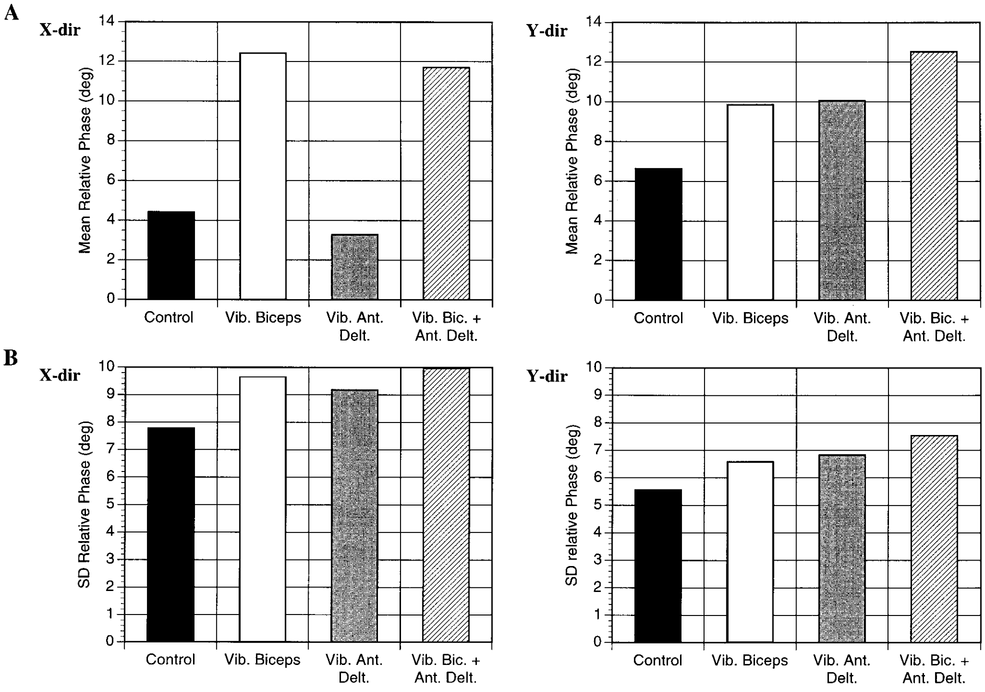

Fig. 6A, B Effect of vibration on temporal coupling of the two arms. Temporal coupling was described by the mean and SD of the relative phase between the two limbs. *Each bar* represents the grand mean of nine subjects. The required mean relative phase was 0°, which corresponds to the in-phase coordination pattern. Positive values of relative phase indicate a phase lead of the dominant limb. *Black bars* represent the control condition; *white bars*, biceps vibration; *light gray bars*, anterior deltoid vibration; *hatched bars*, simultaneous vibration of both muscles

tive relative phase implies that the dominant arm leads the non-dominant arm, which proved to be the case in all four proprioceptive conditions.

Without tendon vibration, the natural tendency of subjects was for the dominant hand to lead the non-dominant hand by about 5° (Fig. 6A, black bar). Vibration enhanced the phase lead of the dominant hand, as shown in Fig. 6A for the x-component of hand movements (left panel) as well as the y-component (right panel). In the x-direction, biceps vibration substantially increased the phase lead of the dominant hand, whereas anterior deltoid vibration produced a small decrease in phase lead. In the y-direction, both biceps and anterior deltoid increased the phase lead of the dominant hand, and these effects appeared to be partially additive during simultaneous vibration of both muscles. These observations were confirmed with a 4×2 (Condition × Axis) ANOVA, which showed a significant main effect for Condition (Table 2). Post hoc tests revealed that each vibration condition resulted in a different relative phase value, relative to the control condition ($P<0.05$). Vibration of the anterior deltoid resulted in a significantly smaller change in relative phasing than the two other vibration conditions ($P<0.05$), presumably as a result of the lack of effect in the x-direction. The main effect for Axis was not significant. There was a significant interaction effect between Condition and Axis, presumably because vibration of the anterior deltoid in the x-direction resulted in a decrease in relative phase compared to the control condition.

The stability of the coordination pattern was also affected by tendon vibration, as shown by an increased variability in the relative phase between the two hands due to vibration of either biceps and/or anterior deltoid (Fig. 6B). A 4×2 (Condition × Axis) ANOVA with repeated measures showed that vibration resulted in a significant increase in variability (Table 2). Post hoc tests confirmed that all three vibration conditions increased the variability of interlimb phasing compared to the control condition ($P<0.01$).

Simultaneous vibration of the two muscles increased the relative phase variability more than biceps vibration alone ($P<0.05$). The relative phase variability in the x-direction was greater than that in the y-direction, which is consistent with a significant effect for Axis. The interaction effect was not significant.

Control experiment 1: vibration of the non-dominant arm

A first control experiment was performed to study whether the previously observed effect on interlimb coupling was dependent on the arm vibrated (i.e., dominant versus non-dominant). The findings revealed that vibration of the non-dominant arm had an opposite effect on the relative phasing between the arms to that shown by vibration of the dominant arm (Fig. 7). Compared to the control trials (black bars), vibration of the non-dominant arm (hatched bar) decreased or even reversed the phase lead of the dominant arm, whereas vibration of the dominant arm (white bar) increased the phase lead (see also Fig. 6A). A repeated measures 3×2 (Condition × Axis) ANOVA revealed that vibration of the non-dominant arm led to a significant decrease of the dominant hand phase lead, $F(1,9)=30.8$, $P<0.01$. Vibration of the dominant arm increased the phase lead, $F(1,9)=28.02$, $P<0.01$.

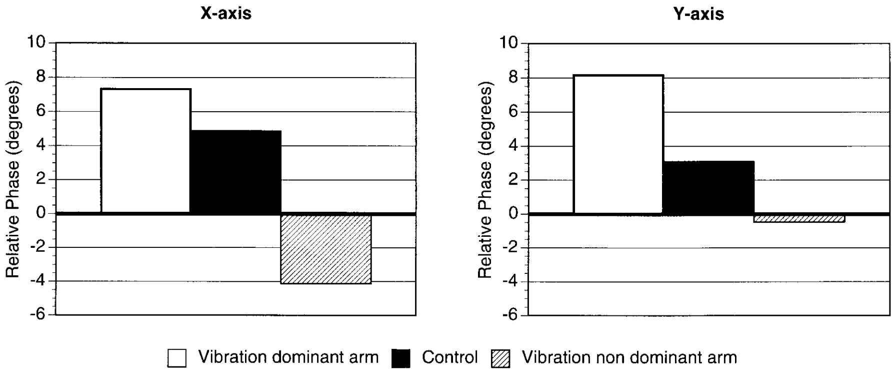

Fig. 7 Effect of vibration of the dominant arm versus vibration of the non-dominant arm on relative phase between the arms. The relative phase of the x-axis component of hand movement is shown *on the left* and that of the y-axis component is shown *on the right*. *Each bar* represents the grand mean of ten subjects. In each group of three bars, *the leftmost bar* represents the relative phase during vibration of the dominant biceps, *the middle bar* represents the control condition, and *the rightmost bar* represents vibration of the non-dominant biceps

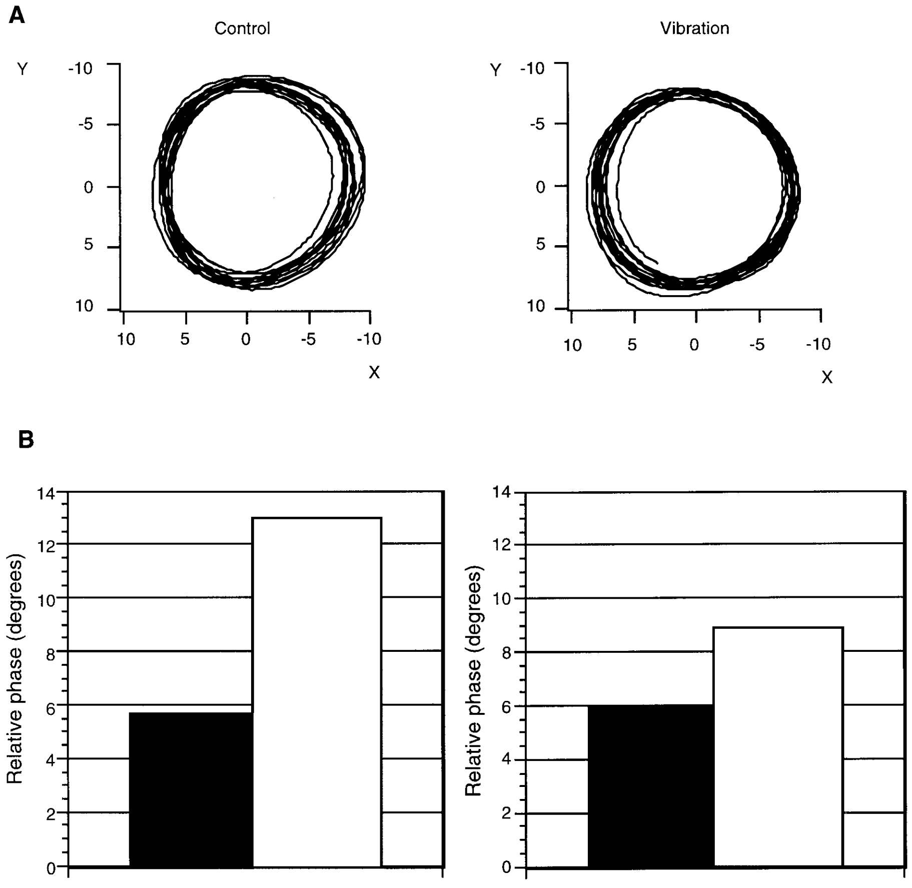

Fig. 8A, B Effect of vibration on relative phasing between the arms when subjects could see the dominant, vibrated arm. *The top two panels* **(A)** show the dominant, viewed hand movement of a representative subject from a control trial (*left*) and a vibration trial (*right*). *In the bottom panels* **(B)**, *each bar* represents the grand mean of ten subjects of the relative phase between the arms. *In each pair of bars, the left bar* represents the control condition and *the right bar* vibration of the dominant biceps

Control experiment 2: vibration with vision of the vibrated arm

A second control experiment was performed to determine whether changes in interlimb coupling as a result of vibration were associated with changes in spatial characteristics. When subjects were allowed to see the vibrated arm, but not the non-vibrated arm, vibration did not distort the spatial characteristics of circles drawn by the dominant, vibrated arm ($P>0.05$) (Fig. 8A), as compared to the condition in which the vibrated arm could not be seen (see Fig. 1). However, vibration still resulted in a change in the relative phasing between the arms, increasing the phase lead of the dominant arm from 5–13° in the x-direction and from 6–9° in the y-direction during biceps vibration, $F(1,9)=23.89$, $P<9.01$ (Fig. 8B). This increase in phase lead is comparable to that found when neither arm could be seen (see Fig. 6A).

Discussion

In the study of unilateral circle drawing described in the preceding paper (Verschueren et al. 1998), the spatial characteristics of hand movements were found to be influenced by tendon vibration of the performing arm. In the bimanual circle-drawing study described in this paper, we found that, in addition to the previously demonstrated spatial effects on the performing arm, tendon vibration influenced the temporal coupling of the two hand movements. In contrast, the spatial characteristics of contralateral hand movement were relatively unaffected by vibration.

Spatial coordination of bimanual circle drawing and the role of proprioception

Tendon vibration during bimanual circle drawing might reveal contralateral influences of proprioceptive input in two ways. First, undisturbed proprioceptive input from the non-vibrated arm could change the unilateral effects of vibration in the vibrated arm (see Verschueren et al. 1998). Second, proprioceptive input from the vibrated arm could influence the spatial characteristics of hand movement in the non-vibrated arm.

Spatial proprioceptive influences of the non-vibrated arm on the vibrated arm

During bimanual circle drawing, the spatial characteristics of circles drawn by the vibrated arm were almost identical to those observed during unilateral circle drawing (Verschueren et al. 1998). The average *x*-axis diameter of the circles drawn with the vibrated arm decreased by 0.88 cm during biceps and anterior deltoid vibration in unimanual circle drawing (Verschueren et al. 1998, see Fig. 4) compared to 0.93 cm during bimanual circle drawing (Fig. 2). Similarly, the average *y*-axis diameter of circles drawn with the vibrated arm decreased by 0.96 cm during biceps and anterior deltoid vibration in unimanual circle drawing compared to 1.07 cm during bimanual circle drawing. The circularity (i.e., SD of curvature and *x*- and *y*-axis relative phase) of circles drawn by the vibrated arm was similar for unimanual and bimanual circle drawing (cf. Figs. 3 and 4, and Verschueren et al. 1998, Fig. 6). Finally, the hand of the vibrated arm drifted inward toward the midline by almost the identical amount in bimanual and unimanual circle drawing (cf. Fig. 5 and Verschueren et al. 1998, Fig. 5). Thus, the undisturbed sensory input from the non-vibrated arm had virtually no modulatory or corrective effect on the disturbances to circles drawn with the vibrated arm.

Spatial proprioceptive influences of the vibrated arm on the non-vibrated arm

In bilateral circle drawing, vibration of muscles in the dominant arm had a minimal effect on the spatial characteristics of circles drawn by the non-dominant hand. The circularity (i.e., SD of curvature and *x*- and *y*-axis relative phase) of figures drawn by the contralateral hand was unaffected by vibration of the dominant arm. Nor did vibration cause any significant drift of the contralateral hand, implying that the position of each hand in extrinsic space was independently controlled in the present task. The only contralateral spatial effect of vibration was an increase in circle diameter in the non-dominant hand, in contrast to a decrease in the diameter of circles drawn by the dominant hand. However, this effect only reached significance when both the biceps and anterior deltoid were vibrated, which might explain why some previous studies using single muscle vibration failed to document contralateral vibration effects (e.g., Bullen and Brunt 1986). Thus, the change in spatial characteristics of circles drawn by the hand contralateral to the vibrated arm was limited to the diameter of the circles, and this change was in the opposite direction to that for the vibrated arm, consistent with several previous studies reporting contralateral effects of vibration (Al-Senawi and Cooke 1985; Lackner 1984) being opposite to those seen in the vibrated arm (e.g., Capaday and Cooke 1981; Inglis and Frank 1990; Sittig et al. 1985).

Taken together, the results of vibration on the spatial characteristics of bimanual movement suggest that the spatial control of the two arms by proprioception is relatively independent, whereby proprioceptive information of one arm does not have an effect on the spatial characteristics of the other arm movement.

Temporal coordination of bimanual circle drawing by proprioception

The results of the present study show that vibration influenced the temporal coupling of the two limbs, demonstrating that proprioception contributes to interlimb coordination during bimanual circle drawing. Vibration applied to a tendon of the dominant limb influenced the mean as well as the SD of the relative phase between the two limbs, suggesting that the temporal control of the two arms was mediated by proprioception.

The SD of relative phase increased as a result of tendon vibration (Fig. 6B), implying that proprioceptive information is important for preserving the stability of the coordination pattern between the limbs. Such an hypothesis was previously forwarded by Wilson (1961) and Wendler (1974) for the coordination between the wings of the flying locust and for the coordination of hand-foot movements in humans by Baldissera et al. (1991) and Swinnen et al. (1995). While rhythmic patterns of motor output can be generated without sensory feedback by a central network, these patterns become vulnerable when sensory input is not available (Grillner 1985).

In trials where proprioceptive input was undisturbed by tendon vibration (i.e., control trials), the circles drawn by the dominant hand led those drawn by the non-dominant hand (Fig. 6A). Previous studies have reported this asynchrony between the dominant and the non-dominant arms during bimanual circle or ellipse drawing (Semjen et al. 1995; Stucchi and Viviani 1993; Swinnen et al. 1996, 1997; Viviani et al. 1998) and during line drawing (Swinnen et al. 1998). The origin of this asynchrony, however, remains controversial. Semjen et al. (1995) hypothesized that the higher maximal movement frequency and the higher preferred inherent frequency of the dominant limb might result in the phase lead of the faster, dominant arm with respect to the slower, non-dominant arm. Alternatively, Stucchi and Viviani (1993) proposed that bilateral cyclical movements are timed by a lateralized "functional module" and that the asynchrony arises from the transmission of time-keeping information from one cortical hemisphere to the other. Recently, Viviani and coworkers (1998) found asymmetric neural activity in some portions of motor and premotor areas of both hemispheres during bimanual coordination, which led them to suggest that this timekeeping information is originating in only one hemisphere. Swinnen et al. (1996) found that manipulating visual cueing affected the phase offsets between the limbs: the temporal asynchrony between the limbs was largest when subjects directed their gaze at the dominant limb and smallest when focusing on the non-dominant limb. However, they noted that vision was not the only source of sensory information influencing the phase offset, as such offsets were also observed when the subjects were blindfolded. Collectively, these studies indicate that the phase offsets observed in unperturbed cyclical movements of the limbs are attributable to both central and sensory mechanisms.

In the present study, the finding that tendon vibration applied to muscles of the dominant arm increased the phase lead of the dominant limb above that in trials without vibration – suggests that proprioceptive information is used to coordinate the timing characteristics of this bimanual task. Conversely, vibration applied to muscles in the non-dominant arm resulted in a decrease in phase lead of the dominant arm. Thus, proprioceptive input from each arm is involved in bimanual coordination. The direction of the effect of dominant arm vibration (i.e., increased phase lead of the dominant arm) is consistent with that occurring in the absence of tendon vibration, whereas the direction of the effect of non-dominant arm vibration is opposite. Thus, there is a fundamental difference in the role of dominant and non-dominant arm proprioception in interlimb coordination of the circle-drawing task. The phase offset that occurs under normal conditions (i.e., no tendon vibration) could be accounted for, at least in part, by processing and transmission of proprioceptive information from one arm control center to the other.

More specifically, we hypothesize that a proprioceptive monitoring mechanism is used by the CNS whereby relative phase offsets exceeding a certain threshold may trigger corrections in order to maintain a stable phase relationship between the arms (Swinnen et al. 1996). The results of a number of previous studies suggest proprioceptive triggering as a mechanism for interlimb coordination. It has been shown in cats that initiation of the swing phase depends on the critical positioning of the ipsilateral hip (Grillner and Rossignol 1978; Hiebert et al. 1996; Sherrington 1910) and the appropriate phase of the contralateral step cycle (Grillner and Rossignol 1978). In both mesencephalic (Kulagin and Shik 1970) and spinal cats (Forssberg et al. 1980) walking on a split speed treadmill, the animals adjusted the stride length of each limb, suggesting the action of a proprioceptive triggering mechanism. In cats, a proprioceptive triggering mechanism appears to prevent the initiation of the swing phase until the leg is unloaded by weight-bearing on the other legs (Pearson and Duysens 1976). In human locomotion, Nashner (1980) showed that short-latency stumbling responses evoked from the stance leg produced reciprocal compensatory responses in each leg. In insects, proprioceptive triggering has also been shown to play a role in interlimb coordination during walking (Bassler 1986, 1987) and flying (Wendler 1974; Wilson 1961; Wolf and Pearson 1988). Thus, proprioceptive triggering appears to be a general feature in the control of locomotion and other bilateral cyclical motor behaviors. Finally, proprioceptive triggering has also been proposed in studies on intersegmental coordination (Cordo 1990; Cordo et al. 1994).

The results of the bimanual circle-drawing experiment suggest that the spatial and temporal characteristics of the hand movements are independently controlled. In the experiment where the subject was unable to see the arms, vibration of the dominant arm distorted the spatial characteristics of hand movements produced by the dominant arm at the same time that it distorted the temporal coupling of the two arms. It is possible, therefore, that these two distortions are related. However, in the experiment where the subject could see the dominant, vibrated arm, the temporal coupling between the two arms (Fig. 8B) was still disturbed, despite the absence of any spatial disturbance to hand movements produced by the vibrated arm (Fig. 8A). Thus, the increased phase lead of the dominant arm, relative to the non-dominant arm, must be a direct effect of disturbed proprioceptive input, and not an indirect one as a result of the change in spatial characteristics of the vibrated arm.

To summarize the results of this bimanual study, the effects of vibration on the spatial characteristics of circles drawn by the ipsilateral arm were similar to the results observed during unilateral circle drawing (Verschueren et al. 1998), whereas the effects on the contralateral arm were minimal. These findings indicate that the control of the spatial characteristics of the present circle-drawing task is primarily a unilateral function. Tendon vibration also changed the phase relation between the two hands, increasing the normally occurring phase lead of the dominant arm when vibration was applied to the dominant arm and reversing the phase lead of the dominant arm to a phase lag when vibration was applied to the non-dominant arm. Thus, the two arms appear temporally coupled by proprioception – possibly by a proprioceptive monitoring mechanism – independently of the spatial control of circle drawing.

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