

The coordination of bimanual prehension movements in a centrally deafferented patient

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Summary

Many everyday tasks require that we use our hands cooperatively, for example, when unscrewing a jar. For tasks where both hands are required to perform the same action, a common motor programme can be used. However, where each hand needs to perform a different action, some degree of independent control of each hand is required. We examined the coordination of bimanual movement kinematics in a female patient recovering from a cerebrovascular accident involving anterior regions of the parietal lobe of the right hemisphere, which resulted

in a dense hemianaesthesia of her left arm. Our results indicate that unimanual movements executed by our patient using her non-sensate hand are relatively unimpaired. In contrast, during bimanual movements, reaches executed by our patient using her non-sensate hand show gross directional errors and spatiotemporal irregularities, including the inappropriate coupling of movement velocities. These data are discussed with reference to the role played by limb proprioception in the planning and control of prehension movements.

Keywords: bimanual movements; reach-to-grasp; deafferentation; hemianaesthesia; parietal cortex

Abbreviations: BA = Brodmann area; BIT = Behavioural Inattention Test; MD = movement duration; PGA = peak grip aperture; SI = primary somatosensory cortex; SII = secondary somatosensory cortex; TTPGA% = time taken to reach peak grip aperture expressed as a percentage of total movement time; TTPV = time taken to reach peak movement velocity; WAIS-R = Wechsler Adult Intelligence Scale—Revised

Introduction

Planning and execution of bimanual movements

When we execute a unimanual reaching movement to a target position, the duration of the movement is frequently found to depend on the ratio of movement amplitude to target size (a formula known as Fitts' Law). Movement duration (MD) is shorter when the distance is small and/or the target is large (sometimes referred to as having a low index-of-difficulty), compared with when the distance is longer and/or the target object is smaller (referred to as having a high index-of-difficulty). Bimanual movements in which both hands execute movements of the same index-of-difficulty also conform to this rule, while bimanual movements of mixed index-of-difficulty do not (Kelso *et al.*, 1979, 1983; Jackson *et al.*, 1999). During bimanual movements subjects tend naturally to synchronize their hands, even when they are not explicitly instructed to do so (Keele, 1986). As a consequence, MD as well as time to movement onset are often similar for both

hands. The hand reaching for the difficult target takes less time than it would when reaching to the same target under unimanual conditions, whereas the hand reaching to the easy target takes more time than it would for a unimanual reach. While it has been argued that there can be significant departures from synchrony when the limbs are moving to mixed difficulty targets (Marteniuk *et al.*, 1984), it should be noted that the absolute differences in movement onset times and MD between the limbs is usually small (~100 ms or less).

How might this degree of temporal synchronization be achieved? Two broad classes of explanation can be distinguished: one suggests that coordination of movement components is planned in advance of movement onset and based upon temporal synchronization (e.g. Jeannerod, 1981, 1984; Hoff and Arbib, 1993); the other proposes that coordination is achieved by the on-line control of movement

parameters based upon continuous sampling of spatial information (e.g. Bootsma and van Wieringen, 1992; Zaai *et al.*, 1999). While these models differ quite substantially in their account of how temporal synchronization is achieved, proprioceptive signals are likely to be critical for effective synchronization in either case. Recent findings from the visual attention literature demonstrate that individuals are limited in their ability to attend to more than one object at a time (Duncan, 1984). Duncan and colleagues propose that visual information related to different objects results in competition between those objects, which is characterized as a reduction in the efficient processing of each object (Duncan *et al.*, 1997). One obvious limiting factor during the execution of bimanual movements is the need to control and maintain the synchronicity of two actions unfolding in parallel. One possible role for proprioception in this case would be to allow bimanual movements to be executed without the need to allocate attentional resources.

Proprioception and the coordination of upper-limb movements

The sensorimotor system controlling upper-limb movements may use both visual and proprioceptive inputs to formulate motor commands. However, movement accuracy is maximized when both are available (Rossetti *et al.*, 1994, 1995). Visual information can serve to calibrate proprioceptive knowledge of initial limb position (Rossetti *et al.*, 1994, 1995) and to make on-line corrections to a kinaesthetically controlled hand path (Goodale *et al.*, 1986). Recent evidence also suggests that proprioceptive signals can function to update 'visual' representations of peripersonal space (Carey and Allan, 1996). It should be noted, however, that the precise role played by both visual and proprioceptive signals may vary with task demands such as the requirement for accuracy or the need for manipulation.

The role played by proprioception in limb movement control has previously been investigated by studying how movements are affected by the removal of proprioceptive signals. Studies of single joint movements have suggested that neither proprioceptive nor visual information is entirely necessary for movement initiation or for computing the final position of the limb. For example, deafferented monkeys can execute simple aimed movements with relative accuracy, even in the absence of vision (Polit and Bizzi, 1979). However, it should be noted that in this experiment the animals were highly trained and the terminal accuracy of the movements did not approach normal levels. Similar results have been obtained in human subjects with a peripheral deafferentation due to large-fibre sensory neuropathy—a condition which results in the degeneration of the large afferent fibres, causing severe impairment or loss of somatosensation but with intact motor function (e.g. Forget and Lamarre, 1987; Rothwell *et al.*, 1982; Sanes *et al.*, 1985; Nougier *et al.*, 1996). Like deafferented monkeys, such

patients are able to initiate and execute simple flexion-extension movements, without vision. However, even when vision is available, movement trajectories are often variable and end-point accuracy reduced. Furthermore, studies of deafferented patients suggest that proprioceptive information may be particularly important for controlling naturalistic movements involving multiple joints (Ghez and Sainburg, 1995).

Few studies to date have examined reach-to-grasp movements in deafferented patients. Gentilucci and colleagues tested a patient (M.B.) with a peripheral neuropathy affecting both hands and forearms, and for whom shoulder and elbow movements could be detected only at extreme ranges. Their results indicated that while M.B.'s movement trajectories showed increased variability, the kinematic parameters for the transport phase of her movements were largely normal, at least until peak deceleration was reached. Thus, the amplitude of her peak velocity values were equivalent to those of control subjects and occurred at an equivalent point during the movement. Furthermore, her peak velocity values were shown to be scaled for movement amplitude as was the case for control subjects. M.B.'s movement kinematics during the decelerative phase of the movement were, however, markedly different from those observed for the control subjects. She made frequent adjustments to her movements and the overall length of the deceleration phase of her movements was substantially increased. Grasp phase kinematics in this patient were also impaired. M.B.'s grip aperture was more variable than controls and she achieved maximum grip aperture later than control subjects. However, like the control subjects, M.B.'s grip aperture was scaled for object size (Gentilucci *et al.*, 1994). This finding is consistent with the distinction proposed by Paillard between morphokinetic and topokinetic movements, i.e. movements of a particular form which do not require spatial accuracy versus movements to a specific position which necessitate spatial accuracy of the deafferented limb. Only the latter appear to be impaired after peripheral deafferentation (Paillard *et al.*, 1991)

Jeannerod and colleagues also studied reach-to-grasp movements in a patient (R.S.) suffering from a sensory loss to the fingers and wrist of her right hand (Jeannerod *et al.*, 1984). Several factors, however, differentiate this patient from patient M.B. First, R.S.'s deafferentation was central in origin and arose as a result of a lesion to her left parietal cortex, involving the primary somatosensory cortex (SI), the secondary somatosensory cortex (SII), Brodmann area (BA) 5 and probably much of BA 40. Secondly, R.S. perceived somatosensory signals from her forearm and shoulder, and was able to detect accurately the direction of passive movements at the shoulder. Finally, R.S.'s somatosensory loss was restricted to her right side. Despite these differences, R.S.'s reach-to-grasp movements showed many similarities to those of M.B. For example, when reaching with her affected limb R.S. showed a prolonged deceleration phase to her movements. However, in contrast to M.B., the overall

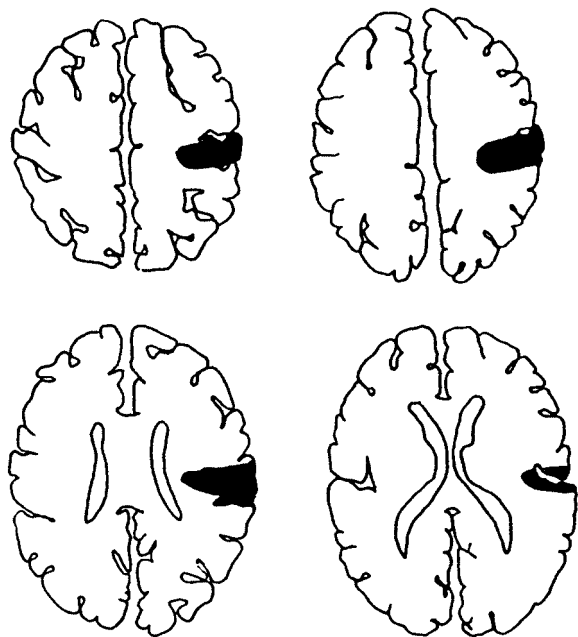


Fig. 1 Patient D.B.'s lesion reconstruction plotted on to standard templates. The angle and position of each cut relative to the inferior orbitomeatal line can be obtained by referring to Damasio and Damasio (Damasio and Damasio, 1989).

amplitude of R.S.'s movement velocities were lower than normal, even when vision of her hand was provided. Moreover, she was unable to form a precision grip. When vision of her hand was permitted, R.S. grasped the target object using a whole hand grip. Without vision, R.S. was inaccurate and missed the target object (her hand remained searching above the target).

The earlier work with non-human primates together with the few studies which have examined the execution of multi-joint arm movements in deafferented patients, suggest that proprioception is likely to play an important role in controlling naturalistic forms of hand action such as prehension. One form of naturalistic hand action where proprioception might be expected to be critical is bimanual movements in which it is required that separate effectors be synchronized (Haggard and Wing, 1991). In this paper we investigate the role of proprioception in the coordination of bimanual prehension movements by examining how such movements are affected in a patient suffering from a dense hemianaesthesia involving loss of sensation (including position and motion sense) throughout the upper arm, forearm and hand regions of her left arm, following a central lesion.

Subjects

Case study: patient D.B.

D.B. is a 72-year-old right-handed woman who, 3 months prior to testing, suffered a focal infarct of the right anterior parietal lobe. The lesion has been reconstructed from CT scans using standard templates (Damasio and Damasio, 1989) and is presented in Fig. 1. Prior to behavioural testing, D.B.

was examined neurologically and assessed on a number of standard neuropsychological tests. In addition, D.B.'s somatosensory and motor function was assessed using a range of behavioural tasks on several occasions prior to testing. The main findings from these standard examinations are summarized below.

General cognitive function

Verbal intelligence, language, reading, spelling and short-term memory were all normal. Specifically, in the National Adult Reading Test D.B. had a predicted verbal IQ of 117 and a predicted performance IQ of 115. Her performance in the short version of the Minnesota Test revealed no impairments. Her error scores were: serial item identification, 0/6; oral reading (words), 0/15; picture naming, 0/20; and written spelling, 0/20. In the Wechsler Adult Intelligence Scale—Revised (WAIS-R) D.B.'s scaled scores for the verbal tests were: information, 10/20; digit span, 8/20; and vocabulary, 12/20. These scores are all within 1 SD of the norm. D.B.'s visual perceptual functions were also normal to a large extent. She exhibited moderate impairment in WAIS-R tasks involving judgements of the spatial relationship between items. Her scaled scores for the WAIS-R performance tests were: picture completion, 6/20; block design, 6/20; and object assembly, 6/20. These scores are all 1 SD or more below the norm.

The existence of spatial attentional impairments was assessed using the Behavioural Inattention Test (BIT) which confirmed that D.B. did not show any evidence of a contralesional hemispatial inattention deficit. In specific subtests of the BIT, patient D.B. scored as follows (items correct): line cancellation, left 18/18, right 18/18; letter cancellation, left 16/20, right 17/20; star cancellation, left 27/27, right 23/27; line bisection, 9/9; and figure/shape copying, 4/4. We also explicitly tested D.B. for visual extinction and for distortions of her representation of objects using a version of the size-judgement task reported by Milner and Harvey (Milner and Harvey, 1995). In this task two stimuli (i.e. horizontal bars, vertical bars, circles or random shapes) were presented simultaneously on a computer monitor and remained on the screen until a response was recorded. D.B. was required to detect which of the two stimuli was smaller or larger than the other. In one-third of trials the right-hand stimulus was smaller, while in a further third of trials the left-hand stimulus was smaller. In the remaining trials the stimuli were of equal size. D.B.'s error scores for this task were as follows: left stimulus, 0/20; right stimulus, 1/20. In trials where the two stimuli were the same size, D.B. chose the left stimulus on eight out of 24 occasions (note that she was not permitted to report that they were the same size and was instructed to guess if they appeared to be of similar size). These data confirm that D.B.'s size judgements were normal in both her ipsilesional and contralesional visual fields, and importantly, that she does not exhibit any evidence of visual extinction.

Table 1 Summary of patient D.B.'s somatosensory and motor assessments

Task	Right arm	Left arm
Somatosensation (eyes closed)		
Pain detection	+	-
Hot/cold discrimination	+	-
Somatosensory discrimination		
Fingertip	+	-
Hand	87.5%	-
Forearm	87.5%	-
Somatosensory localisation		
Contralateral hand	-	-
Contralateral shoulder	+	-
Contralateral knee	+	-
Nose	+	-
Tactile object identification		
Mug	+	-
Toothbrush	+	-
Door key	+	-
Fork	+	-
Proprioception (eyes closed)		
Joint motion discrimination		
Forefinger	+	-
Wrist	+	-
Elbow	+	-
Copy limb posture (eyes closed) [‡]	+	-*
Motor function		
Copy gestures (eyes open)		
Meaningful	+	+?
Abstract	+	+?
Pantomime common actions (eyes open)		
Comb hair	+	+
Wash face	+	+
Brush teeth	+	+
Answer telephone	+	+
Open door with key	+	-
Use a hammer	+	-
Drink from a cup	+	-
Bimanual coordination [§]	+	+ [†]

- = 100% negative response; + = 100% positive response.

*D.B. was able to mimic postures of her sensate arm using her non-sensate arm provided that she was allowed to look at her non-sensate arm while performing the task; [†]it was noted that D.B. consistently looked at her left (non-sensate) hand while performing this task; [‡]target limb posture positioned by the experimenter; [§]repetitive alternation of each hand between 'fist' and 'palm flat' hand positions.

Somatosensory and motor function

The results of D.B.'s somatosensory and motor assessments are presented in Table 1. At the time of testing she had a dense hemianaesthesia involving the left hand, forearm and upper arm (to approximately midway between elbow and shoulder joints). As a consequence she was completely unable to detect or discriminate between a range of somatosensory stimuli applied to this limb, including superficial pinpricks, hot/cold temperature probes and light rubbing of the skin. Somatosensory (two-point) discrimination was investigated by asking D.B. to report, without vision and for both of her

upper limbs, whether her skin had been pricked using one pin or two (including catch trials).

D.B. was also completely unable to detect or discriminate between passive rotations of the index finger of her left hand, her left wrist or left elbow (testing initially began with small movements and increased to rotations of 50°, all of which were completed undetected by D.B. for her non-sensate limb). Despite this somatosensory loss, D.B. was able to execute complex movements using her non-sensate limb, particularly if she was permitted to look at it prior to, or during, movement execution. Thus, she was easily able to copy hand gestures made by the experimenter, and following a verbal command, to pantomime common actions (a set of 12 different actions, e.g. comb her hair, brush her teeth, answer the telephone, use a hammer). Finally, her ability to execute a series of coordinated bimanual hand movements (each hand alternating between a 'fist' and a 'palm flat' hand position) was not impaired when she was able to see her non-sensate hand (she was not tested on this task without vision of her hand). Neurological examination failed to demonstrate any weakness in D.B.'s non-sensate limb.

Control subjects

Seven control subjects, two females and five males, with a mean age of 69.1 years, were recruited from the School of Psychology, University of Wales, Bangor, community participant panel. All subjects were right handed (Edinburgh Handedness Inventory) and had normal or corrected to normal vision including stereopsis (Randot Stereopsis test). All subjects, including D.B., gave informed consent to participate in the study, which was approved by the Ethical Committee of the University of Wales.

Apparatus and stimuli

Subjects were seated at a 1000 mm² table and executed prehension movements towards target objects presented in the frontal plane (red wooden dowels 50 mm high with a diameter of 22.5 mm). Reaches with the right hand were made from a foam-rubber backed metal pedal (225 × 120 mm) positioned approximately in line with the subject's right shoulder. Reaches with the left hand were made from a similar pedal positioned in line with the subject's left shoulder. The centre-to-centre separation between the pedals was 400 mm. Target objects could be positioned at one of two distances from the starting positions of the hands and to the left or the right of the subject's mid-sagittal plane (see Fig. 2). Note that reaches using the right hand were always executed towards targets presented in right space and reaches using the left hand to targets in left space. At no time therefore did subjects reach with their right hand into left space or vice versa. For the control subjects, targets were positioned at either 200 mm (near) or 300 mm (far). Due to restrictions caused by being seated in a wheelchair, patient

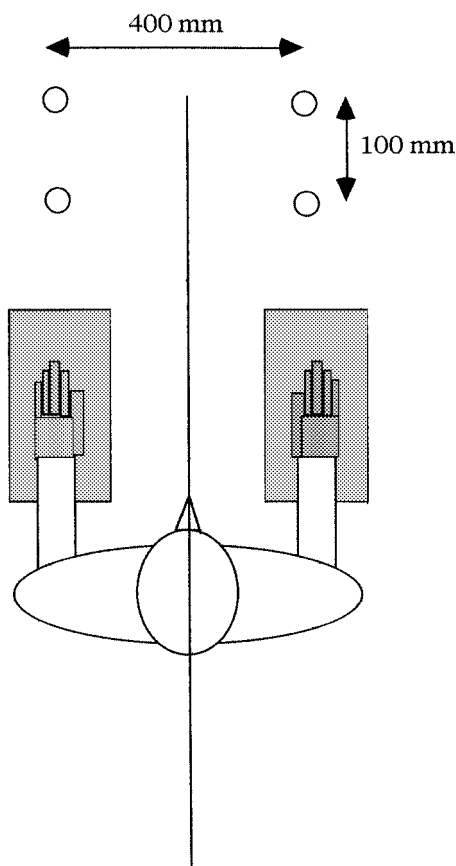


Fig. 2 Schematic representation of the task. Prehension movements were executed from a foam-rubber backed pedal towards wooden dowels presented to the right or left of the mid-sagittal axis.

D.B. reached to targets positioned at either 200 mm (near) or 250 mm (mid) from the start position of the hand.

All subjects executed four types of prehension movement: unimanual reaches using the right hand, unimanual reaches using the left hand, congruent bimanual reaches and incongruent bimanual reaches. During unimanual reaches subjects reached, using either their right or left hand, for a single target object presented in the appropriate hemisphere. During congruent bimanual trials subjects reached, using both right and left hands, for two target objects, one presented in each hemisphere. Furthermore, during congruent trials only, both targets were presented at the same distance from the subject (i.e. both near or both far/mid target locations). In contrast, the target object locations always differed from one another for incongruent bimanual trials, i.e. right hand, far target (mid for D.B.) and left hand, near target, or vice versa.

Each subject completed six trials of each trial type \times target position permutation as follows: 24 unimanual trials (12 trials with each hand and 12 trials to each target distance), 24 bimanual trials (12 congruent trials and 12 incongruent trials). For bimanual trials, the number of near and far reaches with each hand was counterbalanced. Subjects began each trial with the hand placed flat upon the starting pedals, oriented along the sagittal plane and with the thumb closed against

their index finger. To control viewing conditions, subjects wore a set of glasses which were fitted with liquid crystal lenses throughout the experiment. Each trial commenced with the glasses clearing. It is important to note that occlusion with these lenses did not significantly decrease levels of illumination to the eye. For control subjects, the order of presentation of trials for each block was individually randomized for each subject. For patient D.B. the order of conditions was randomized in an ABA design. Subjects were instructed to reach as quickly as possible while maintaining accuracy. A short practice session was conducted prior to the presentation of the experimental trials.

Movement recording and data analysis

Hand movements were recorded using a MacReflex infrared motion-analysis system with a sampling rate of 50 Hz. Reflective markers, 5×5 mm, were placed on the distal portion of the thumbnail, on the distal portion of the index finger and on the wrist of each hand. Additional markers were also fixed to the target objects. The 3D spatial coordinates of these markers were analysed off-line using custom software. Data were low pass filtered using a 4th-order Butterworth filter (cut-off frequency of 10 Hz).

Dependent measures

Kinematic parameters were initially calculated for each hand separately. Movement onset was defined as the first frame in which the wrist marker exceeded a velocity of 25 mm/s in the direction of movement. Movement end-point was defined as the first frame in which horizontal displacement of the target marker exceeded 1.0 mm. MD was defined as movement end-point minus movement onset. The following dependent measures were computed from the 3D coordinates for the markers placed on the thumbnail, index finger and wrist, and were used to analyse the kinematics of the grasp phase of the prehension task: (i) peak grip aperture (PGA) between index finger and thumb (measured in mm); and (ii) the time taken to reach PGA expressed as a percentage of total movement time (TTPGA%). The following dependent measures were computed from the 3D coordinates for the wrist marker and were used to analyse the kinematics of the transport phase: (i) peak velocity in the direction of movement; and (ii) absolute time (in milliseconds) between movement onset and the point where peak velocity was achieved, i.e. time taken to reach peak movement velocity (TTPV).

Planned comparisons

As the purpose of this study was to investigate the role of proprioception on the coordination of bimanual movements, a series of planned comparisons (using linear contrasts between means) were conducted to examine differences between the patient's sensate and non-sensate hand on

unimanual compared with bimanual reaches. In each case separate comparisons were run for the patient and control subjects. The first set of comparisons consisted of the following contrasts: (i) unimanual left reaches versus unimanual right reaches; (ii) bimanual left congruent versus bimanual right congruent reaches; (iii) bimanual left incongruent reaches versus bimanual right incongruent reaches. To examine the effect of making bimanual movements and the influence of movement congruency, we compared: (i) unimanual reaches versus bimanual reaches; and (ii) congruent bimanual versus incongruent bimanual reaches. Finally, to examine the coupling of bimanual movements we examined how scaling of kinematic parameters to target distance varied across condition by conducting the following contrasts: (i) unimanual near versus far reaches; (ii) bimanual congruent near versus far reaches; (iii) bimanual incongruent near versus far reaches.

Results

Transport phase kinematics

Movement duration

Control subjects. Mean movement duration values are presented in Figs 3 and 4. The results of the planned comparisons revealed that MDs for both the left and right hands did not differ for any of the movement conditions [maximum $F(1,6) = 1.5$, $P = 0.2$]. MDs (Fig. 3B) were significantly longer for bimanual reaches compared with unimanual reaches [$F(1,6) = 20.5$, $P < 0.001$], while MDs for congruent bimanual reaches did not differ from those for incongruent bimanual reaches [$F(1,6) < 1$, $P > 0.1$].

The planned comparisons revealed that MDs were scaled for movement amplitude, for unimanual [$F(1,6) = 57.1$, $P < 0.0001$], congruent bimanual [$F(1,6) = 6.22$, $P < 0.0001$] and incongruent bimanual reaches [$F(1,6) = 11.0$, $P > 0.1$]. However, as Fig. 4B makes clear, the mean MDs for near and far target locations became more similar (approximately midway between the mean MDs observed for the far and near target locations in the congruent bimanual condition) during incongruent bimanual reaches.

Patient D.B. The planned comparisons showed that patient D.B., like the control subjects, exhibited longer movement times (Fig. 3A) for bimanual reaches compared with unimanual reaches [$F(1,5) = 14.12$, $P < 0.01$]. Like the control subjects her MDs for congruent bimanual reaches did not differ from those for incongruent bimanual reaches [$F(1,5) < 1$, $P > 0.1$]. Planned comparisons confirmed that the MDs of D.B.'s right and left hands did not differ for unimanual reaches [$F(1,5) = 1$, $P = 0.7$]. In contrast, MDs for her non-sensate left hand were significantly slowed during bimanual congruent [$F(1,5) = 5.8$, $P < 0.05$] and bimanual incongruent reaches [$F(1,5) = 16.52$, $P < 0.01$]. This suggests that D.B. does not couple the MD across her hands during bimanual reaches as the performance of her right and

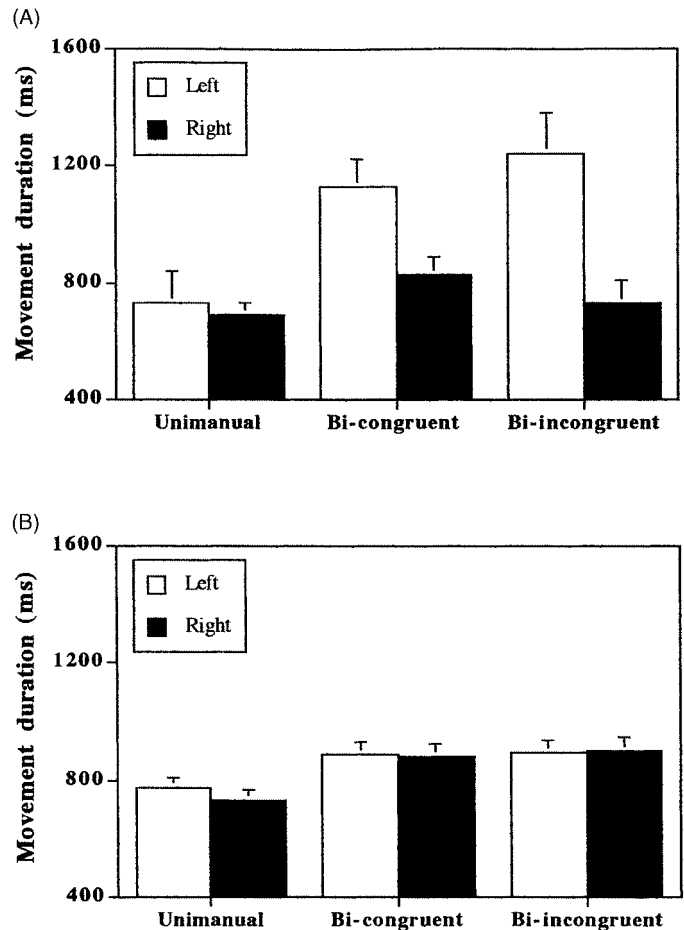


Fig. 3 (A) Mean MDs for reaches executed by patient D.B. using her right and left hands in each of the three movement conditions. (B) MDs for reaches executed by control subjects ($n = 7$) using their right and left hands in each of the three movement conditions. Error bars represent the standard error of the mean.

left hands becomes less similar during bimanual reaches compared with unimanual reaches.

Finally, whereas D.B.'s MDs were scaled for movement amplitude during unimanual [$F(1,5) = 7.6$, $P < 0.05$] and incongruent bimanual movements [$F(1,5) = 7.9$, $P > 0.05$], they did not scale for distance during congruent bimanual movements [$F(1,5) = 0.4$, $P = 0.5$]. Again, this finding suggests that patient D.B. does not couple her movements normally during bimanual reaches.

Peak velocity

Control subjects. Mean peak velocity values are presented in Figs 5 and 6. The analyses revealed that right hand peak wrist velocities were significantly greater than those of the left hand for bimanual reaches [minimum $F(1,6) = 6.9$, $P < 0.05$] and that peak velocities were significantly greater for unimanual compared with bimanual reaches [$F(1,6) = 4.6$, $P < 0.05$]. However, peak velocities for congruent reaches did not differ from those for incongruent reaches [$F(1,6) < 1$, $P = 0.5$].

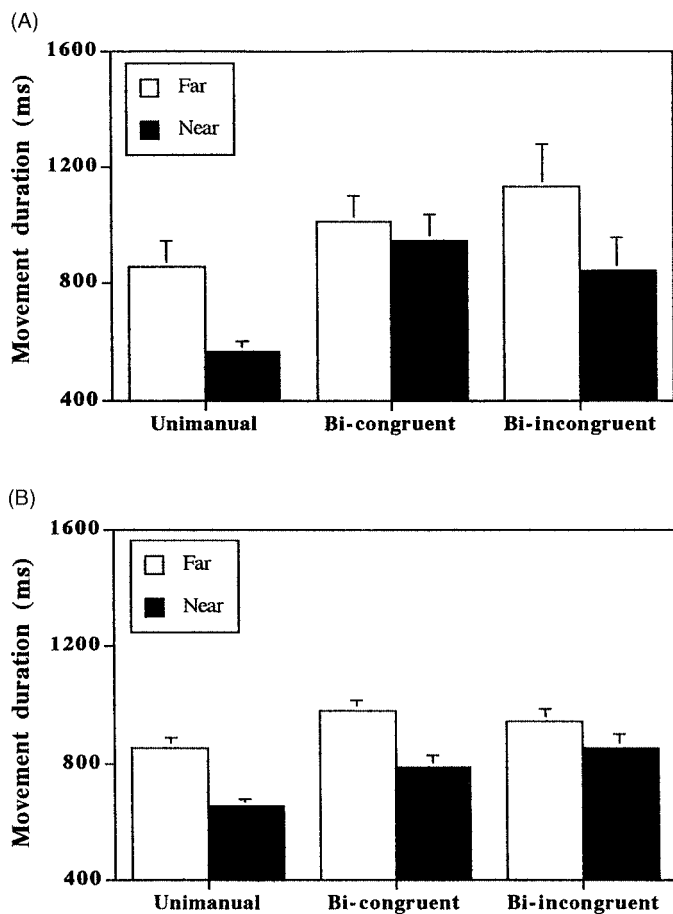


Fig. 4 (A) Mean MDs for reaches directed to the far and near target locations in each of the three movement conditions. (B) MDs for reaches directed to the far and near target locations in each of the three movement conditions. Error bars represent the standard error of the mean.

Planned comparisons also showed that peak velocities were scaled for movement amplitude for each movement condition, including the incongruent bimanual condition [minimum $F(1,6) = 18.2, P < 0.001$]. These results confirm that in incongruent bimanual trials, where each hand was required to move to a different target distance, control subjects were able to independently scale the velocity of each hand.

Patient D.B. The planned comparisons revealed that during unimanual trials, the velocity of D.B.'s right (sensate) hand was significantly slower than that of her left (non-sensate) hand [means (standard deviation): right hand, 397 (53) mm/s versus left hand, 480 (74) mm/s; $F(1,5) = 9.1, P < 0.01$.] This result is in line with the clinical assessment of D.B. indicating that she does not suffer from any weakness in her non-sensate arm. The planned comparisons also revealed that the velocities for D.B.'s right and left hands did not differ during bimanual congruent [$F(1,5) < 1, P = 0.8$] and more importantly during bimanual incongruent [$F(1,5) < 1, P = 0.3$] reaches. This finding suggests that, unlike control

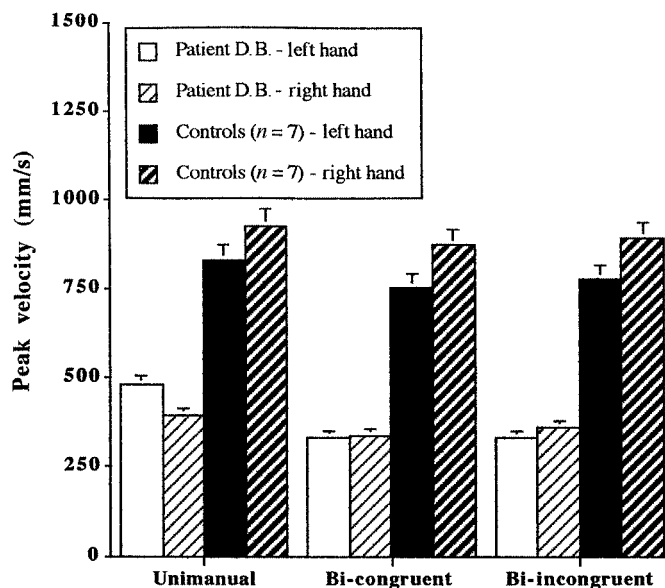


Fig. 5 Peak velocity values for reaches executed by patient D.B. and controls ($n = 7$) using their right and left hands in each of the three movement conditions. Error bars represent the standard error of the mean.

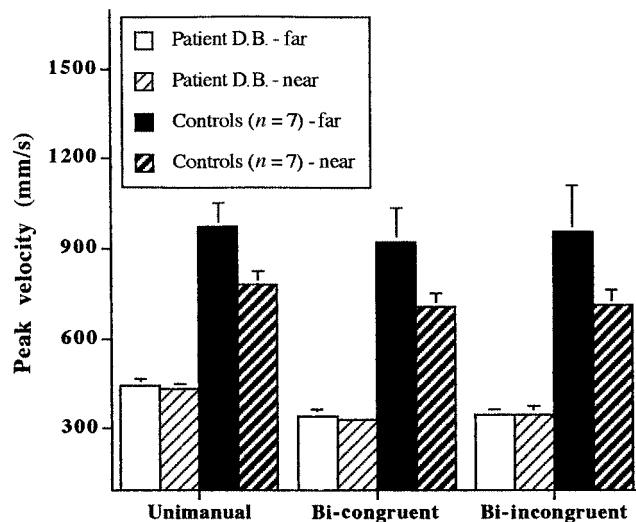


Fig. 6 Peak velocity values for reaches executed by patient D.B. and controls ($n = 7$) to the far and near target locations in each of the three movement conditions. Error bars represent the standard error of the mean.

subjects, D.B. does not independently control the velocity of each hand during incongruent bimanual reaches. Instead she appears to couple together the velocity of each hand leading to MD differences for each hand. However, it is also important to take into account when peak velocity occurs (see below).

As was the case for control subjects, peak wrist velocities were significantly greater for unimanual compared with bimanual reaches [$F(1,5) = 49.8, P < 0.0001$] and peak velocities for congruent bimanual reaches did not differ from those for incongruent bimanual reaches [$F(1,5) < 1, P = 0.6$]. However, in contrast to controls, peak velocities were

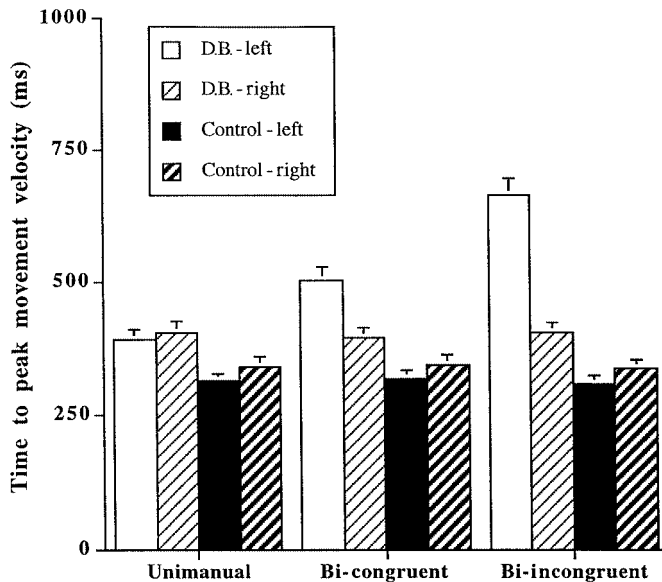


Fig. 7 TTPV (ms) for reaches executed by patient D.B. and controls ($n = 7$) using their right and left hands in each of the three movement conditions. Error bars represent the standard error of the mean.

not scaled for movement amplitude for any of the movement conditions [maximum $F(1,5) < 1$, $P > 0.5$ in all cases]. Again these results suggest that D.B. is inappropriately coupling the velocity of her hands during incongruent bimanual reaches.

TTPV

Control subjects. Relevant means are presented in Fig. 7. For control subjects, TTPV was equivalent for left and right hands across all movement conditions [maximum $F(1,6) 1.5$, $P > 0.1$]. In addition, TTPV did not differ for unimanual and bimanual reaches [means: unimanual, 327 ms versus 328 ms; $F(1,6) = 3.1$, $P > 0.1$] or for congruent and incongruent bimanual reaches [means: congruent, 332 ms versus incongruent, 323 ms; $F(1,6) < 1$, $P > 0.1$]. Finally, TTPV was not scaled for distance for unimanual movements [$F(1,6) < 1$, $P > 0.1$] or incongruent bimanual reaches [$F(1,6) = 3.3$, $P > 0.1$]. However, means for congruent bimanual movements did scale to target object distance [means: far, 363 ms versus near, 301 ms; $F(1,6) = 5.8$, $P < 0.03$].

Patient D.B. TTPV was equivalent for D.B.'s left and right hands for the unimanual and congruent bimanual conditions [maximum $F(1,5) = 1.9$, $P > 0.1$]. However, during incongruent bimanual reaches, TTPV was substantially delayed in D.B.'s left (non-sensate) hand [means: left, 662 ms versus right, 403 ms; $F(1,5) = 10.5$, $P < 0.025$]. Analysis of individual trials revealed that the delayed mean TTPV for reaches executed using her left hand during incongruent bimanual reaches was a result of substantial re-accelerations of her left arm. Thus, D.B. typically showed an initial velocity

peak for her left limb which was coupled to the velocity profile of her right limb. This was frequently followed by one or more further velocity peaks of her left limb. In some cases peak velocity of these later peaks exceeded that of the initial velocity peak. Like control subjects, mean TTPV for patient D.B. did not differ significantly between unimanual and bimanual reaches [means: unimanual, 398 ms versus bimanual, 492 ms; $F(1,5) = 3.1$, $P > 0.1$] or between congruent and incongruent bimanual reaches [means: congruent, 450 ms versus incongruent, 533 ms; $F(1,5) = 1.8$, $P > 0.1$]. Finally, TTPV did not scale for target on unimanual reaches [$F(1,5) < 1$, $P > 0.1$]. However, TTPV occurred later for farther targets compared with near targets during congruent [$F(1,5) = 6.7$, $P < 0.05$] and incongruent bimanual reaches [$F(1,5) = 4.9$, $P = 0.07$].

Grasp phase kinematics

Peak grip aperture

D.B. was instructed to pick up the target dowel(s) using a precision (finger–thumb) grip, removing the dowel(s) from the table surface cleanly. Overall, the maximum aperture of D.B.'s grip was smaller than that of the control subjects. While controls opened their right hand wide to unimanual targets [$F(1,6) = 5.9$, $P = 0.05$], patient D.B. opened her left (non-sensate) hand wider in this condition [$F(1,5) = 14.6$, $P = 0.01$]. Patient D.B. and controls showed comparable right- and left-hand PGAs during bimanual reaches. Finally, PGA was not affected by target distance for control subjects [maximum $F(1,5) = 2.3$, $P = 0.2$] or patient D.B. [maximum $F(1,5) = 0.6$, $P = 0.5$]. It should be noted that D.B. was generally quite accurate at performing the reach-to-grasp task, although in a number of trials she knocked over the dowel instead of lifting it cleanly from the table surface.

TTPGA%

Control subjects. TTPGA% was equivalent for left and right hands across unimanual and congruent bimanual movement conditions [maximum $F(1,6) < 1$, $P > 0.1$]. However, in incongruent bimanual reaches the subjects' right hand reached maximum grip aperture earlier than their left hand [$F(1,6) = 4.8$, $P < 0.05$]. TTPGA% also occurred earlier during bimanual compared with unimanual reaches [means: unimanual, 77% versus bimanual, 72%; $F(1,6) = 6.7$, $P < 0.025$], but congruent and incongruent bimanual reaches did not differ from one another [$F(1,6) = 2.5$, $P > 0.1$]. Finally, during unimanual trials TTPGA% occurred at 77% of MD for both near and far reaches [$F(1,6) < 1$, $P > 0.1$]. However, during bimanual trials there was a tendency for TTPGA% to occur earlier for far reaches. This effect was significant for incongruent bimanual reaches [$F(1,6) = 5.2$, $P < 0.05$].

Patient D.B. Patient D.B. tended to reach maximum grip aperture later than control subjects (means: controls, 77% versus D.B., 86%). TTPGA% was equivalent for D.B.'s left and right hands across all movement conditions [maximum $F(1,5) = 4$, $P = 0.1$], did not differ in unimanual trials compared with bimanual trials [means: unimanual, 87% versus bimanual, 85%; $F(1,5) < 1$, $P > 0.1$] and was equivalent for congruent and incongruent bimanual reaches [$F(1,5) = 1.8$, $P > 0.1$]. Finally, TTPGA% was not affected by target–object distance [$F(1,5) = 3.5$, $P > 0.1$].

Patient D.B.: hand path/velocity analyses

The results outlined above demonstrate that: (i) MDs for patient D.B.'s right (sensate) hand are comparable with those of control subjects across all movement conditions; (ii) MDs for D.B.'s left (non-sensate) hand only differ from those of controls during bimanual reaches; (iii) unlike control subjects, D.B. does not couple the MDs of her left and right hands during bimanual movements; instead, she appears to couple hand movement velocities during bimanual movements.

This pattern of effects can be better understood by viewing D.B.'s hand paths during bimanual movements (Fig. 8). The upper panels of Fig. 8 (Fig. 8A and C) show hand paths from several congruent (same distance) bimanual trials. Inspection of these panels shows that, whereas reaches made with her right hand are approximately straight, reaches made with her left (non-sensate) hand are grossly inaccurate. This does not, however, appear to result from a simple misreaching impairment. The lower panels of Fig. 8 (Fig. 8B and D) show unimanual reaches made by D.B. using left and right hands, and executed to the same target locations as illustrated in Fig. 8A and C. Inspection of these panels shows that unimanual reaches made by D.B. using her left (non-sensate) hand do not show the gross inaccuracies observed during bimanual reaches.

We have previously argued that the kinds of bimanual action investigated in the current study impose information processing limitations which are not associated with similar kinds of unimanual action (Jackson *et al.*, 1999). Inspection of the hand paths presented in Fig. 8 suggest that D.B.'s misreaching deficit is largely confined to bimanual movements. Thus, there is now considerable evidence to attest to the difficulty of attending to more than a single object at any one time. For example, subjects find it easier to report the presence of a pair of stimulus properties when these are present on a single object, compared with when they occur on different objects (Duncan, 1984). Therefore, D.B.'s impairment during bimanual trials may result from an inability to simultaneously attend to two unfolding movements directed towards different target objects. Support for this suggestion is obtained by examining D.B.'s movement velocity profiles for congruent bimanual movements. Figure 9 presents three representative pairs of velocity profiles, each one showing the time-locked changes in movement velocity for D.B.'s right and left hands. Figure 10 presents spatial

hand paths for patient D.B. and a representative control subject. In Fig. 9 each panel illustrates a single congruent bimanual trial in which each hand is required to move an identical distance in an identical direction but from different start positions. Inspection of this figure reveals several important findings. First, in all three examples the movement onset of each hand (indicated by the leftmost pair of circle symbols) occurred at a similar point in time. This pattern of coupling together the movement onset of each hand is commonly reported for bimanual reaching movements (Keele, 1986) and was observed in all of D.B.'s bimanual trials. Secondly, the slopes of the acceleration phase of the movement (i.e. TTPV) for each hand and the point in time when peak velocity occurred, were clearly similar in each case, even when the MD of each hand varied considerably. Thirdly, the velocity profiles in each panel clearly show that despite the coupling of the early phase of D.B.'s reaches, later aspects of her reaches are not coupled. Thus, the point in which each hand makes contact with the target object (indicated by the rightmost pair of circle symbols) is vastly different in all cases, and in each case one or other of D.B.'s hands is required to re-accelerate to obtain the target. An important point to note, however, is that the hand which re-accelerates is not constant. In Fig. 9A and C, D.B.'s left (non-sensate) hand re-accelerates to obtain the target only after her right hand has obtained its target, whereas Fig. 9B shows the reverse situation, in which D.B.'s left (non-sensate) hand obtains its target first, after which her right hand re-accelerates to obtain the right-hand target object. These data suggest that D.B. can couple the movements of each hand during the early phase of bimanual movements. However, later phases of the movement (most likely associated with target acquisition) may require continuous control of each hand. The data strongly suggest that D.B. cannot simultaneously monitor more than one reaching movement at a time; as a consequence, the target acquisition phase of each hand is executed serially. Most likely this results from D.B.'s reliance on vision to control the final phase of her prehension movements.

General discussion

The aim of the current study was to investigate the role played by proprioceptive signals in the planning and control of bimanual movements directed towards two objects. We examined the ability of a woman (D.B.) recovering from a cerebrovascular accident which resulted in a dense hemianaesthesia of her left arm, to plan and control bimanual reach-to-grasp movements. Our results demonstrated that patient D.B.'s ability to execute unimanual reach-to-grasp movements using her non-sensate hand was comparable with that of control subjects, and also to her ability to execute movements using her sensate hand. However, D.B. showed a marked impairment in her ability to execute bimanual reach-to-grasp movements. Specifically, in contrast to control subjects who reliably couple the reaching movement of each

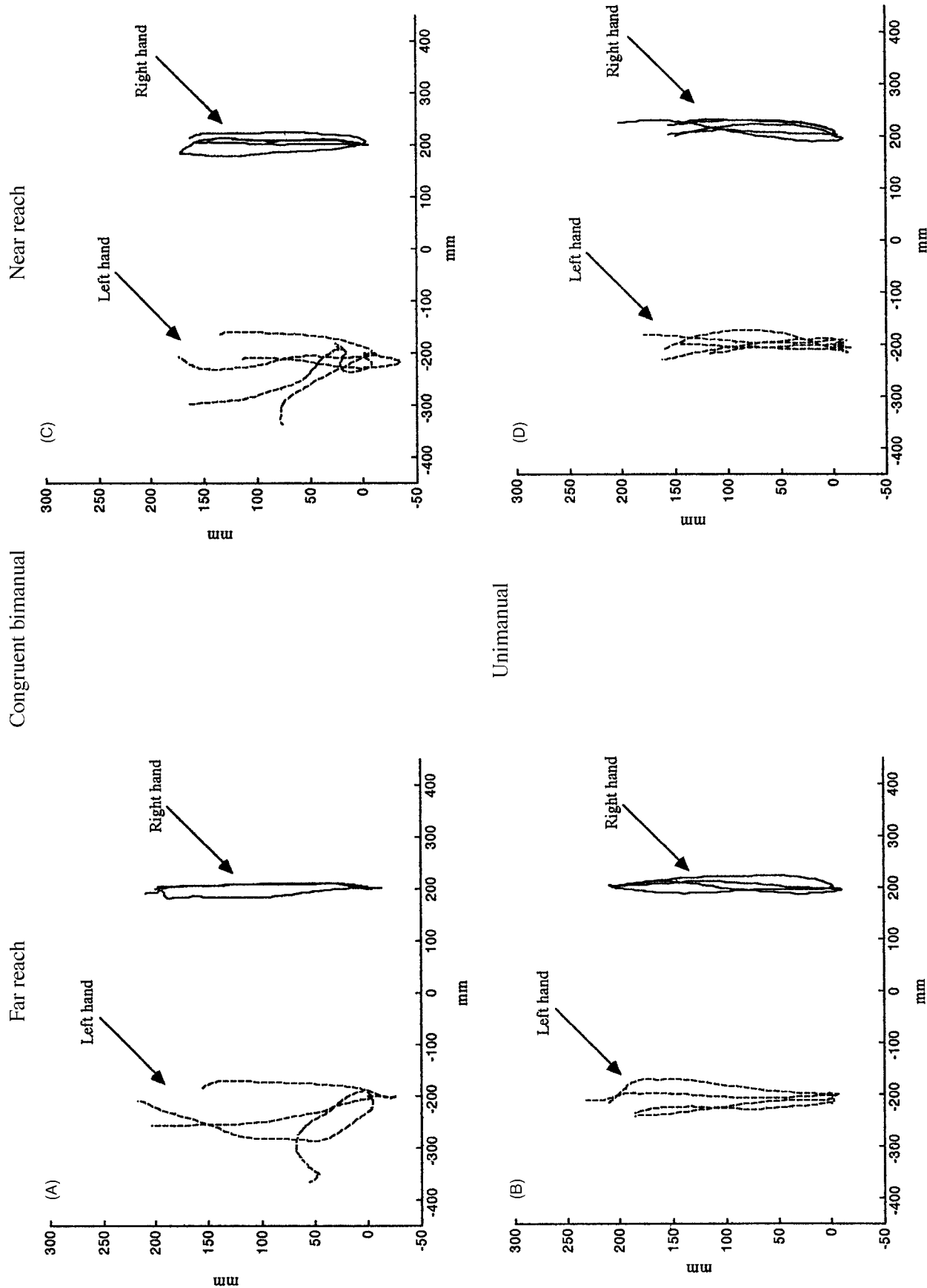


Fig. 8. x-y plots showing representative spatial paths of the wrist markers during reaches executed by patient D.B. using her right and left hands. The upper panels show congruent bimanual movements to the far (A) and near (C) target positions. The lower panels show unimanual reaches to the far (B) and near (D) locations.

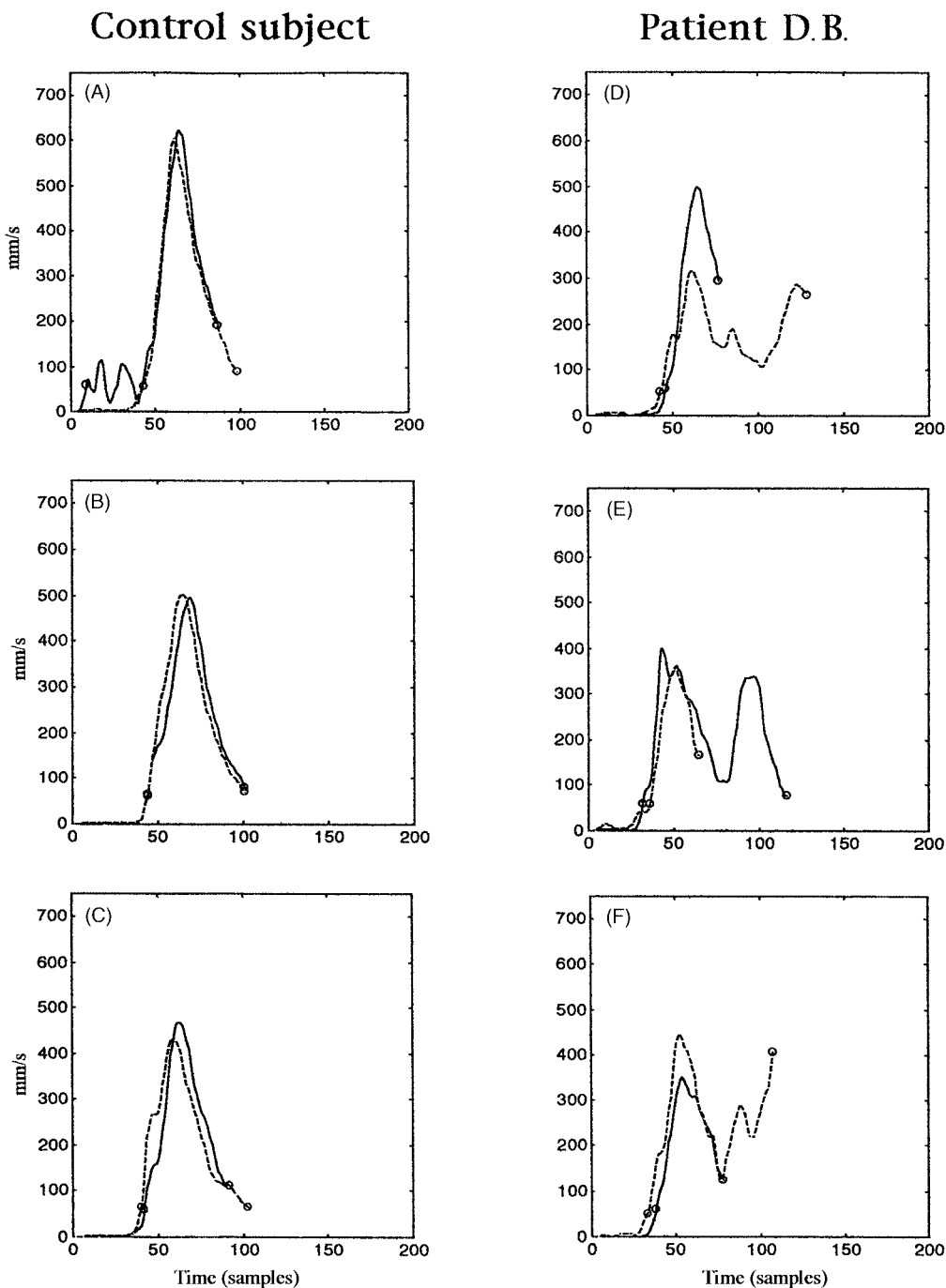


Fig. 9 Several representative velocity profiles for the left (broken line) and right (continuous line) hands of a single control subject executing visually guided congruent bimanual reaches (A, B and C). The leftmost open circle symbols indicate movement onset for each hand. The rightmost open circle symbols indicate the point at which each hand reaches the target object. These profiles clearly illustrate the degree of synchronization observed during bimanual reaching movements. The right panels show representative velocity profiles for patient D.B. under identical conditions (D, E and F).

hand so that movements begin and end at approximately the same time (Kelso *et al.*, 1979, 1983; Jackson *et al.*, 1999), patient D.B. failed to show appropriate coupling of the MDs of each hand. Instead, she produced movements in which the initial accelerative phase of the movements of each hand were coupled but later target-approach phases were de-

coupled. Of particular interest was the consistent finding that D.B. coupled the initial movement velocities of each hand during bimanual movements, even where this was inappropriate, as in the case of trials where each hand was required to execute a movement of a different amplitude.

As noted above, two general frameworks have been

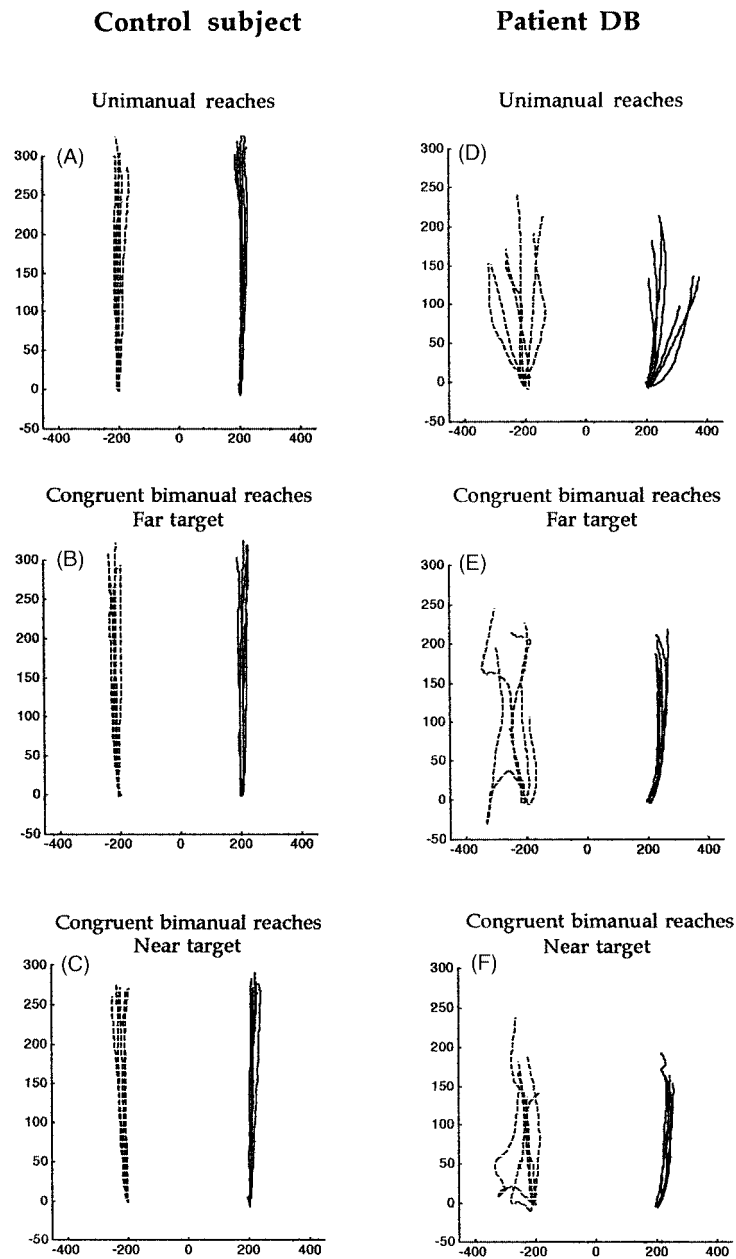


Fig. 10 The left panels (A, B and C) each show x - y plots showing spatial paths of the wrist markers during reaches executed by a single control subject using her right (continuous lines) and left (broken lines) hands. The right panels (D, E and F) show x - y plots for patient D.B.; plots are shown for unimanual movements (D), congruent bimanual movements to the mid target location (E) and congruent bimanual movements to the near target location (F).

proposed to explain how the movement coordination might be brought about during the execution of prehension movements (Jackson *et al.*, 1999). One framework, which we term the temporal planning model, proposes that the coordination of movement components is planned in advance of movement onset and based upon a common time-frame for each movement (e.g. Hoff and Arbib, 1993). Our finding that patient D.B. shows normal coupling of movement onset is compatible with this view and confirms that proprioceptive signals coding the initial position of the limb are unnecessary for synchronizing movement initiation. This finding also

confirms previous suggestions, based upon the study of unimanual reach-to-grasp movements in a deafferented individual, that the initial stages of reach-to-grasp movements are executed under feedforward control (Gentilucci *et al.*, 1994).

Based upon the finding that in healthy adults the kinematics of unimanual reach-to-grasp movements differ from those of bimanual reach-to-grasp movements having the same index-of-difficulty, we have previously argued that a sensorimotor mechanism is utilized during bimanual movements which is not required during unimanual movements (Jackson *et al.*,

1999). Furthermore, we have suggested that this mechanism exists to maintain inter-limb coordination during movement execution and have speculated that this mechanism is most likely based upon proprioceptive coding of limb position and motion (see also Haggard and Wing, 1991). Our finding in the current study that patient D.B. exhibits a specific deficit for executing bimanual movements also runs counter to the view that bimanual movements are synchronized through the computation, prior to movement onset, of a single motor programme which binds each effector to a common time-frame. Instead, our results indicate that proprioceptive signals may be necessary to maintain coordination of each limb during movement execution, at least during the later (target-acquisition) phase of the movement.

An alternative to temporal planning models are continuous control models which hold that movement coordination might arise from the fact that independently controlled movements might rely on common sources of information (e.g. Zaal *et al.*, 1999). One such signal may be a time-to-contact or motor error signal, in which moment-by-moment changes in the spatial separation between the moving effector and target are used as a control signal. Support for this view was obtained in a recent study by Zaal and colleagues who compared movement kinematics for reaches executed to static targets (presented at different amplitudes) with movements directed to targets which, at movement onset, began to move away from the subject at one of several constant velocities (thereby increasing the resultant movement amplitude). Their results showed that MD did not differ in the moving target condition for objects moving at different velocities. Instead, MDs were shown to be scaled to the initial distance between hand and target and not to the resultant movement amplitude of the reach. In contrast, movement velocity was shown to scale for both the initial distance between hand and target, and also for target object velocity. From these findings, Zaal and colleagues concluded that movement velocity is subject to on-line control, which is based upon perceptual information signalling both a change in position and hand movement velocity relative to the target object (Zaal *et al.*, 1999).

It should be noted that this study by Zaal and colleagues (Zaal *et al.*, 1999) was based upon an examination of unimanual movements directed to a single target object. In order to account for the case in which bimanual movements are simultaneously directed towards two spatially separated target objects, it is necessary to provide an account of how subjects might monitor two continuously varying time-to-contact signals. This issue is considered below in the context of the current study.

Competitive processing and the control of bimanual movements

The integrated competition theory introduced by Duncan and colleagues proposes that visual information produces activity within multiple brain systems, within which activations

related to different objects compete with one another. Such competition is characterized in behavioural terms as interference characterized by a reduction in the efficient processing of each object. It is therefore suggested that mechanisms exist to reduce competition so that 'For the sensorimotor network as a whole, the tendency is to settle into a state in which different brain systems have converged to work on the same dominant object, analysing its multiple visual properties and implications for action. . . . At the neural level, there should be widespread maintenance of the selected object's representation, accompanied by widespread suppression of response to ignored objects' (Duncan *et al.*, 1997).

One obvious limiting factor during bimanual prehension movements directed towards different target objects would be the need for the visuomotor system to continuously sample two time-to-contact signals. A solution to this problem might be for the sensorimotor system to adopt an intermittent sampling strategy during bimanual movements, where the time-to-contact signal for each hand is independently sampled by switching attention between target objects during movement execution. Two predictions can be generated from such a model: first, there should be a clear cost in performing bimanual prehension movements compared with unimanual movements and secondly, there should be no additional costs of performing incongruent compared with congruent reaches. While both of these predictions have been confirmed in previous studies (Jackson *et al.*, 1999) and are consistent with the findings of the current study, an intermittent sampling strategy is incompatible with the 'integrated competition theory' which, as currently formulated, would predict sequential reaches to each target. It is therefore of interest to note that patient D.B. executes bimanual reaches in exactly the manner predicted by the integrated competition theory, i.e. in contrast with control subjects, patient D.B. executes the target acquisition phase of each of her reaches serially.

In order to understand D.B.'s behaviour it is useful to first consider why healthy adults do not complete bimanual reaches serially, in the manner observed for D.B. An alternative to the intermittent sampling strategy, which avoids the problem of monitoring two time-to-contact signals, might be for the sensorimotor system to reconfigure the task so that only one time-to-contact signal need be monitored. This could be achieved by coupling together each limb so that they were constrained to act as a single functional unit (Kelso *et al.*, 1979). Each limb could commence moving at the same time, but might move at different velocities so as to arrive at their respective targets simultaneously. Within this model, only one object need be viewed to derive a time-to-contact signal appropriate for both limbs. Such a model would, however, not be compatible with a visual time-to-contact signal. Instead, it is more likely that any motor error signal coding time-to-contact would be based upon the integration of visual cues indicating target location and the felt position of the limb. In D.B.'s case, as proprioceptive cues coding the position of her non-sensate limb were not available, she

would either be forced to make use of visual cues signalling target location and the spatial position of her non-sensate limb or to make use of proprioceptive cues arising in her sensate limb. This latter alternative might account for our finding that D.B. couples together the velocity profiles of each limb during bimanual movements, even where this is inappropriate, as in the case of incongruent reaches.

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