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Bimanual Coordination During Rhythmic Movements in the Absence of Somatosensory Feedback

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Spencer, Rebecca M. C., Richard B. Ivry, Daniel Cattaert, and Andras Semjen. Bimanual coordination during rhythmic movements in the absence of somatosensory feedback. *J Neurophysiol* 94: 2901–2910, 2005. First published July 13, 2005; doi:10.1152/jn.00363.2005. We investigated the role of somatosensory feedback during bimanual coordination by testing a bilaterally deafferented patient, a unilaterally deafferented patient, and three control participants on a repetitive bimanual circle-drawing task. Circles were drawn symmetrically or asymmetrically at varying speeds with full, partial, or no vision of the hands. Strong temporal coupling was observed between the hands at all movement rates during symmetrical drawing and at the comfortable movement rate during asymmetrical drawing in all participants. When making asymmetric movements at the comfortable and faster rates, the patients and controls exhibited similar evidence of pattern instability, including a reduction in temporal coupling and trajectory deformation. The patients differed from controls on measures of spatial coupling and variability. The amplitudes and shapes of the two circles were less similar across limbs for the patients than the controls and the circles produced by the patients tended to drift in extrinsic space across successive cycles. These results indicate that somatosensory feedback is not critical for achieving temporal coupling between the hands nor does it contribute significantly to the disruption of asymmetrical coordination at faster movement rates. However, spatial consistency and position, both within and between limbs, were disrupted in the absence of somatosensory feedback.

INTRODUCTION

Studies involving bimanual periodic movements have shown that two patterns of coordination, in-phase and antiphase, exhibit spontaneous stability. With respect to the sagittal plane of the body, in-phase movements are symmetric and typically involve the simultaneous activation of homologous muscles. Antiphase movements are asymmetric, with muscle activation patterns typically 180° out of phase. A fundamental observation in the motor control literature is that these two patterns are not equally stable. For in-phase movements, the variability of relative phase remains low and relatively constant across a large range of movement frequencies. In contrast, for antiphase movements, relative phase variability increases as frequency increases and, at a critical frequency, spontaneous transitions from anti- to in-phase movements are observed (reviewed in Schoener and Kelso 1988).

Although the dynamics of hand coordination were originally developed for single-joint, oscillatory movements (Kelso 1984), many recent studies have used a two-dimensional bimanual circle-drawing task in which movements are made either symmetrically with one hand circling clockwise and the other, counterclockwise, or asymmetrically, with both hands circling clockwise or counterclockwise (Carson et al. 1997; Semjen et al. 1995). The reduced stability of the asymmetric pattern is seen at high frequencies, manifest not only in increased phase variability between the hands but also in trajectory deformations. These are especially evident in the movements produced by the nondominant hand (e.g., Franz et al. 2002; Swinnen et al. 1996).

Although formal models have addressed the abstract dynamics of pattern stability during bimanual coordination tasks (Beek et al. 2002; Haken et al. 1985), the underlying neurological mechanisms have been the subject of recent investigations. One physiological account has associated the susceptibility of the asymmetric pattern to neural cross talk, whereby the movement commands assigned to one hand spread to the neural centers controlling the other hand (Heuer 1993; Swinnen 1992). Cattaert et al. (1999) modeled such effects by assuming a spontaneous tendency for coactivation of homologous muscle groups of the upper limbs. This coactivation would generate cross talk that would be mutually facilitatory for commands associated with symmetric movements and in conflict for commands associated with asymmetric movements. A possible neural locus for these interactions might be at the spinal level where input from the dominant crossed corticospinal fibers might be influenced by a smaller, yet significant input from uncrossed descending fibers (Cattaert et al. 1999). Consistent with this conjecture, a group of participants with a relatively high degree of ipsilateral corticospinal excitability were more unstable in drawing asymmetric circles than participants who showed minimal evidence of ipsilateral corticospinal excitability (Kagerer et al. 2003).

However, the results of a study involving split-brain patients suggest that the critical neural interactions occur at a cortical level rather than at a spinal level (Kennerley et al. 2002). These patients showed no preference for the symmetric pattern in the bimanual circle-drawing task. Indeed, temporal coupling was appreciably attenuated, with the hands adopting different movement frequencies during either symmetrical or asymmetrical movements. This result suggests that interhemispheric communication by the corpus callosum is an essential pathway for bimanual coordination, at least for tasks involving continuous, periodic movements.

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An interoperative study of a patient during collosal resection illustrated the role of the corpus callosum in conveying spatial information; asymmetric trajectories improved after resection of the posterior collosal fibers (Eliassen et al. 1999). More specifically, we have proposed (Ivry et al. 2004) that interactions arise between abstract spatial codes that are invoked during the preparation and execution of the movement trajectories. For example, the codes for the two hands, if defined in egocentric coordinates, might be more compatible for symmetric patterns (e.g., "move both hands inward, then both outward") than for asymmetric patterns (e.g., "move right hand inward and left hand outward"). This hypothesis focuses on interactions between the spatial codes defining the movement goals. In support of this hypothesis, asymmetric movements not only exhibit reduced stability during movement execution but also entail costs before movement initiation (Heuer 1993). Furthermore, it has been suggested that the location of this interference occurs, at least in part, in the parietal cortex (Wenderoth et al. 2004).

Sensory information could provide another source of information for bimanual coordination. Pattern stability might be maintained by the exchange of proprioceptive, kinesthetic, and tactile information arising from the moving limbs (Baldissera et al. 1991; Cohen 1971; Kelso et al. 1991). For example, evaluating the relative phase of the hands (i.e., whether one hand leads or lags the other hand) might rely on registering, continuously or intermittently, their relative positions, or some higher-order derivative, in an egocentric reference system. The ease with which such information can be compared under different coordination modes might be one factor determining the coordination dynamics in bimanual actions (Semjen et al. 1995). For example, the greater stability of in-phase movements might, at least in part, result if it is easier to compare sensory signals from homologous muscles than from nonhomologous muscles.

To investigate the role of movement-related somatosensory feedback during bimanual coordination, two patients with sensory disturbances were tested on the bimanual circle-drawing task. One patient had severe bilateral sensory neuropathy, essentially rendering the individual deafferented. The other patient had milder sensory loss on one side with the impairment most pronounced in the arm and digits. If somatosensory signals are important for bimanual coordination, the patients' performance should be quite different from that observed in control participants. The tasks were performed with full vision, partial vision, or no vision of the hands. In this manner, we sought to also evaluate the role of visual feedback and, in particular, whether this sensory source might substitute for somatosensory information.

METHODS

Participants

Five participants were tested, two patients with sensory disturbances and three age-matched controls. The control participants and Patient 1 were tested in Marseille and Patient 2 was tested in Berkeley. All participants were self-reported right-handers. The control participants were members of the laboratory staff and had no previous practice on the circle-drawing task. All participants were tested in a single session.

Patient 1, a 54-yr-old female, has suffered from an extensive sensory polyneuropathy since age 29. The disease primarily affects large myelinated sensory fibers. A full clinical report can be found in Cole and Paillard (1995; see also Forget and Lamarre 1987). Clinical investigations and electrophysiological tests have consistently demonstrated a total loss of touch, vibration, pressure, and kinesthetic senses and no tendon reflexes in the four limbs. The trunk region is moderately impaired. Pain and temperature sensation persists and motor fibers appear to be unaffected. Given the extent of the neuropathy, she is confined to a wheelchair. However, she is able to perform everyday manual tasks quite satisfactorily under constant visual guidance.

Patient 2, a 65-yr-old male had sensory impairment in the right arm, extending to the shoulder, and less extensive sensory loss in the right leg after a left parietal stroke at age 55. Neurological examination revealed a loss of sensation of touch and position, and a mild loss of vibration sense. Pain and temperature sensation remained intact. Although clumsy, he reported performing daily activities without assistance. Patient 2 is also right-handed, although he now writes and performs other daily activities with his left, unaffected hand.

This work was approved by the local ethics committees and was performed in accordance with the ethical standards established in the 1964 Declaration of Helsinki. Informed consent was obtained from all participants before testing.

Task

The participant was seated at a table. Taped to the table surface was a target sheet consisting of two circles that served as drawing templates. Each circle was 50 mm in diameter and the center-to-center distance between the circles was 15 cm. The task consisted of tracing the template continuously with the index fingers of both hands for 15 s. The instructions emphasized that the templates served to indicate the approximate size and location of the circles to be drawn, rather than to precisely constrain the movement trajectory. The movements started and stopped on the verbal instructions of the experimenter and were executed with the forearms and elbows positioned slightly above the table surface.

The experimental conditions are summarized in Fig. 1. The circling task was performed in two coordination modes: symmetrical (the left hand moved counterclockwise, the right hand clockwise) and asymmetrical (both hands moved clockwise). Both coordination conditions were performed under three vision conditions: full vision of the hands, vision restricted to the one hand ("partial"), and no vision of the hands. In the no-vision trials, the participants were instructed to close the eyes after they drew two complete circles. In the partial-vision trials, a screen prevented the participant from seeing one arm. For Patient 1 and controls, the partial condition was tested with the right

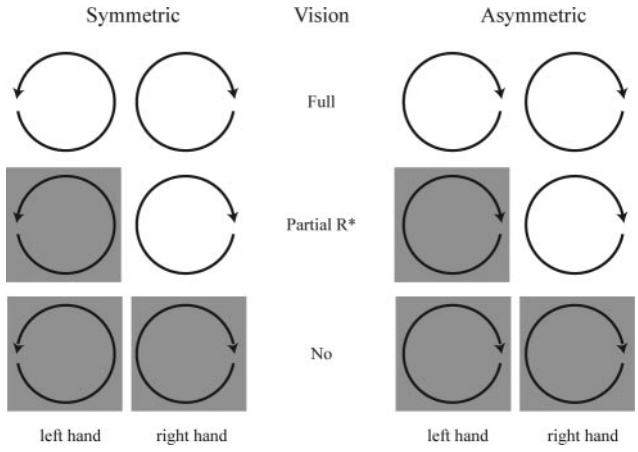

FIG. 1. Task illustration. Shading illustrates shielding of vision for the specified limb. Note that Patient 2 was also tested in a condition in which vision was limited to the left hand only (not shown).

hand occluded. Because Patient 2 has unilateral sensory loss on the right side of the body, this patient was tested twice in the partial vision condition, once with the right hand occluded and once with the left hand occluded.

The patients performed each condition at two movement rates, one self-selected to be "comfortable" and the other "as fast as possible." The control participants were capable of moving at much faster rates than the patients. However, our goal was to compare performance between groups when the movements were approximately matched in terms of movement rate. Thus we used a metronome to indicate the desired movement rates for the control participants.[1] The metronome consisted of a sequence of brief tones, presented at an interstimulus interval of 1,200 ms for the "comfortable" condition and 600 ms for the "faster" condition. These rates were chosen to reflect rates approximating those of the patients' performance. The metronome was played before a series of trials and was not presented during the actual movements. Participants were instructed to match the metronome speed and, whenever the experimenter noted a marked departure from the target rate, the metronome was played again before the following trial.

Procedure

The experimental conditions were performed in a fixed order, starting with what was anticipated to be the easiest conditions for the patients. All of the movement conditions were first tested at the comfortable rate and then at the faster rate. Within each movement rate, the tasks were presented in the following order: *1*) symmetrical trials followed by asymmetrical trials with full vision; *2*) symmetrical trials followed by asymmetrical trials with partial vision; and *3*) symmetrical trials followed by asymmetrical trials with no vision. Four trials of each type were recorded in succession, with the exception that six trials were obtained for the partial-vision (bimanual) condition for Patient 1 and the control participants. Patient 1 was unable to perform the no-vision condition at the faster rate.

Recording

Trajectories were recorded with the ELITE system (Ferrigno and Pedotti 1985) in the Marseille laboratory and with a miniBird magnetic tracking system (Ascension, Burlington, VT) in the Berkeley laboratory. Markers were affixed on the nail of each index finger and position in three-dimensional (x, y, z) space was sampled at 100 Hz (ELITE system) or 138 Hz (miniBird). The duration of the recording period for each trial was 15 s. The experimenter manually started the recording after two or three cycles of movement had been completed.

Data analysis

The trajectories were reconstructed off-line. Local maxima and minima for the x- and y-dimensions were determined. These were defined by the principal axes of the table surface, with x and y referring respectively to the surfaces parallel and perpendicular to the body axis. These events were used for calculating the primary dependent variables.

Unless otherwise noted, performance differences for patients relative to controls was compared with two (one for Patient 1; one for Patient 2) ANOVAs. For Patient 1 relative to controls, this was a three-way [group (Patient vs. Controls) $\times$ visual condition (full vs. partial-right vs. no) $\times$ coordination mode (symmetric vs. asymmetric)] ANOVA. For Patient 2 relative to controls, the ANOVA had the additional factor of rate (comfortable vs. faster). Comparisons of the performance of Patient 2 in the partial-vision conditions were performed with a three-way [vision (partial-right vs. partial-left) $\times$ coordination mode $\times$ rate] ANOVA.

[1] Control participants also performed the tasks with the instructed rate to move "as fast as possible." However, we report only the rate conditions that matched that of the patients.

RESULTS

Noticeable degradation of the trajectories and increased variability are evident for both symmetric (Fig. 2*A*) and asymmetric (Fig. 2*B*) coordination modes in the absence of vision (gray lines). Of central interest was the contribution of sensory afferents to coordination in this bimanual circling task. We report measures of both temporal and spatial coordination.

Temporal coordination

A cycle was defined as the interval between successive maxima in the y-dimension. Mean cycle duration was calculated for each participant and condition. These values are presented in Table 1.

If the two hands are temporally coupled, the difference in cycle duration for the two limbs should be small on a trial-by-trial basis. The difference in cycle duration was calculated for each trial and the means of the absolute value of these difference scores are plotted in Fig. 3. To statistically analyze the data, we opted to perform two sets of ANOVAs, one comparing Patient 1 to the controls and a second comparing Patient 2 to the controls. This strategy was chosen given the different degree and etiology of the pathology for the two patients. Below, we distinguish between the two analyses as Patient 1 ANOVA and Patient 2 ANOVA.

First, consider the effects of the task variables on temporal coupling. There was a significant increase in the difference between cycle duration for the two hands as rate increased [main effect of rate $F(1,156) = 16.6$, $P < 0.001$ for the Patient 1 ANOVA; $F(1,214) = 17.3$, $P < 0.001$ for the Patient 2 ANOVA]. There was also a main effect of mode, with the difference scores larger in the asymmetric mode [$F(1,156) = 16.9$, $P < 0.001$ and $F(1,214) = 14,7$, $P < 0.001$ for Patient 1 and Patient 2 ANOVAs, respectively]. Moreover, the mode $\times$ rate interaction was significant in the ANOVAs with Patient 1 [$F(1,156) = 14.8$, $P < 0.001$] and Patient 2 [$F(1,214) = 15.1$, $P < 0.001$].

Of primary interest is whether the patients differed from the controls in terms of temporal coupling. Compared with controls, Patient 1 exhibited a similar mean difference in cycle duration [$F(1,156) < 1$], regardless of the visual condition [group $\times$ visual condition (full and partial only) interaction, $F(1,156) < 1$], coordination mode [group $\times$ coordination mode interaction $F(1,156) < 1$], or rate [group $\times$ rate interaction $F(1,156) = 1.17$, $P = 0.28$]. Likewise, Patient 2 performed similar to controls [$F(1,214) < 1$] regardless of the visual condition [$F(2,214) < 1$], coordination mode [$F(1,214) = 3.13$, $P = 0.08$], or rate [$F(1,214) = 1.33$, $P = 0.25$]. Thus in terms of the difference in cycle duration measure, both patients showed similar temporal coupling to that observed in the control participants.

A within-subject comparison is also possible for Patient 2 given that he performed the partial vision condition twice—with vision limited to the right deafferented limb (partial right) or with vision limited to the left, unimpaired limb (partial left). If sensory information is necessary for temporal coupling of the hands, the temporal difference would be greater for the

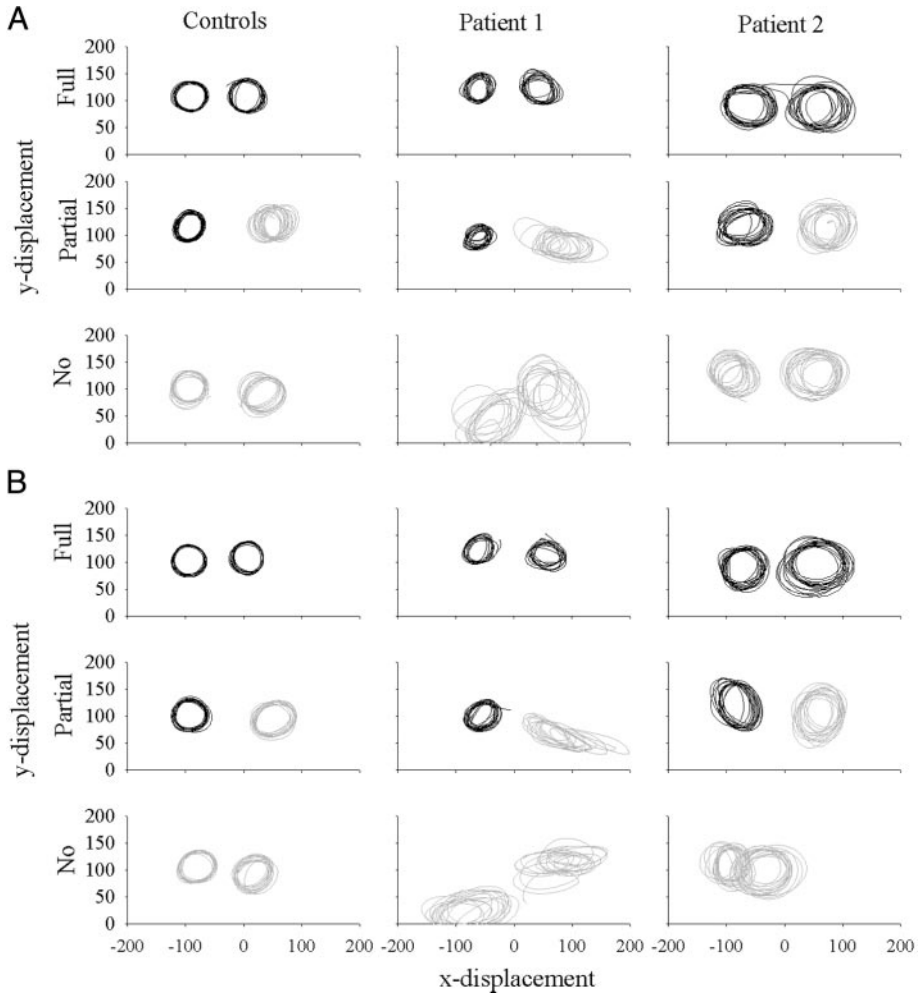

FIG. 2. Exemplar trajectories from the (*A*) symmetric and (*B*) asymmetric conditions, performed at a comfortable rate. Gray lines represent trajectories produced without vision of that limb.

partial left condition because visual and somatosensory information from the right arm would be absent in the partial right condition. Consistent with the between-group comparisons, this was not the case. The main effect of vision condition (partial right vs. partial left) was not significant [$F(1,31) < 1$].

In sum, the patients exhibited temporal coupling similar to the controls regardless of the visual conditions.

Phase coordination

A second way to assess coupling is to measure the relative phase of the two hands. A point sample of relative phase was calculated using the right hand at the maxima in the *y*-dimension on each cycle as the reference point. This measure ignores variation in rate across cycles, focusing instead on the relative position of the two hands when the right hand is farthest from the body. A score of 0° indicates the hands are moving in a synchronous fashion in the *y*-dimension regardless of coordination mode.

The distribution of relative phase values and their variability are presented in Fig. 4. These distributions (shaded area) indicate tight coupling between the limbs with the dominant limb consistently leading the nondominant limb by approximately 5–30° in the symmetric conditions and 0–60° in the

TABLE 1. *Average cycle duration (in ms) for all participants*

	Controls		Patient 1		Patient 2	
	Left	Right	Left	Right	Left	Right
			Symmetric mode			
Comfortable rate						
Full vision	1,246	1,245	1,392	1,395	1,069	1,055
Partial R	943	942	942	943	1,009	995
Partial L					993	990
No vision	1,146	1,146	1,101	1,107	967	966
Full vision	630	629	644	640	723	704
Partial R	588	588	722	722	733	724
Partial L					690	689
No vision	631	630			629	625
			Asymmetric mode			
Faster rate						
Full vision	1,293	1,291	1,450	1,453	1,090	1,092
Partial R	1,039	1,038	1,013	1,003	1,067	1,065
Partial L					1,028	1,022
No vision	1,120	1,117	1,023	1,020	960	960
Full vision	679	586	735	647	792	754
Partial R	678	581	735	686	734	702
Partial L					737	675
No vision	662	605			738	652

Shaded cells indicate conditions in which vision of the specified limb was occluded.

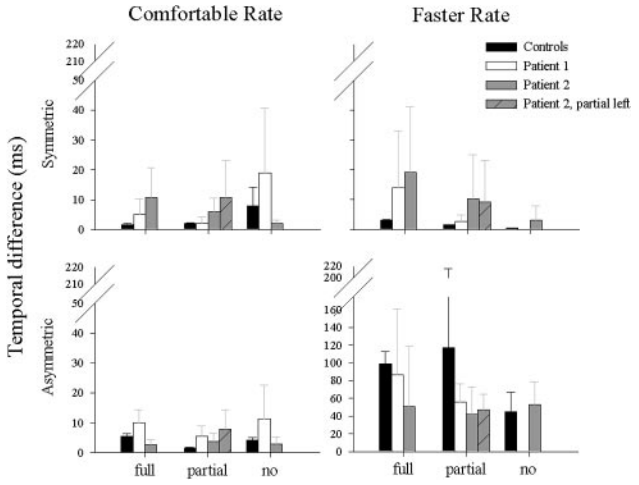

FIG. 3. Average of the absolute difference between left-hand cycle duration and right-hand cycle duration during bimanual circle drawing, as a function of vision, movement, and coordination mode. Gray error bars (on patient data) represent SD across trials. Black error bars (on the control data) represent the SE across subjects. Hatched bars are for performance of Patient 2 in the partial vision condition when the right hand was occluded.

asymmetric conditions. Relative phase varied with rate [Patient 1 ANOVA: $F(1,156) = 10.4$, $P < 0.001$; Patient 2 ANOVA: $F(1,214) = 88.4$, $P < 0.001$] and was greater when vision was obstructed [Patient 1: $F(1,156) = 3.2$, $P = 0.07$; Patient 2: $F(2,214) = 5.7$, $P < 0.001$].

As with the rate difference measure, the patients performed similar to the controls. The results are especially clear for Patient 1 where there was no effect of group [$F(1,156) = 2.7$, $P = 0.11$], nor did the group factor interact with any of the other variables. For Patient 2, the main effect of group was reliable [$F(1,214) = 58.7$, $P < 0.001$] and this factor interacted with coordination mode [$F(1,214) = 23.9$, $P < 0.001$]. When moving symmetrically, Patient 2 had a greater phase lead of the right hand (mean lead of 42°) than the controls (mean lead of 8°). Interestingly, this patient performed similar to controls in the asymmetric mode (mean for Patient 2: 7° phase advance of the right hand from the target phase; mean for controls: 2° phase advance of the right hand from the target phase).

Relative phase variability is reflected in the length of each arrow in Fig. 4 with shorter arrows indicating greater variability. Relative phase variability was influenced by rate [Patient 1 ANOVA: $F(1,156) = 157.1$, $P < 0.001$; Patient 2 ANOVA: $F(1,214) = 124.5$, $P < 0.001$], availability of vision [Patient 1: $F(1,156) = 3.8$, $P = 0.054$; Patient 2: $F(1,214) = 6.6$, $P = 0.002$], and coordination mode [Patient 1: $F(1,156) = 166.5$, $P < 0.001$; Patient 2: $F(1,214) = 107.9$, $P < 0.001$]. Consistent with previous studies, relative phase variability was similar for the symmetric conditions at both rates. However, there was an increase in variability (i.e., reduced stability) during asymmetric circling at the fast rate (Byblow et al. 1999; Carson et al. 1997; Semjen et al. 1995). The mode × rate interaction was significant in both ANOVAs [Patient 1: $F(1,154) = 128.3$, $P < 0.001$; for Patient 2: $F(1,214) = 78.2$, $P < 0.001$].

Variability in the relative phase was greater for both patients relative to controls [Patient 1: $F(1,156) = 34.9$, $P < 0.001$; Patient 2: $F(1,214) = 4.9$, $P = 0.03$]. This difference was not modulated by the availability of vision [group × vision interaction, Patient 1: $F(2,211) = 1.9$, $P = 0.14$; Patient 2: $F(2,214) < 1$]. For Patient 1, the group × coordination mode interaction was not significant [$F(1,211) < 1$]. However, this interaction was significant for Patient 2 [$F(1,214) = 13.9$, $P < 0.001$] and further modulated by rate, as indicated in a significant three-way interaction of group × mode × rate [$F(1,214) = 5.3$, $P = 0.02$]. Compared with controls, Patient 2 exhibited increased

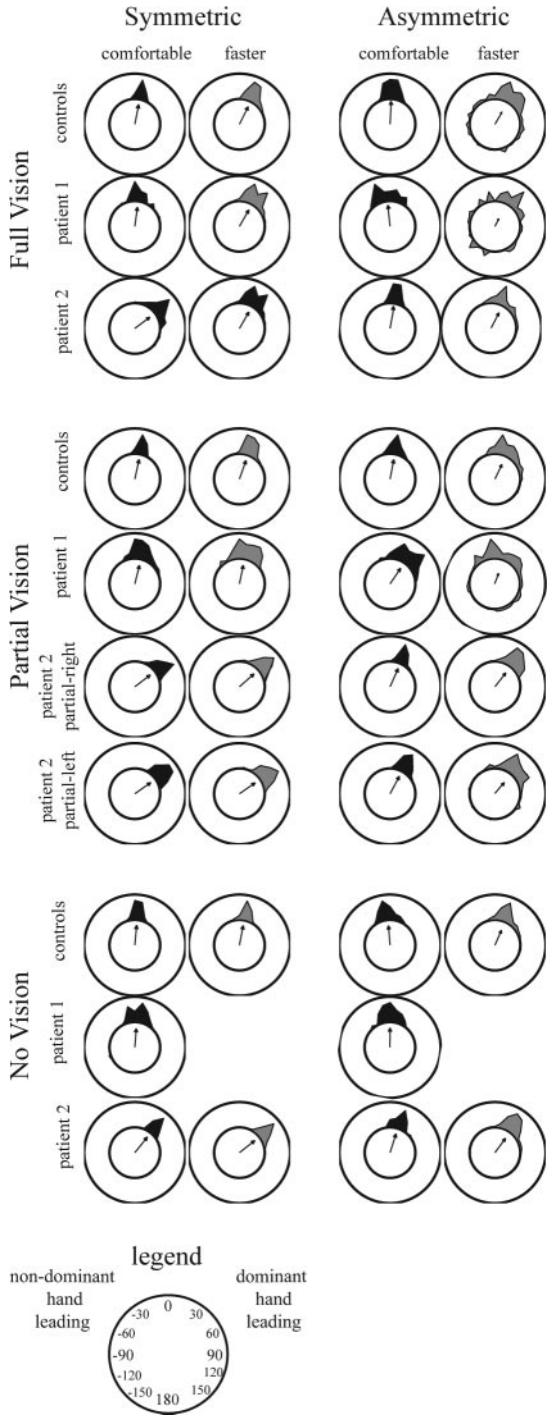

FIG. 4. Relative phase plots. Arrows points to the mean relative phase (see legend), whereas the length of the arrows indicates variability [shorter arrow = higher variability; see Kennerley et al. (2002)]. Relative phase is calculated using a point sample relative to the maximum displacement of the right hand in the *y*-dimension. For both the symmetric and asymmetric coordination modes, the 2 hands should cross this point simultaneously.

TABLE 2. *Average y-amplitude (in mm) for all participants*

	Controls		Patient 1		Patient 2	
	Left	Right	Left	Right	Left	Right
			Symmetric mode			
Comfortable rate						
Full vision	46.8	46.7	69.1	68.8	53.1	54.9
Partial R	47.3	47.1	47.3	47.2	50.9	51.3
Partial L					49.5	50.2
No vision	54.6	52.7	54.3	54.9	48.2	49.2
Full vision	31.6	31.5	32.9	32.0	35.2	36.2
Partial R	29.4	29.4	36.4	36.5	36.1	36.8
Partial L					35.8	34.5
No vision	35.1	35.2			31.4	31.7
			Asymmetric mode			
Faster rate						
Full vision	64.6	65.1	73.4	75.0	54.0	54.9
Partial R	49.7	49.6	51.0	50.5	51.9	52.4
Partial L					50.6	51.2
No vision	50.8	50.7	50.2	51.4	48.2	48.1
Full vision	34.2	29.5	36.8	32.2	38.2	40.2
Partial R	35.6	29.1	36.9	34.5	35.3	35.9
Partial L					35.7	37.2
No vision	36.1	33.8			33.9	37.0

Shaded cells indicate conditions in which vision of the specified limb was occluded.

relative phase variability when circling fast in the asymmetric mode. Thus his loss of stability for this most demanding condition was more marked than that observed in the controls. Patient 2 also exhibited greater relative phase variability in the partial-left condition (impaired hand obscured) compared with the partial-right condition [$F(1,31) = 6.09$, $P = 0.02$]. As indicated by the significant vision (partial-right vs. partial-left) $\times$ rate (comfortable vs. faster) interaction [$F(1,31) = 8.5$, $P = 0.008$], this difference was greatest at the fast rate.

Thus although the relative phase distributions were similar to the controls, the patients did show an increase in relative phase variability, indicating that they were less consistent than the controls regardless of visual conditions.

Spatial coordination

Movement amplitude was defined as the distance between successive maxima and minima in the *y*-dimension with the target amplitude being 50 mm, the diameter of the template circles. The mean amplitude values for each condition are presented in Table 2. In general, the participants approximated the template size in the comfortable rate conditions (see Fig. 2). When moving at the faster rate, the circles were consistently compressed for both patients and controls [Patient 1 ANOVA: $F(1,156) = 482.4$, $P < 0.001$; Patient 2 ANOVA: $F(1,214) = 460.1$, $P < 0.001$]. Amplitude was further modulated by the availability of vision [Patient 1: $F(1,156) = 56.4$, $P < 0.001$; Patient 2: $F(2,214) = 9.0$, $P < 0.001$] and rate [Patient 1: $F(1,156) = 482.4$, $P < 0.001$; Patient 2: $F(1,214) = 456.2$, $P < 0.001$]. One noticeable deviation from the goal amplitude for controls and Patient 1 occurred when moving in the asymmetric mode at the comfortable rate with full vision (see Table 2); however, the mode $\times$ rate $\times$ vision interaction was not significant [Patient 1: $F(1,156) < 1$; Patient 2: $F(2,214) < 1$].

Turning to the comparison of the patients and controls, the main effect of group was significant for Patient 1 [($F(1,156) = 10.1$, $P = 0.002$] but not for Patient 2 [$F(1,214) = 0.1$, $P = 0.76$]. The only factors interacting with group were observed with Patient 2: there was a reliable group $\times$ vision interaction [$F(2,214) = 5.5$, $P < 0.005$] and a significant interaction of group $\times$ rate [$F(1,214) = 23.6$, $P < 0.001$]. Although these interactions were not significant for Patient 1, as noted above, this patient was unable to perform the no-vision condition at the fast rate.

To test the degree of amplitude coupling, the absolute difference in amplitude between hands was calculated on a cycle-by-cycle basis, with the values for a given trial then averaged together (Fig. 5*A*). As with the mean amplitude, the amplitude difference was modulated by coordination mode [Patient 1 ANOVA: $F(1,156) = 17.3$, $P < 0.001$; Patient 2 ANOVA: $F(1,214) = 11.9$, $P < 0.001$]. The main effect of vision approached significance in each ANOVA [Patient 1: $F(1,156) = 2.7$, $P = 0.10$; Patient 2: $F(2,214) = 2.5$, $P = 0.08$].

In terms of the amplitude difference measure, there was a significant main effect of group for Patient 1 [$F(1,156) = 16.9$, $P < 0.001$] and Patient 2 [$F(1,214) = 22.6$, $P < 0.001$]. Thus overall, the patients produced circles of unequal amplitude to a greater degree than the control participants. The group $\times$

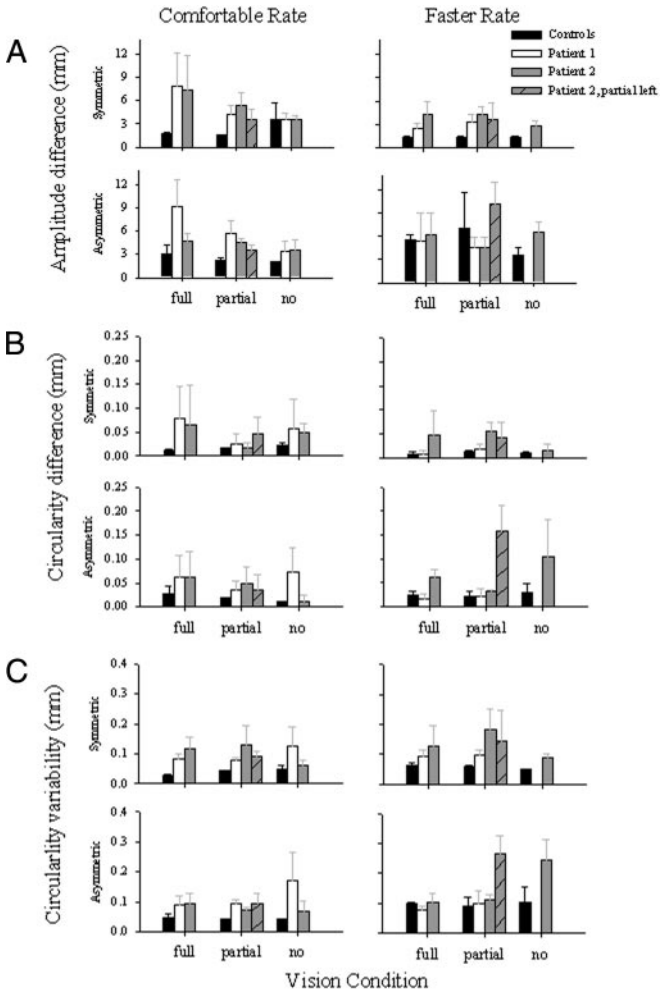

FIG. 5. Amplitude difference (*A*) and circularity difference (*B*) across limbs for each task. *C*: variability (averaged across limbs) of the circularity difference.

vision interaction approached significance for Patient 1 [$F(1,156) = 2.9$, $P = 0.09$] but not for Patient 2 [$F(2,214) < 1$]. Notably, the biggest differences were observed for the full-vision condition. In the within-subject comparison for Patient 2, there was a significant three-way interaction of vision (partial-right vs. partial-left) × mode × rate. In the asymmetric, faster condition, the mean amplitude difference was 0.6 mm when the patient could see his deafferented right arm compared with a mean difference of 1.5 mm when vision of this limb was occluded.

To assess whether each hand produced circles, the within-hand ratio of the *x*-amplitude relative to the *y*-amplitude was computed on a cycle-by-cycle basis. If the trajectory was circular, this value = 1; a value <1 corresponds to an elliptical trajectory with the long axis along the vertical dimension; a value >1 corresponds to an elliptical trajectory with the long axis along the horizontal dimension. As shown in Table 3, the ratio was close to 1 for all participants in all of the conditions.

We next used the circularity measure as a tool to compare the shapes produced by the two limbs. For this analysis, we calculated the absolute circularity difference on each trial. Note that normal individuals have difficulty producing trajectories of mismatching circularity (e.g., a line or ellipse with one hand and a circle with the other; Franz et al. 1991; Walter et al. 2001, 2002). Consistent with this, the mean circularity difference scores were very small for the controls, averaging <0.03 (Fig. 5*B*). However, the circularity difference was dependent on the visual condition [Patient 1 ANOVA: $F(1,156) = 4.2$, $P = 0.04$; Patient 2 ANOVA: $F(2,214) = 4.8$, $P = 0.001$] and movement rate [Patient 1: $F(1,156) = 16.0$, $P < 0.001$; Patient 2: $F(1,214) = 4.1$, $P = 0.04$]. The effect of mode was not significant for Patient 1 [$F(1,156) = 1.7$, $P = 0.19$], although this is likely explained by the fact that this ANOVA does not include the faster circling without vision, and Patient 2 and the controls showed relatively large scores for this condition when circling asymmetrically. Indeed, mode was significant in the ANOVA for Patient 2 [$F(1,214) = 9.2$, $P = 0.003$] and when interacted with rate [$F(1,214) = 10.5$, $P = 0.001$].

TABLE 3. *Average spatial ratio (x-amplitude:y-amplitude) for all participants*

	Controls		Patient 1		Patient 2	
	Left	Right	Left	Right	Left	Right
			Symmetric mode			
Comfortable rate						
Full vision	1.01	1.01	1.03	1.03	1.05	1.00
Partial R	1.00	1.00	1.00	1.01	1.01	1.01
Partial L					1.21	1.01
No vision	1.00	1.00	1.06	1.04	1.01	0.98
Full vision	1.01	1.00	1.00	1.01	1.01	1.00
Partial R	1.01	1.00	1.01	1.01	1.02	1.04
Partial L					0.97	1.01
No vision	1.00	0.99			1.00	0.99
			Asymmetric mode			
Faster rate						
Full vision	0.99	0.99	0.99	0.99	1.02	0.97
Partial R	0.99	1.00	0.99	1.01	1.01	1.00
Partial L					0.97	0.98
No vision	1.00	0.99	0.99	0.97	0.98	0.99
Full vision	1.02	1.00	1.01	1.01	1.10	1.04
Partial R	1.01	1.01	1.00	1.00	1.02	1.00
Partial L					1.07	1.08
No vision	1.02	1.02			1.07	1.01

Shaded cells indicate conditions in which vision of the specified limb was occluded.

The main effect of group was significant for both Patient 1 [$F(1,156) = 11.0$, $P = 0.001$] and Patient 2 [$F(1,214) = 38.6$, $P < 0.001$], indicative of greater spatial uncoupling for the deafferented patients. Moreover, the group × rate interaction was significant for Patient 1 [$F(1,156) = 12.0$, $P < 0.001$] and approached significance for Patient 2 [$F(1,214) = 3.6$, $P = 0.06$]. The group × vision interaction was significant for Patient 2 [$F(1,214) = 7.3$, $P = 0.008$]. Consistent with this, in the within-subject comparison, there was a significant three-way interaction [$F(1,30) = 15.76$, $P = 0.006$]. The amplitude ratio difference was greatest for the condition in which the patient performed asymmetric movements at the faster rate when vision of the deafferented limb was precluded.

Within-hand spatial variability was measured as the variability in the circularity measure (Fig. 5*C*). Overall, variability increased with rate [Patient 1 ANOVA: $F(1,156) = 12.3$, $P < 0.001$; Patient 2 ANOVA: $F(2,214) = 15.0$, $P < 0.001$]. Compared with controls, the patients were more variable in producing circles [Patient 1: $F(1,156) = 25.7$, $P < 0.001$; Patient 2: $F(1,214) = 36.9$, $P < 0.001$]. This increase in variability was relatively consistent across the conditions, as indicated by the lack of significant two-way and higher-order interactions. One exception was that the group × vision interaction was significant for Patient 2 [$F(2,214) = 3.7$, $P = 0.03$]. Surprisingly, Patient 2 was more consistent in the no-vision condition except when circling at the faster rate in the asymmetric condition [group × vision × mode × rate interaction; $F(2,214) = 4.2$, $P = 0.02$].

A noticeable feature of the patient performance depicted in Fig. 2 is the drift in the location of the circle. To quantify this, the center of the circle was located on a cycle-by-cycle basis. The measure of spatial drift was the average distance between the centers of successive circles. These values are depicted in Fig. 6. Drift was significantly greater for the patients relative to controls, as indicated by a main effect of group for the ANOVA (with the hand as an additional variable) for Patient 1 relative to controls [$F(1,283) = 15.6$, $P < 0.001$] and for Patient 2 relative to controls [$F(1,384) = 240.1$, $P < 0.001$]. Likewise, there was a significant main effect of vision condition [Patient 1 and controls: $F(1,283) = 11.7$, $P < 0.001$; Patient 2 and controls: $F(2,384) = 9.3$, $P < 0.001$]. The group × vision interaction was significant for Patient 2 relative to controls [$F(2,384) = 4.7$, $P = 0.01$] but not for Patient 1 relative to controls [$F(1,283) = 1.8$, $P = 0.18$]. Interestingly, for Patient 2 relative to controls, the three-way interaction of group × vision × hand was near significance [$F(2,384) = 3.5$, $P = 0.06$]. Patient 2 tended to exhibit asymmetric drift in the partial vision conditions.

The ANOVA comparing the performance of Patient 2 in the partial left and partial right conditions revealed a near-significant main effect of vision [$F(1,48) = 3.7$, $P = 0.06$]. The main effects of coordination mode, rate, and hand were not significant [mode: $F(1,48) = 1.5$, $P = 0.23$; rate: $F(1,48) = 2.8$, $P = 0.1$; hand: $F(1,48) < 1$]. Of interest is the interaction between hand and vision condition (partial left vs. partial right). It would be expected that drift should be greatest for the unseen hand (right hand in partial left; left hand in partial right). This interaction was near significance [$F(1,48) = 3.4$, $P = 0.07$].

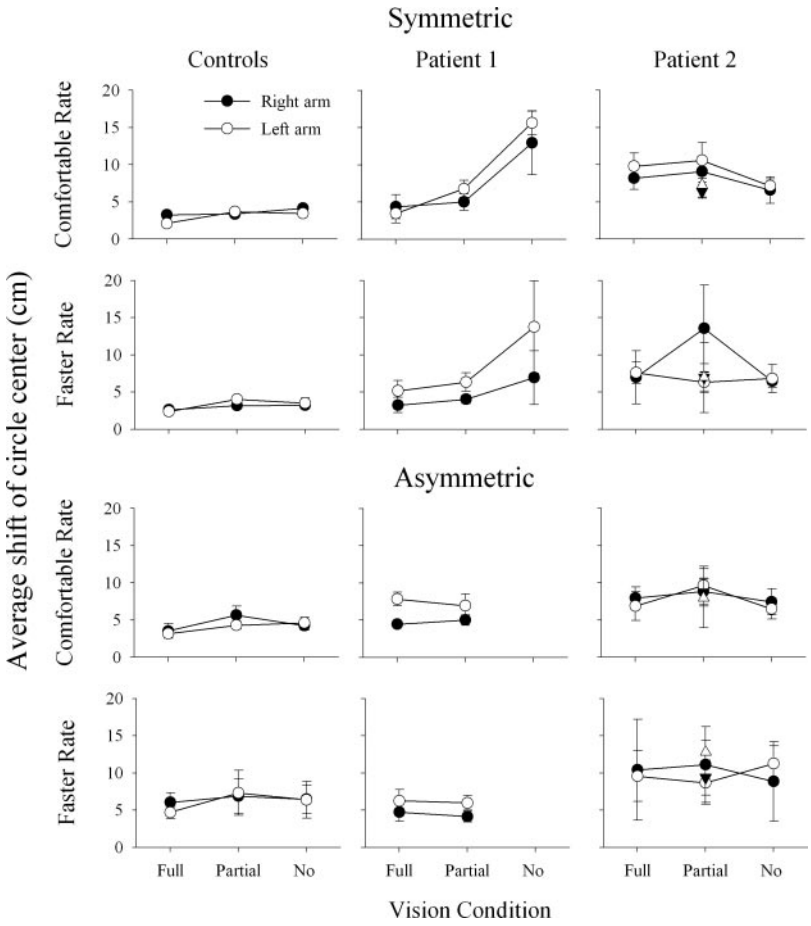

FIG. 6. Average cycle-by-cycle drift in the location of the center of the circle across groups and conditions.

To summarize, these spatial measures indicate that the patients generally exhibited less spatial coupling than the control participants. The patients produced circles that were more unequal in amplitude than the controls. Moreover, the amplitude ratio difference scores suggest that this lack of symmetry in shape was not just a scaling problem: for both patients, the two shapes were less likely to be of similar circularity. These effects can be seen in Fig. 2. With full vision, Patient 2 produced circles of different amplitude in the asymmetric condition; with partial vision, the right-hand movement for Patient 1 is more elliptic than the left-hand movement.

DISCUSSION

We tested two individuals with severe somatosensory impairments on a bimanual circle-drawing task. Although there were some subtle differences between the patients and controls, the most striking feature of the results is the absence of serious impairment in either patient. The relative sparing of bimanual coordination was observed in the patient with unilateral sensory loss as well as the individual who is functionally deafferented in both limbs. Moreover, precluding visual information did not produce marked changes in performance. These results suggest that, in large part, the coordination of bimanual movements reflects the operation of descending control signals that can operate in an open-loop manner.

Previous studies involving deafferented patients, some of which included Patient 1, have led to similar conclusions. For example, Rothwell et al. (1982), in their seminal study, demonstrated that a deafferented patient similar to Patient 1 was able to produce complex unimanual trajectories, such as those shown in Fig. 8, or continuous circles, even when vision was precluded. Subsequent work has shown that reaching (Sanes et al. 1985) and pointing (Bard et al. 1999) errors are scarcely different in deafferented patients than in controls. It is important to note that this work does not suggest that afferent information is irrelevant. Without feedback, errors accumulate over time (Rothwell et al. 1982) and learning is likely to be limited. Moreover, as evident in our study, the movements are more variable spatially (e.g., Jackson et al. 2000; Noigier et al. 1996). Nonetheless, the current study adds to these previous studies in showing the prominent features of bimanual coordination are present in the absence of somatosensory and visual information.

The patients adopted a common frequency for the two hands during the bimanual circling task, similar to the control participants and previous reports (Byblow et al. 1999; Carson et al. 1997; Semjen et al. 1995). Moreover, the degree of temporal coupling was stronger during symmetric movements than that during asymmetric movements. The preserved temporal coordination in patients with severe somatosensory impairment stands in contrast to that observed in callosotomy patients. The latter exhibited frequency unlocking (thus phase wrapping; see Batchelet 1981; Haken 1983) between the hands during circle drawing, with little evidence of any difference in performance between the symmetric and asymmetric conditions (Kennerley et al. 2002). Taken together, these patient studies suggest that

temporal coupling during bimanual circle drawing requires the interhemispheric integration of control signals across the corpus callosum. These signals, however, do not appear to involve the comparison of feedback signals from the ongoing movements.

What might be the nature of these control signals? One possibility is that during bimanual circling movements, a common angular velocity (or stiffness) is specified for the movements of the two hands. This form of control has been proposed for tasks involving continuous movements, distinct from the manner in which regularities in timing are achieved for repetitive movements that involve discontinuities (Ivry et al. 2002). Although bimanual coordination by the specification of a target angular velocity could be achieved if efferent commands originated in a common hemisphere (see Cattaert et al. 1999; Ivry and Richardson 2002; Stucchi and Viviani 1993), the temporal uncoupling observed in split-brain patients suggests that each hemisphere is capable of controlling the contralateral limb. Temporal coordination would, as such, require the transcallosal coordination and integration of these commands.

A recent study by Drewing et al. (2004) is also consistent with the idea that temporal coordination does not require somatosensory information. As in the current study, the two movements were strongly coupled. Moreover, within-hand variability was reduced during bimanual tapping, compared with unimanual tapping. This result is predicted by an open-loop model in which independent timing signals are generated for each hand and then integrated as a means of achieving temporal synchronization (Helmuth and Ivry 1996; Ivry and Richardson 2002). Even though there are reasons to believe the control processes are distinct for discrete, tappinglike movements and continuous movements (Spencer et al. 2003), the results of the current study and Drewing et al. (2004) emphasize the relatively minor role for somatosensory information in temporal coordination.

In terms of spatial coupling, we did observe some differences between the performance of the patients and the control participants. First, the patients tended to produce movements of unequal amplitudes to a greater degree than the controls. Second, there was a greater difference in the degree of circularity for the movements of the two limbs. Moreover, the patients were more variable on this latter measure across cycles. These results suggest that the integration of somatosensory signals from the two hands might be important for fine-tuning and maintaining the movement trajectories. In this view, the integration of descending commands to the two limbs can suffice to sustain the basic temporal pattern on a cyclical basis. For example, the control signal might indicate, at least implicitly, the transition from extension to flexion. Spatial uncoupling could result from the accumulation of error in the execution of these descending commands. Such errors could be manifest as a deformation of the trajectories or drift in the workspace.

When neurologically healthy individuals draw circles unimanually in the absence of vision, the circles become smaller and their amplitude more variable (Zelaznik and Lantero 1996). Likewise, during bimanual circle drawing, the circles become smaller and relative phase variability increases (see also Carson et al. 2005; Swinnen et al. 1996). This is consistent with the differences we observed between the visual conditions. In the absence of somatosensory information, the role of vision might be enhanced. However, whereas phase and amplitude coupling were more variable in the patients, we failed to find a group $\times$ vision interaction. Notably, the within-subject comparisons for performance of Patient 2 were significant, indicating that vision can adjust the phase and amplitude of the movements.

In previous reports of Patient 1, in the absence of vision, trajectories maintained the approximate required shape, although the size and location varied (Teasdale et al. 1993, 1994). Similarly, precluding vision during tapping in another deafferented patient led to an increase in movement amplitude and force, whereas the rhythm was unaffected (Billon et al. 1996). Vision has also been shown to enhance the performance of deafferented patients in unimanual arm movements (Noigier et al. 1996; Sainberg et al. 1993) and bimanual reaching and grasping tasks (Ghez et al. 1995; Simoneau et al. 1999). Although vision aids performance in these tasks, it does not always improve it to the extent of unimpaired performance (Ghez and Sainberg 1995; Noigier et al. 1996; Teasdale et al. 1994).

Taken together, observations of the role of vision in the performance of deafferented patients has led to the idea that somatosensory information may be essential for the spatial scaling of a kinematic goal or template (i.e., the circular trajectory in the current study) and the on-line compensation of directional and metric errors (drift) that occur during movement execution (Bard et al. 1995; Teasdale et al. 1993). Consistent with this idea, proprioceptive cues can mediate the perception of movement trajectories (Roll and Gilhodes 1995). In blindfolded participants, muscle vibration during bimanual circle drawing produces a spatial drift of the vibrated arm, thus altering the movement diameter and producing a shift in mean relative phase and increase in phase variability (Verschueren and Swinnen 2001; Verschueren et al. 1999a,b). The present results are consistent with these findings in healthy individuals because we observed increased spatial drift and amplitude variability in two deafferented patients. Proprioceptive feedback, and perhaps somatosensation in general, may be essential for fine-tuning the shape of the movement trajectory and maintaining position in extrinsic space.

What remains unclear is whether these adjustments are restricted to each hand or whether these signals are used to make adjustments to maintain bimanual coordination. In the current study, the inability to use somatosensory information to adjust movement amplitude or circularity would produce an increase in the between-hand difference scores of these measures, even if such signals were not used to coordinate performance between the hands. Alternatively, feedback information might be used to initiate corrective processes when the spatial and/or temporal differences between the hands exceeds some critical value (Verschueren and Swinnen 2001).

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