

## On the space-time structure of human interlimb co-ordination

J. A. SCOTT KELSO, CAROL A. PUTNAM\* AND DAVID GOODMAN†

*Haskins Laboratories, New Haven, Connecticut, and Departments of Psychology and Biobehavioral Sciences, University of Connecticut, Storrs, Connecticut, USA*

\* *Biomechanics Laboratory, Dalhousie University, Halifax, Nova Scotia, Canada.*  
 † *Department of Kinesiology, Simon Fraser University, Burnaby, British Columbia, Canada.*

In three experiments we show, using behavioural measures of movement outcome, as well as movement trajectory information and resultant kinematic profiles, that there is a strong tendency for the limbs to be co-ordinated as a unitary structure even under conditions where the movements are of disparate difficulty. Environmental constraints (an obstacle placed in the path of one limb, but not in the other) are shown to modulate the space-time behaviour of both limbs (Experiment II). Our results obtain for symmetrical (Experiment I) as well as asymmetrical movements that involve non-homologous muscle groups (Experiment III). These findings suggest that in multi-joint limb movements, the many degrees of freedom are organised to function temporarily as a single coherent unit that is uniquely specific to the task demands placed on it. For movements in general, and two-handed movements in particular, such units are revealed in a partitioning of the relevant force demands for each component (a force scaling characteristic) and a preservation of the internal "topology" of the action, as indexed by the relative timing among components. These features, as well as systematic deviations from perfect synchrony between the limbs can be rationalised by a model that assumes the limbs behave qualitatively like non-linear oscillators.

### Introduction

Many of the actions that humans perform require the co-operation of the upper limbs, but generally speaking, little attention has been devoted to seeking principles that might underlie human inter-limb co-ordination. Although some interesting studies of bimanual tapping performance have appeared recently (e.g. Peters, 1981; Yamanishi, Kawato and Suzuki, 1980), by far the greatest research effort has been directed toward understanding the mechanisms associated with single limb movements, most involving only one degree of freedom (e.g. Bizzi, Dev, Morasso and Polit, 1978; Cooke, 1980; Fel'dman, 1966, 1980; Kelso, 1977; Kelso and Holt, 1980).

Of course, there is a long history of work on the co-ordination among the appendages of vertebrates and invertebrates, the results of which have been especially impressive (for review, see Delcomyn, 1980). As an instance, Wilson's research on insect locomotion revealed, in principle, how the many surface kinematic details of gait

could be synthesised out of a tonically activated network of coupled oscillators (Wilson, 1966; see also Grillner, 1975; Stein, 1977). Even here, however, the nature of coupling processes among limbs remains somewhat obscure, a situation that may be remedied when non-linear oscillator theory is more fully developed and exploited (cf. Pavlidis, 1973; Winfree, 1980). Indeed, some preliminary steps have already been taken to apply this framework to an understanding of human rhythmical movement (Kelso, Holt, Rubin and Kugler, 1981; Yamanishi *et al.*, 1980).

Although the work on animal neuromotor systems is obviously important to gain a fuller understanding of biological co-ordination in complex systems possessing many degrees of freedom, it seems useful to proceed with investigations on the human front as well, in the hope that general principles may emerge. With this in mind, in 1979 we introduced a paradigm that we felt might have broad potential for exploring the processes underlying the control of both limbs when they work together to accomplish a task (Kelso, Southard and Goodman, 1979a,b). The question that we asked was a very simple one. Suppose subjects are required to produce movements of the upper limbs toward targets of widely disparate difficulty as quickly and accurately as possible, how will they respond? A formulation developed for reciprocal tapping tasks by Fitts (1954) relating movement duration, movement amplitude and target precision demands allowed us to examine the issue experimentally. The equation relating these variables is:

$$MT = a + b \log_2 (2A/W)$$

where  $A$  is the amplitude of movement;  
 $W$  corresponds to target width;  
 $a$  and  $b$  are constants; and  
 $MT$  is movement time.

For limbs operating singly, the obvious prediction from the above relationship is that movement time depends on the ratio of movement amplitude to movement precision. But now consider a situation in which one limb, say the left, moves a short distance to a large target (termed easy) while the other moves a longer distance to a small target (termed hard). For the single limb case, movement time in the easy condition, according to Fitts' Law will obviously be much shorter than in the hard condition. However, when the two conditions are combined, Kelso *et al.* (1979a,b) did not find that the limb producing a short movement to an easy target arrived earlier than its more difficult counterpart as one might expect. Instead, there was a strong tendency for *both* movements to be initiated and terminated synchronously. Indeed, an examination of the movement times indicated that the hand moving to the difficult target moved more rapidly in the combined, easy-hard condition than its single limb control, while the easy hand obviously slowed down—as if the limbs were adopting a common temporal metric.

It is important to point out that the limb moving to the easy target did not appear to "hover" over the target or "wait" for its difficult counterpart but rather moved at quite different speed. High-speed cinematography (200 frames/s) and consequent examination of horizontal displacement, velocity and acceleration patterns over time revealed that the limbs under easy-difficult target conditions reached peak velocity

and peak acceleration at practically the same time during movements. Thus, although different spatial demands for the two limbs affected the magnitude of forces produced by each limb, the absolute timing and the segmental durations of movement components, that is, the *timing relations* between the two limbs remained quite constant.

The idea that motor co-ordination involves a reduction of the degrees of freedom of the sensorimotor system, not into prefabricated sets of reflexes, but into *functional* groupings of muscles constrained to act as a single unit [termed functional synergies (e.g. Gelfand, Gurfinkel, Tsetlin and Shik, 1971; Saltzman, 1979) or co-ordinative structures (e.g. Fowler, 1977; Turvey, Shaw and Mace, 1978)] stems originally from Bernstein (1967) and has undergone theoretical extension by Greene (1972), Boylls (1975), Turvey (1977) and others. To paraphrase Boylls (1975), functional synergies are collectives of muscles, all of which share a common pool of afferent and/or efferent information that are deployed as a unit in a motor task. In spite of powerful logical arguments that they are the significant units of action, it is only recently that rigorous analysis of muscle-joint collectives has taken place (cf. Kelso, 1981, for recent review of their existence in activities ranging from posture and locomotion to speech and handwriting).

The Kelso *et al.* (1979a,b) experiments reveal what appears to be the chief signature of a functional synergy, namely that when a group of muscles co-operate as a single, coherent structure to accomplish a task, *the internal timing relations among muscles and kinematic components are preserved invariantly over changes in the magnitude of activity in individual components*. However, it is fair to say that the kinematic evidence on which this claim is based is rather sparse. In the early experiments (Kelso *et al.*, 1979a,b) we were restricted by limitations imposed by high speed cinematography and tedious frame-by-frame analysis. In fact, only the kinematics on the horizontal plane were examined over a series of six trials on a single subject. One of the goals of the present experiments was to supplement this very preliminary evidence with a much more detailed analysis of the movement trajectories of two limbs and their kinematic behaviour on both horizontal and vertical planes. The first experiment reported here is a "behavioural replication" of our earlier work, but used a pulsed light emitting diode (LED) technique to capture the space-time trajectories of the limbs. A second experiment explored more directly the influence of environmental constraints on the dynamic behaviour of the hypothesised functional unit. If indeed the action system solves the two-handed task by controlling the limbs as a single structure, then the introduction of an obstacle which one limb must "jump over" to reach the target, may have (at least initially) concomitant modulatory effects on the other unconstrained limb.<sup>1</sup> The obstacle in this case can be interpreted as placing a contextual constraint on the degrees of freedom of the *unit* rather than the individual limb.

All our experiments up to now have examined *symmetrical* movements of the

<sup>1</sup> We do not claim that the types of constraints observed in our two-handed movement task cannot be broken down with practice, or by instructional strategies, or by loading the limbs differentially, or by removing visual information, etc. We do claim that, faced with the task of controlling many muscles in the two-handed task, the perceptual-motor system tends to solve *this particular problem* naturally, by co-ordinating the limbs as a single unit. These experiments are directed toward an understanding and classification of natural constraints on multi-degree of freedom systems. They do not speak to the many apparently arbitrary activities that subjects can perform in laboratory situations.

upper limbs involving primarily extension of the forearm-wrist-hand linkages away from the body midline (Kelso *et al.*, 1979a, Experiment I), flexion toward the body midline (Experiment II) or forward reaching movements in the sagittal plane (Experiment III). The symmetry constraint is a powerful one in human movement, manifested for example in the so-called "mirror movements" exhibited by small children and certain brain-damaged populations (cf. Woods and Teuber, 1978). It is also omnipresent in the two-handed signs of American Sign Language. According to Klima and Bellugi (1979), "The symmetry constraint specifies that in a two-handed sign, if both hands move and are active, they must perform roughly the same motor acts" (p. 64). It would seem an important extension of the work on symmetrical limb movements to examine also the co-ordination of asymmetrical movements which involve non-homologous muscle groups. In Experiment III, we show that they too exhibit a space-time structure similar to that observed for symmetrical movements.

## Experiment I

### *Methods*

#### *Subjects*

The subjects were seven right-handed unpaid volunteers ranging in age between 18 and 25 years.

#### *Apparatus*

We have described the apparatus in detail in previous papers (Kelso, Southard and Goodman, 1979a). It consists of a plexiglass base mounted on a standard table with two home keys and two moveable target keys. The home keys are centered in the base, 4.5 cm apart. In Experiment I, two combinations of target size by target distance were used. The easy target was 7.2 cm wide and positioned 6 cm from its corresponding home key. The hard target was 3.6 cm wide and positioned 24 cm from its corresponding home key. A single target was used in one-handed conditions and two targets were used in the two-handed conditions. Thus, four different two-handed conditions were possible: (a) two-handed easy, (b) two-handed hard, (c) two-handed mixed, hard target on right, easy on left, and (d) two-handed mixed, hard target on left, easy on right. A red light-emitting diode served as the warning light and the sound from a Minisonalert provided the stimulus to move. The onsets of warning light and stimulus tone were controlled by a Digital Equipment Corporation PDP 8/A computer that also collected initiation times, movement times, and total response times. The targets were painted white and were perfectly visible even though the experiment took place in a dimly lit room in order to facilitate the collection of photographic data on movement trajectories.

Light emitting diodes (LEDs) were firmly attached to the dorsal side of the index fingertip of each hand. The LEDs were set to pulse synchronously at a calibrated frequency of 200 Hz. In addition, two LEDs were attached to the target apparatus a known distance apart and within the field of view of the camera in order to provide a linear scale and horizontal reference line. A 35 mm Yashika camera, fitted with a Vivitar 50 mm lens (F stop 2.8) was positioned 2.0 m from the target apparatus so that its optical axis was perpendicular to the plane containing the midpoints of the starting buttons and the targets. The camera was loaded with Kodachrome color slide film (tungsten ASA rating 160). To film each trial, the camera shutter (set on bulb stop) was opened just prior to the start of each movement and was closed immediately after the targets were contacted. As a result, all LED flashes for the duration of any one trial were exposed on a single frame.

### *Task*

The subject's task was identical to the one used in our previous studies of interlimb co-ordination (Kelso *et al.*, 1979a,b). Instructions to subjects were to move their index fingers from the home keys to the target keys as fast and as accurately as possible after receiving a stimulus to move. There were no instructions to move simultaneously in two-handed conditions. The movements themselves primarily involved extension of the forearm-wrist-hand linkage in the lateral plane. For one-handed conditions, the subject depressed the left home key with the left index finger, or the right home key with the right index finger, and, on receiving the stimulus to move proceeded to the designated target, touching it only with the index finger. For two-handed conditions, the subject depressed both home keys with the index fingers and proceeded to hit the respective targets following the onset of the auditory stimulus.

### *Procedure*

As in our previous two-handed studies eight experimental conditions were used which varied depending on whether a single limb or both limbs were involved or whether the movement was easy or hard. All subjects performed 20 trials preceded by five practice trials in each of the eight conditions. The last four trials of each condition were photographed using the procedures outlined above. Each stimulus was preceded by a 1-s to 3-s variable foreperiod and there was an intertrial interval of 5 s. A 3-min rest period was given between each condition.

A within-subject design was used with all seven subjects performing in all experimental conditions, whose order was randomised. From the 20 trials in each condition, mean initiation time, movement time and total response time were computed for each hand. Individual trials initiated prior to or within 30 ms of the stimulus to move were considered anticipations and excluded from the analysis. Similarly, trials with an initiation time greater than 800 ms, or trials in which a target was missed were also excluded. There were four one-handed and four two-handed conditions, making a total of 12 separate means for each subject and each dependent variable.

For the kinematic analysis, each film frame was projected perpendicularly on an opaque screen of a Graf/Pen sonic digitizer. The X and Y co-ordinates were recorded from the image of the LEDs, each representing the location of a fingertip at the end of successive 5 ms intervals. Each XY co-ordinate was scaled to the actual displacement and stored on tape. The digitised data were smoothed by fitting cubic spline functions to the horizontal and vertical displacement-time data for each hand. An International Mathematical and Statistical libraries subroutine called ICSSCU was used to perform data smoothing. Finally, the smoothed displacement-time data functions were mathematically differentiated every 5 ms to arrive at horizontal and vertical velocity-time and acceleration-time functions.

## *Results and Discussion*

Two separate aspects of the data are addressed below. The first involves an analysis of the behavioural data and speaks to the issue of whether or not subjects initiate and terminate movements simultaneously, especially under conditions in which the task demands are quite different. The second aspect concerns the kinematic analysis, which allows us to examine the space-time trajectories of the movements themselves.

### *Analysis of the behavioural data*

The mean initiation times, movement times, and total response times are shown for each condition in Figure 1. Pre-planned contrasts using Dunn's procedure (Kirk, 1968, p. 79) were used to assess the contrasts of interest. This procedure consists of splitting up the alpha level among a set of planned comparisons and does not require a

Total response time	Movement time	Initiation time	Left target	Home keys	Right target	Initiation time	Movement time	Total response time
				• • □ <sup>1</sup>		223	93	316
317	91	226	2 □	• •				
				• •	□ <sup>3</sup>	245	159	404
396	160	236	4 □	• •				
321	96	225	6 □	• • □ <sup>5</sup>		219	101	320
421	169	252	8 □	• •	□ <sup>7</sup>	249	176	425
406	158	248	10 □	• • □ <sup>9</sup>		247	138	385
374	131	243	12 □	• •	□ <sup>11</sup>	236	158	394

FIGURE 1. Mean initiation time, movement time, and total response time (in ms) for single and two-handed movements directed away from the body midline. (For actual dimensions of targets and their distances from the home keys, refer to text).

prior significant overall F-ratio. The mean square error was computed for all dependent variables and then, depending on the number of means (in this case 12), the number of desired comparisons (in this case 6) and the degrees of freedom for experimental error (in this case 77) a *d*-value is calculated which must be exceeded by a given difference between means to be significant.

(a) *Initiation time analysis.* For initiation time, *MSe* was 318.8, *d* = 26 ms, *P* < 0.05. No significant overall hand differences (left versus right, mean differences < 5 ms, *P* > 0.05) were found. In two-handed conditions of equal difficulty, the hands initiated the movements at approximately the same time, as revealed by the non-significance of all comparisons (all *P*s > 0.05). The average time difference in initiating the movements of the separate hands in the two-hand easy trials (5 vs. 6) was 6 ms, while in the two-hand difficult trials (7 vs. 8) it was only 3 ms. In the conditions in which each hand was performing tasks of varying difficulty, the easy hand was initiated 3 ms earlier on the average than the difficult one (9 and 12 vs. 10 and 11), a finding that replicates our earlier work (Kelso *et al.*, 1979a,b).

It is conceivable, however, that these small differences between the hands are in part artifactual because they reflect algebraic differences which may have cancelled each other out when the mean was calculated over 20 trials. In a further analysis of the initiation-time data, absolute time differences between each hand were tabulated and placed into time bins. Table I shows that the hands were initiated within 20 ms of each other on over 93% of the valid individual trials, even in conditions of mixed difficulty.

Further evidence for the co-operation of the limbs is provided by the correlations between the two hands computed for each individual subject and presented in Table II. These correlations were extremely high with only one out of a possible 28 below *r* = 0.97. The similarity in initiation behaviour of the two limbs that we have found

has also been obtained by others. Peters (1981), for example, has shown in a high speed cinematographic analysis of bimanual tapping that the hands are initiated near simultaneously, a result which he interprets as evidence in favour of a common activation source for the two hands.

(b) *Movement time analysis.* The pre-planned contrasts of the movement time data produced results consistent with our previous findings (Kelso *et al.*, 1979a,b). MSe was 227.2,  $d = 22$  ms,  $P < 0.05$ ;  $d = 26.6$  ms,  $P < 0.01$ , for single mean comparisons. One-handed easy movement times (1 and 2) were much faster than their difficult counterparts (3 and 4) as Fitts' formulation (Fitts, 1954) predicts (mean difference = 67.5 ms,  $P < 0.01$ ). This effect was also evident when examining two-handed movements of the same difficulty (5 and 6 vs. 7 and 8, mean difference = 74 ms,  $P < 0.01$ ). As expected, the movement times of each hand when performing two-handed tasks of similar difficulty were not significantly different (mean difference for the easy-easy task = 5 ms,  $P > 0.05$ , and for the hard-hard task = 7 ms,  $P > 0.05$ ). Moreover, the mean difference of 23 ms between the two hands when performing tasks of differing difficulty was also non-significant ( $P > 0.05$ ), although there is a clear tendency for the easy hand to reach its target first.

Some insight into the interpretation of the null effect under mixed conditions is obtained by noting that the movement time of the hand performing the easy task of the mixed difficulty task (9 and 12) is considerably elevated over the easy-easy counterpart (5 and 6) (mean difference = 36 ms,  $P < 0.01$ ). In contrast, when examining the hand performing the hard task in the same conditions, the movement times, while not

TABLE I  
*Number of individual trials (and percentage of total trials)  
in which the absolute time differences between hands was  
less than the tabled value (in ms)*

		Absolute difference between hands						Percentage invalid trials
Condition	<10	<20	<30	<40	<50	>50		
Initiation time	Easy-easy	101 (85)	117 (98)	119 (100)			0 (0)	6
	Hard-easy	97 (79)	115 (94)	121 (98)	122 (99)	123 (100)	0 (0)	8
	Easy-hard	96 (70)	122 (98)	123 (99)	123 (99)	124 (100)	0 (0)	11
	Hard-easy	89 (71)	111 (88)	123 (98)	125 (99)	126 (100)	0 (0)	10
Movement time	Easy-easy	77 (63)	110 (89)	120 (98)	122 (94)	123 (100)	0	6
	Hard-hard	58 (49)	87 (73)	103 (87)	112 (94)	116 (98)	3 (3)	8
	Easy-hard	34 (28)	63 (51)	88 (72)	109 (89)	119 (97)	5 (4)	11
	Hard-easy	33 (27)	59 (48)	86 (69)	108 (87)	116 (94)	9 (7)	10
Total response time	Easy-easy	99 (81)	118 (96)	123 (100)	123 (100)	123 (100)	0	6
	Hard-hard	64 (54)	94 (79)	119 (92)	114 (96)	116 (98)	3 (3)	8
	Easy-hard	38 (37)	77 (62)	89 (72)	110 (89)	117 (94)	7 (6)	11
	Hard-easy	42 (33)	80 (64)	106 (84)	115 (91)	118 (94)	8 (6)	10

TABLE II  
*Correlations of left versus right hand for each subject over the valid trials in each of the four two-handed conditions*

Subject	Easy-easy			Hard-hard			Easy-hard			Hard-easy		
	IT <sup>a</sup>	MT <sup>b</sup>	TRT <sup>c</sup>	IT	MT	TRT	IT	MT	TRT	IT	MT	TRT
S <sub>1</sub>	0.99	0.84	0.98	0.99	0.78	0.98	0.97	0.67	0.95	0.97	0.92	0.98
S <sub>2</sub>	0.99	0.50	0.98	0.99	0.78	0.95	0.97	0.83	0.95	0.98	0.45	0.87
S <sub>3</sub>	0.99	0.98	0.98	0.98	0.94	0.98	0.99	0.82	0.97	0.99	0.59	0.98
S <sub>4</sub>	0.97	0.56	0.74	0.99	0.67	0.97	0.99	0.72	0.98	0.99	0.11	0.67
S <sub>5</sub>	0.99	0.77	0.99	0.99	0.96	0.98	0.92	0.28	0.89	0.99	0.76	0.82
S <sub>6</sub>	0.99	0.88	0.99	0.99	0.65	0.93	0.99	0.49	0.97	0.99	0.75	0.97
S <sub>7</sub>	0.99	0.75	0.99	0.99	0.75	0.93	0.98	0.51	0.96	0.97	0.76	0.94

<sup>a</sup> Initiation time in ms.

<sup>b</sup> Movement time in ms.

<sup>c</sup> Total response time in ms.

significantly different (mean difference = 14.5 ms,  $P > 0.05$ ), are reduced compared to their hard-hard counterpart movements. As in our previous experiments, these data suggest that it is not only the easy hand which slows to the level of its more difficult counterpart, rather, *both* hands adjust, admittedly to varying degrees, as if the motor system were adopting a common time scaling for two-handed movements.

As with the initiation times, the absolute difference between movement times for each hand in the paired movements was tabulated (see Table I). The proportion of trials in which movements were made within 10 ms of each other was somewhat lower for the condition of mixed difficulty (27%) than for the conditions of equal difficulty (62% for easy-easy; 49% for the hard-hard). However, even in the conditions of mixed difficulty, approximately 70% of the movements were made within 30 ms of each other. The movement time correlations for each hand in the two-handed condition are presented in Table II. Although not as high as the correlations for initiation times, 20 of the 28 individual correlations were significant ( $P < 0.05$ ), with no significant differences across the four conditions.

(c) *Total response time.* The outcome of the total response time analysis was very similar to that of the movement time data. All significant effects in the movement time analysis were also significant in the total response time analysis. For the combined condition, the mean time difference between easy and difficult targets was 20 ms which mirrors our earlier data (Kelso *et al.*, 1979a) and is not significant at the 0.05 level (MSe = 628.0,  $d = 36$  ms,  $P < 0.05$ ). Co-ordinating the movements of both hands in the combined condition eliminated 80% of the difference in total response time found between the easy-easy and hard-hard conditions.

With respect to the tabulation of the absolute time differences of each hand (see Table I), since the initiation times for each hand were so similar, the total response-time effects were almost identical to those of the movement times. As expected, the individual subject correlations for response times were high (see Table II), and all were significant at the 0.05 level.



*Kinematic Analysis*

The last four trials of each subject in each condition were filmed as described previously. We have chosen to illustrate the results of two subjects, although we used mean data (over all seven subjects) for the analysis of kinematic features. The trajectories for subjects MB and PH are shown in Figures 2 and 3, respectively. These trajectories, with minor exceptions, were typical of all subjects. Although we have made no attempt to quantify the shape of the trajectories themselves, it is clear that the patterns for each limb are extremely reproducible from trial to trial. Moreover, the trajectories between limbs are very similar under conditions in which the target difficulty is identical for each limb. Even in the combined easy-hard condition, although the paths of the two trajectories are obviously different, their form looks

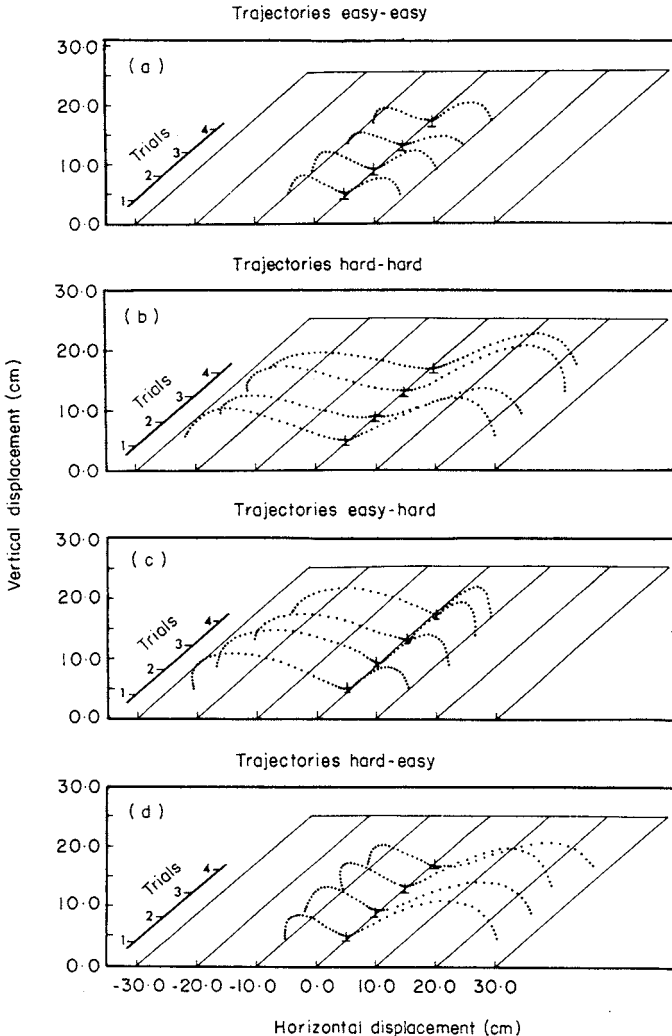


FIGURE 2. Movement trajectories for subject M.B. plotted on the horizontal and vertical displacement plane for the four two-handed conditions. Dots refer to light-emitting-diode pulses sampled at 200 Hz.

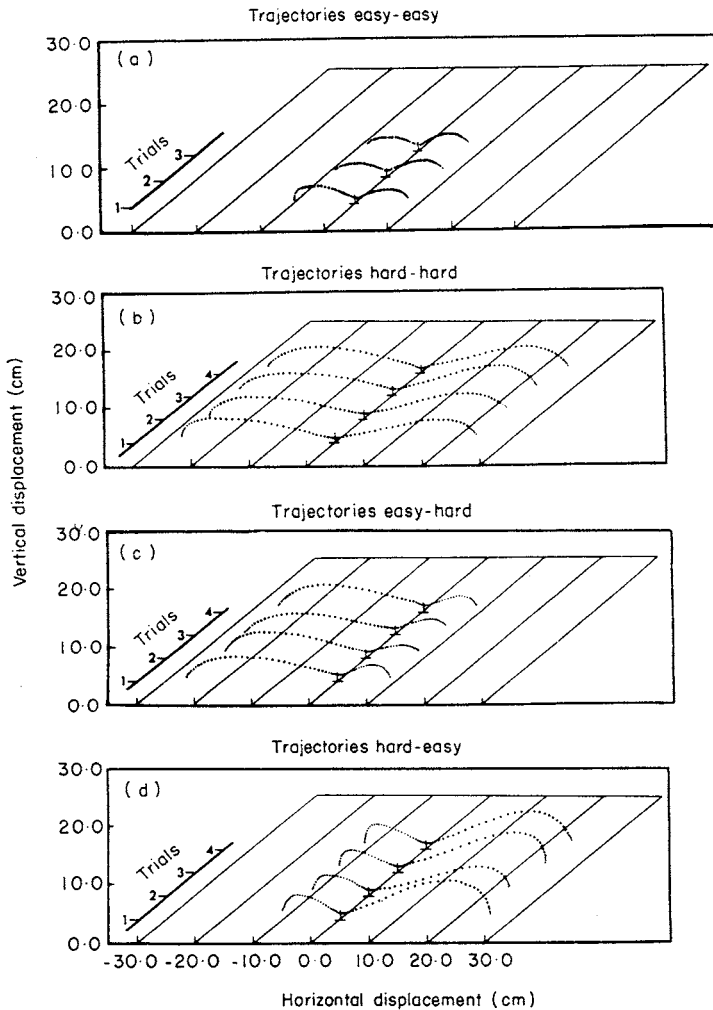


FIGURE 3. Movement trajectories for subject P.H. plotted on the horizontal and vertical displacement plane for the four two-handed conditions. Dots refer to light-emitting-diode pulses sampled at 200 Hz. One trial was lost in the easy-easy conditions due to poor film processing.

remarkably alike as if one were an expanded (or contracted) version of the other. A further notable feature of all the trajectories is that they are smooth and continuous (as judged by the relative spacing between dots) and exhibit no evidence of any "feedback" corrections, an observation that fits the rapid movement times in this experiment.

Knowing the time course of the trajectories, the horizontal and vertical components of the displacement, velocity, and acceleration over time were derived as described in the Methods section. These are depicted in Figures 4 and 5, again for the same two subjects (see figure legends for plotting convention). In both conditions in which the left and right hands perform the same task, it is apparent that the kinematics are quite

similar. Of greater interest however, are the conditions of mixed difficulty. Note in Figures 4 and 5 that there is remarkable similarity in each pair of displacement curves, as if one curve is scaled to the other. There are a number of other kinematic parameters that remain relatively invariant between the limbs. One is the time of peak velocity in the horizontal direction, i.e. the time at which the movement changes from positive to negative acceleration (the same temporal locus as the zero crossing of the acceleration-time curve), which is almost coincidental for both hands in each separate condition. Thus the limbs start their braking action at approximately the same time (see also Lestienne, 1979).

A second kinematic descriptor is the point of maximum vertical displacement which corresponds to the transition between the ascent and descent of the movement and the time of zero vertical velocity. Note in Figures 4 and 5 that once again this point in time is also virtually coincidental for both hands. Two further kinematic descriptors of interest are the times of peak vertical velocity in the positive (upward) and negative (downward) directions. Once again, we see a relatively tight correspondence in timing across both limbs.

The mean times-to-peak of the four kinematic variables discussed above are presented in Table III. Note that in the single hand conditions the times to peak of these parameters are quite disparate from each other. As expected, the difference is also apparent in two-handed movements of equal difficulty. However, when the hands move to different targets the time differences between the two hands are reduced considerably. For instance, the time to peak vertical velocity difference is reduced from 21.0 ms in the single hand condition to 8 ms in the two-handed condition. Like the behavioural data, the two limbs exhibit a kind of "mutual synchronisation" under mixed difficulty conditions, with the easy hand slowing down to a much greater degree than the hard hand speeding up.

## Experiment II

One obvious test of the claim that the limbs, under certain conditions, are co-ordinated and controlled as a single unitary structure is to manipulate a part of the structure to determine if the behaviour of the unit or only the part is modulated. We have examined this idea in other work on rhythmical hand movements (Kelso *et al.*, 1981) by perturbing one limb mechanically (a torque that changed the direction of motion) and then observing if the phase relations of the limbs were affected by the perturbation. Quite remarkably, both limbs returned to synchrony almost immediately. The tack in the present experiment was a little different. Rather than introducing a mechanical perturbation we placed an obstacle in the path of one limb while requiring both limbs to move to their respective targets. Although obstacle height was somewhat arbitrarily chosen (about the height of a beer bottle), and was the same for all subjects, we predicted nevertheless that the obstacle would exert a mutual influence on *both* limbs, that is, the unit as a whole.

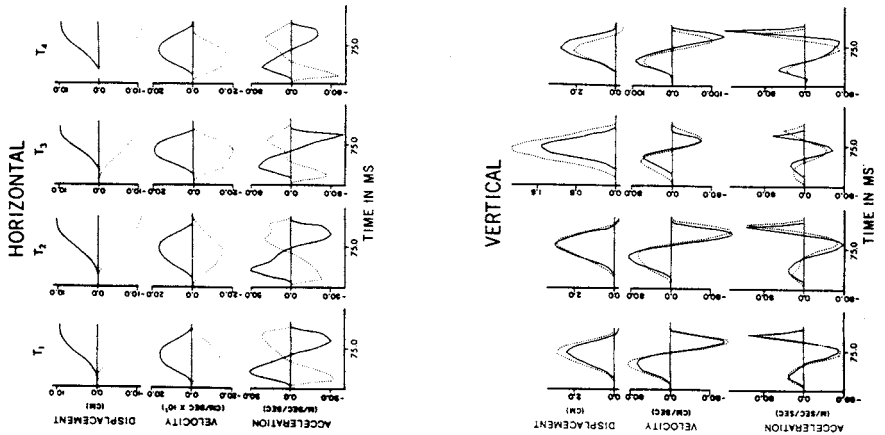
### *Methods*

#### *Subjects*

Seven subjects, all of whom had participated in the previous experiment, served as subjects in Experiment II.

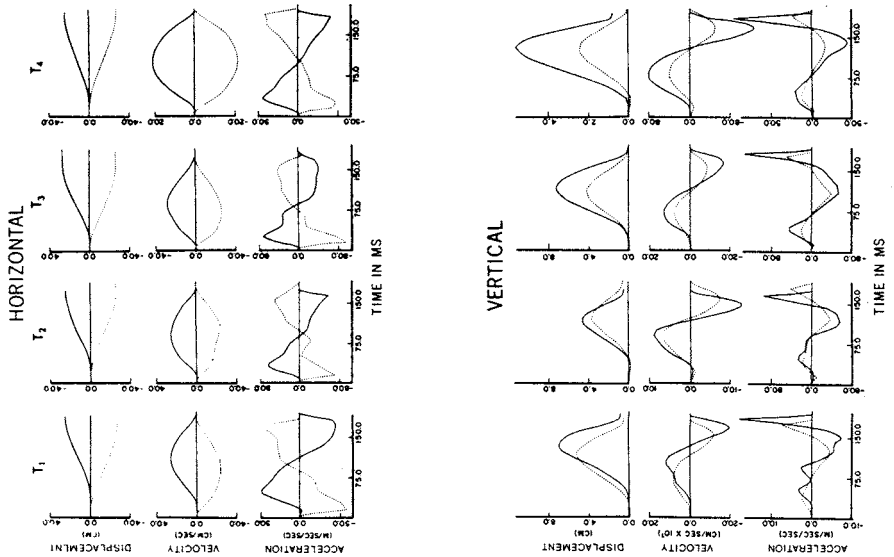
A.

KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (EASY-EASY)

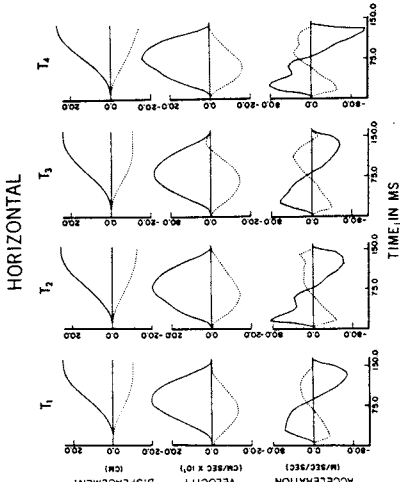


B.

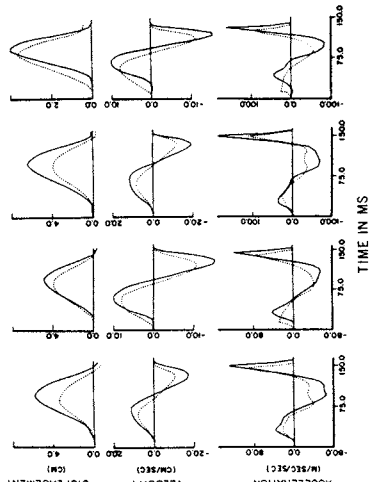
KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (HARD-HARD)



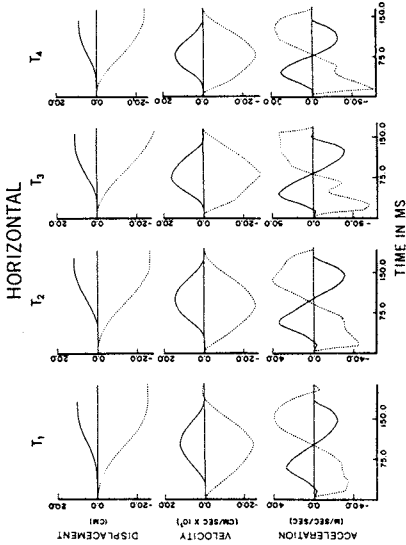
D. KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (HARD-EASY)



VERTICAL



C. KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (EASY-HARD)



VERTICAL

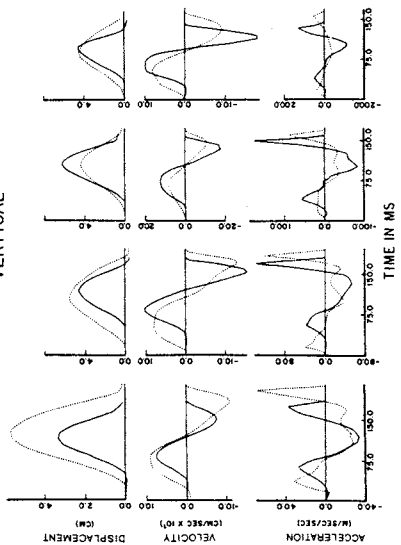
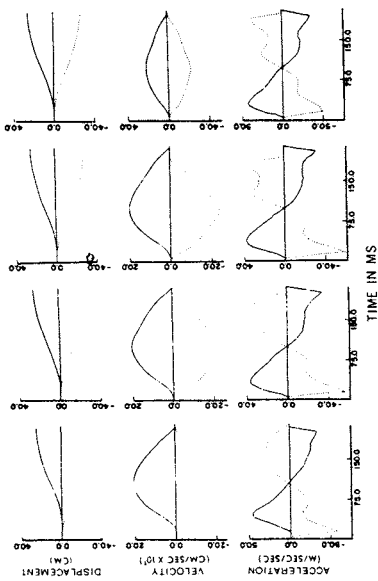


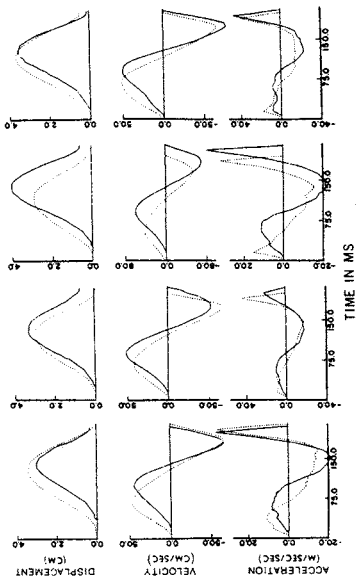
FIGURE 4. The patterns of horizontal and vertical displacement, velocity and acceleration over time for the two-handed movement trajectories of subject M.B. (for derivation procedures refer to text). The last four trials in each condition were filmed and are displayed here. . . . ., left; ———, right.

B. KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (HARD-HARD)

HORIZONTAL

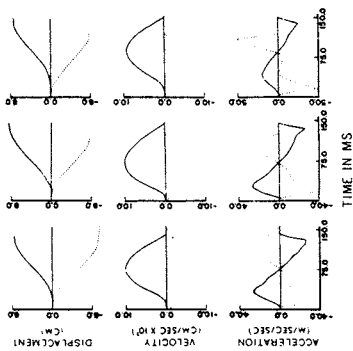


VERTICAL

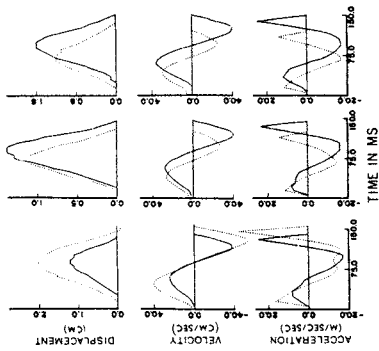


A. KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (EASY-EASY)

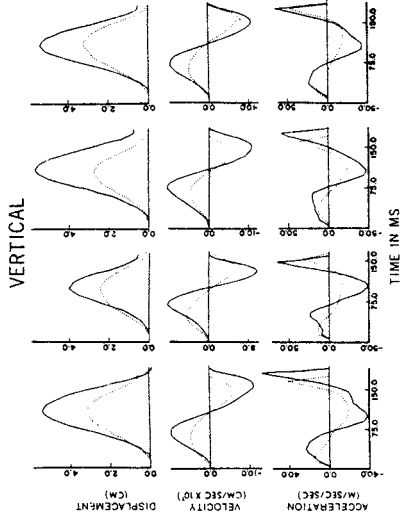
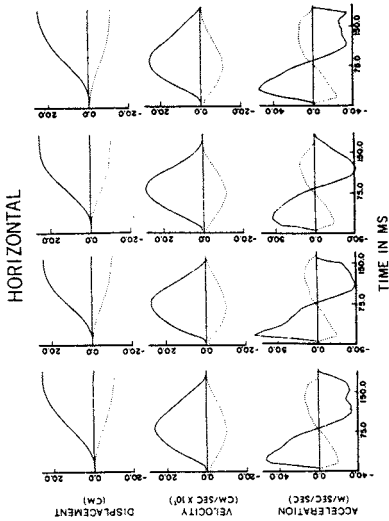
HORIZONTAL



VERTICAL



D. KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (HARD-EASY)



KINEMATIC ANALYSIS OF TWO-HANDED MOVEMENTS (EASY-HARD)

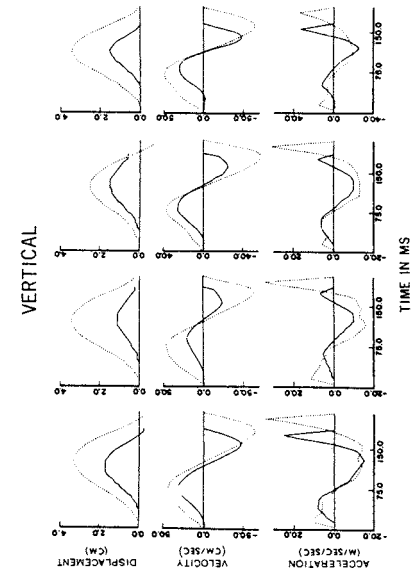
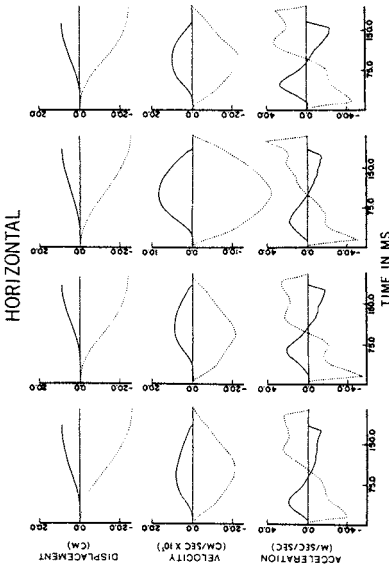


FIGURE 5. The patterns of horizontal and vertical displacement, velocity and acceleration over time for the two-handed movement trajectories of subject P.H. (for derivation procedures refer to text). The last four trials in each condition were filmed and are displayed here. . . . ., left; —, right.

TABLE III  
*Mean times to peak (in ms) of kinematic descriptors<sup>a</sup>*

Movement conditions	Kinematic descriptor			
	Vertical displacement	Horizontal velocity	Vertical velocity 1	Vertical velocity 2
Single-easy	47	33	21	72
Single-hard	90	64	42	137
Two-Hand Same				
Easy	43	39	19	68
Easy	53	40	24	74
Hard	90	62	43	139
Hard	91	62	43	139
Two-Hand Mixed				
Easy	68	42	30	106
Hard	82	57	38	129

<sup>a</sup> Refer to text for details.

### *Apparatus*

The apparatus used in the first experiment was also employed in this experiment with the following two modifications. First, only one target size by target distance was utilised (3.6 cm target, 24 cm from the home keys). Second, a barrier (18 cm high by 7.5 cm wide) was placed mid-way between the home key and the target key. (We will refer to this as the "hurdle" condition.) As in the first experiment, light-emitting diodes were attached to the fingers in order to provide trajectory information.

### *Task*

Instructions to the subject were to move from the home key to the target key as quickly and as accurately as possible, without touching the barrier, following the onset of a stimulus to move. Again, nothing was said to the subject regarding simultaneity in the dual-limb case. There were two conditions: (a) a single-hand condition over the barrier, and (b) a two-hand condition, with the barrier erected only on one side.

### *Procedure*

All subjects performed both of the conditions in a random order. Four of the subjects had the hurdle on the left side, while the other three had the hurdle on the right side. Twenty trials, which were not preceded by any practice trials, were performed in each of the conditions. The first two trials, two of the middle trials (trials 8 and 9) and the final two trials were filmed in the two-handed condition. For each trial there was a ready light followed by a 1- to 3-s variable foreperiod, and the stimulus to move. Each trial was separated by a 5-s inter-trial interval.

### *Results and Discussion*

As in Experiment 1, first we present the behavioural findings followed by the kinematic data. Mean initiation time, movement time, and total response time are shown for the four conditions in Figure 6. In two-handed movements, the limb moving over the hurdle was initiated slightly before the contralateral limb (mean difference = 9.5 ms). This early departure, however, was offset by a longer



Total response time	Movement time	Initiation time	Left target	Home keys	Right target	Initiation time	Movement time	Total response time
457	203	254	□ ← - - - - - ● ●	● ●	□	245	253	499
551	277	274	□ ← - - - - - ● ●	● ●	□	284	219	503
				● ●	□	229	240	469
535	286	249	□ ← - - - - - ● ●	● ●				

FIGURE 6. Mean initiation time, movement time, and total response time (in ms) for an experiment in which one limb must traverse an obstacle (solid line) while the other (dashed line) is left free to vary (refer to text for distances, target dimensions, and obstacle height).

movement time for the limb traversing the hurdle (mean difference = 54 ms,  $P < 0.01$ ) which was reflected in a significant total response-time difference of 45 ms, ( $P < 0.01$ ).

Thus, while we find that the imposition of a hurdle in the movement trajectory of the limbs disrupts the simultaneity effects we had witnessed in Experiment I and in our previous studies (Kelso, Southard and Goodman, 1979a,b), it is also apparent that there is a compensatory effect on the non-hurdle limb. This observation comes about by comparing times in the hurdle condition to those in the non-hurdle conditions of Experiment I. For instance, the movement times and total response times of the non-hurdle hand in the hurdle conditions were elevated 38.5 and 57 ms, respectively, over the counterpart conditions of Experiment I (7 and 8 in Figure 1).

A further observation of the individual subjects' data (see Table IV) reveals a large

TABLE IV  
*Individual mean data (in ms) for hurdle and non-hurdle trials*

	Initiation time		Movement time		Total response time	
	Non-hurdle	Hurdle	Non-hurdle	Hurdle	Non-hurdle	Hurdle
Hurdle on right						
SP	280	274	204	233	484	507
RH	287	277	258	292	545	570
TH	215	203	188	245	402	447
GH	233	229	165	244	398	473
Mean	254	246	204	254	457	499
Hurdle on left						
MB	249	239	240	261	489	499
SB	332	331	255	290	587	621
PH	272	253	163	280	434	533
Mean	284	274	219	277	503	551

disparity between the timing relationships of the limbs across the different subjects. The mean difference in total response times for the hurdle versus the non-hurdle limb ranged from a low of 10 ms (subject MB) to a high of 99 ms (subject PH). This suggests that at least some subjects (e.g. TH, GH and especially PH) may have adopted a rather different strategy than the one adopted by subjects in our earlier studies (Experiment I and Kelso *et al.*, 1979a,b). As indicated in Table IV, initiation times for PH show a sizeable temporal disparity between the hands, with the hurdle hand being initiated some 19 ms before its non-hurdle counterpart. Rather than initiating the movements simultaneously, subject PH appears to perform the two movements in a 1-2 manner rather than as a unified pair.<sup>2</sup> This may be one of the reasons for the differences observed among subjects. Also, the movement times of subjects TH, GH and PH are sufficiently different between the hurdle and non-hurdle limbs to suggest that the parameters for the two limbs may be specified separately. The movements required by the task may have been perceived as sufficiently different from each other that the powerful symmetry constraint between the limbs no longer holds, hence the two hands may not participate in the same co-ordinative structure.

On the other hand, other subjects do appear to co-ordinate the limbs as a single unit. The movement time and total response time differences between the limbs are much smaller for subjects SP, RH, MB and SB (means = 32 ms and 23 ms, respectively) than for PH, GH and TH (means = 81 ms and 73 ms, respectively). Although the trajectories of both limbs are modified by the hurdle, the effects are much stronger for the former grouping of subjects than the latter. To illustrate, the limb trajectories and consequent kinematics are presented for subjects PH and MB in Figures 7 and 8. There are dramatic differences between the two displays. For PH, shown in Figure 7, the non-hurdle limb reaches a maximum vertical displacement of less than one-half of the limb traversing the hurdle. Even so, and especially on the first trial, the vertical displacement for the non-hurdle limb is amplified more than usual (compare Figure 5 for the same subject performing under hard-hard conditions). In contrast, for subject MB, shown in Figure 8, the trajectories of both limbs are very alike across trials, and the kinematic similarities between both limbs are strikingly apparent.

### Experiment III

Because all the published experiments using this paradigm have examined symmetrical movements of limbs, and because the symmetry constraint seems to be such a powerful one in movement (see Introduction), we felt that it would be useful also to examine asymmetrical movements that involve non-homologous muscles. On the face of it, there are not too many reasons to predict different results for such movements. Skilled pianists, for example, appear to be able to move their hands in the same or different directions with equal facility. It is still possible, however, that non-homologous muscle groups may be less effectively controlled as a functional unit in our task, or indeed that they are controlled in a more independent way. We explore this issue in the final experiment of this series.

<sup>2</sup> It is worth noting that subject PH had considerable ballet experience as a consequence of which she may have been more capable of controlling the limbs independently in this task.

Trajectories (hurdle on left only)

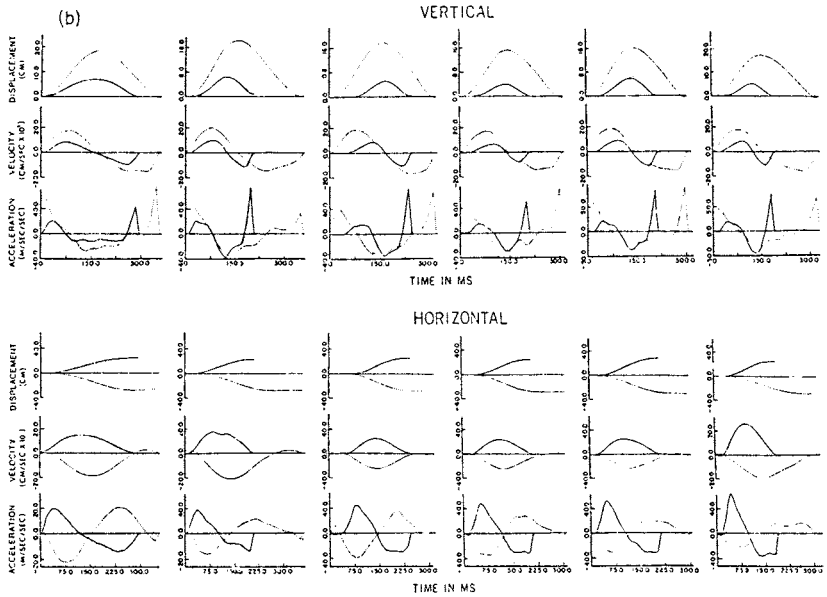
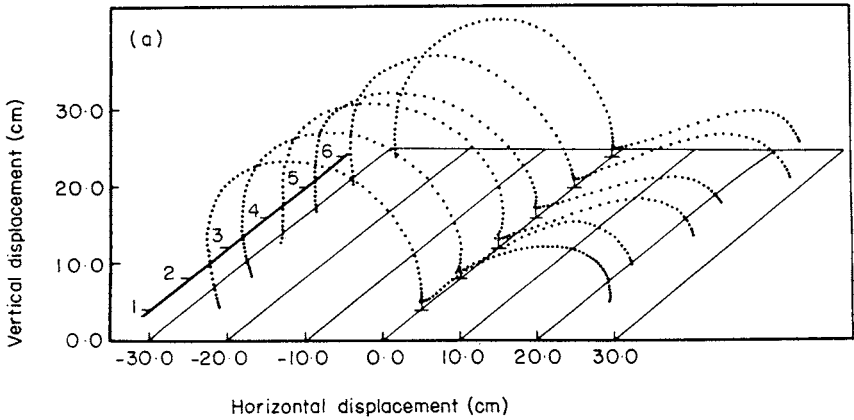


FIGURE 7. (a) Movement trajectories and (b) consequent kinematic profiles of subject P.H. Trials 1 through 6 on z-axis correspond to filmed trials 1 and 2, 8 and 9, 19 and 20. Hurdle on left only. . . . , hurdle; —, non hurdle.

*Methods*

*Subjects*

Subjects were ten right-handed volunteers between the ages of 20 and 32 years, none of whom had participated in any of the previous two-handed experiments.

*Task*

The two-handed apparatus described previously was modified somewhat for this experiment which involved asymmetrical movements of the limbs. The base of the apparatus was split into

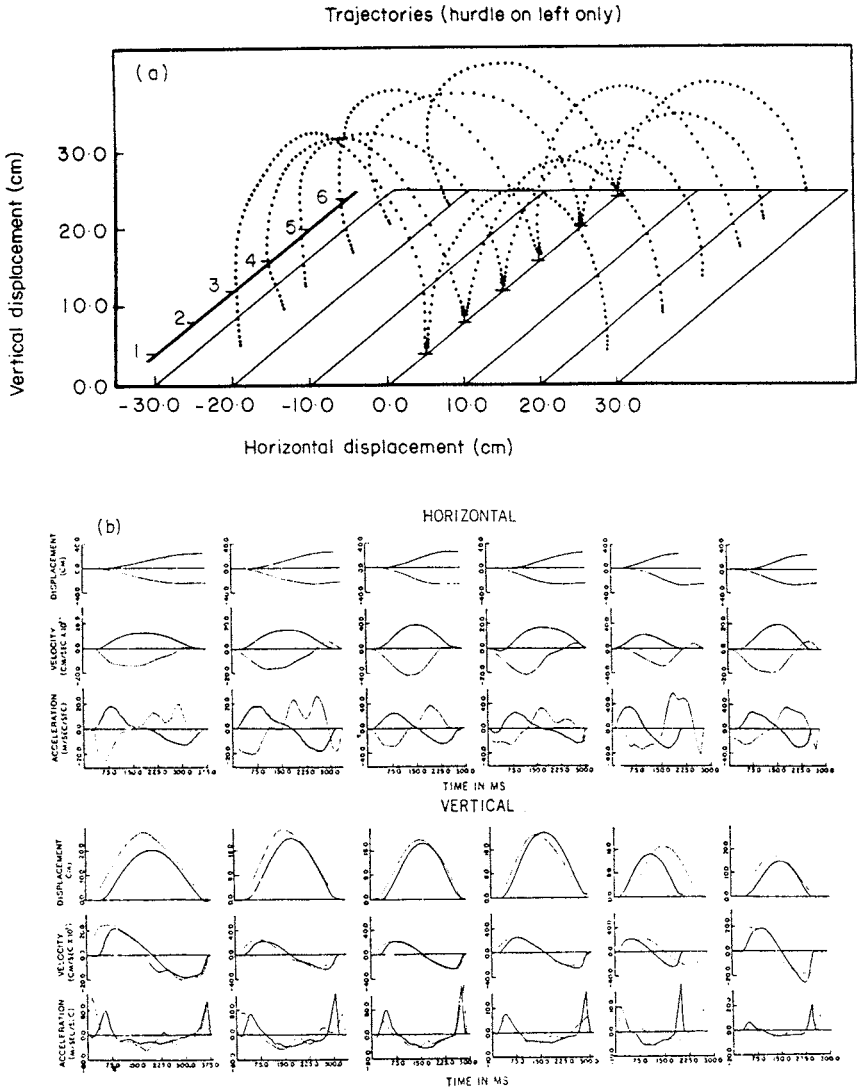


FIGURE 8. (a) Movement trajectories and (b) consequent kinematic profiles of subject M.B. Trials 1 through 6 on z-axis correspond to filmed trials 1 and 2, 8 and 9, and 19 and 20. Hurdle on left only . . . . hurdle; —, non-hurdle.

two identical halves, such that each housed a home key and a target key which was positioned either near or far from the home key. The two bases were then placed side by side and oriented so that the home keys were located opposite the left shoulder of the subject, and the target keys extended laterally to the right. Thus, movements of both hands were always to the right, and involved primarily flexion of the left arm and extension of the right. As in our previous studies, two distance by target sizes were used, resulting in both an easy task (7.2 cm target, centred 6 cm from the home key) and a hard task (3.6 cm target, centred 24 cm from the home key). Filming was not conducted for this experiment. Other than these modifications, the apparatus remained identical to that of Experiment I.

All combinations involving single and two hands and easy and hard targets were performed by each subject. Instructions to subjects were identical to those described previously. In each of the eight resulting conditions, there were 25 trials; the first five were considered to be practice trials and excluded from statistical analysis. One half of the subjects performed the task such that the right hand was always associated with the home key/target key arrangement closest to the body, while the left hand was assigned to the home key/target key farthest from the body. This assignment was reversed for the remaining subjects.

### *Results and Discussion*

Mean initiation times, movement times, and total response times are shown for each condition in Figure 9. Our main concern was whether the findings of simultaneity of initiation and termination of movement found in our previous work extended to asymmetrical movements in which non-homologous muscle groups were used. The basic findings were indeed replicated. No significant differences in initiation times were found between hands, the largest mean difference = 8 ms,  $P > 0.05$  ( $MSe = 395.2$ ,  $d = 23$  ms,  $P < 0.05$ ).

As expected, movements to the hard target took longer than movements to the easy target, both in the single hand conditions (mean difference = 64 ms,  $P < 0.01$ ), and the two hand conditions in which the movements were identical (mean difference = 66 ms,  $P < 0.01$ ,  $MSe = 912.2$ ,  $d_{0.01} = 48$  ms). This rather large difference in movement times between the easy and hard conditions was reduced considerably when the two movements were executed under conditions of mixed difficulty (mean difference = 15 ms,  $P > 0.05$ ). These results then mirror the major aspects of our earlier work on symmetrical movements, and provide little reason to assume that the organisation for asymmetrical movements is qualitatively different.

### *General Discussion*

Our intent in these experiments was to elaborate the processes underlying the control and coordination of both limbs when they cooperate together in a task that places very different spatial demands on each limb. A key feature of the approach was to combine behavioural measures of movement outcome (e.g. initiation time, movement time) with information about space-time trajectories, followed by a kinematic analysis of the movement trajectories themselves. Although there is a long history of work on the analysis of human motion (e.g. Marey, 1894), only quite recently have engineers and neuroscientists come to recognise its importance for understanding the logical operations through which the nervous system participates in the organisation of skilled movements (e.g. Abend, Bizzi and Morasso, in press; Soechting and Lacquaniti, 1981).

A central and continuing aspect of our work, following the lead of Bernstein (1967), is to examine movements in which many degrees of freedom are involved, in an attempt to identify the "significant functional units" of co-ordination (cf. Greene, 1971). After Gelfand and Tsetlin (1971, see also Bernstein, Chapter 6), we envisage the variables that define these functional units or co-ordinative structures as falling into two classes: *essential* variables which determine the form of the function (also referred to as the structural prescription of movement, cf. Boylls, 1975; Kelso *et al.*, 1979a,b; Turvey, Shaw and Mace, 1978) and *non-essential* variables which specify marked changes in

Condition	Home keys	Easy target	Hard target	Initiation time	Movement time	Total response time
1	●	→ □ 1		240	120	360
2	●	→ □ 2		224	103	327
3	●	→ □ 3		228	183	411
4	●	→ □ 4		233	169	402
5	●	→ □ 5		249	141	390
	●	→ □ 6		253	139	392
6	●	→ □ 7		253	207	460
	●	→ □ 8		248	205	453
7	●	→ □ 9		249	176	425
	●	→ □ 10		241	183	424
8	●	→ □ 11		271	229	500
	●	→ □ 12		273	204	477

FIGURE 9. Mean initiation time, movement time, and total response time (in ms) for single and two-handed lateral movements to the right. Two-handed conditions require asymmetrical movements involving non-homologous muscle groups.

the values of the function, but leave its topological properties essentially unchanged (the metrical prescription).

A main way to discover the signature of co-ordinative structures is to alter the metrics of the motor activity (e.g. speed it up, do it more forcefully, alter its spatial requirements) and observe which variables are modified, and which variables or relations among variables remain unchanged. Note that changing the metrical properties of an action could obscure its basic form by altering properties of individual components that might otherwise remain stable. Alternatively, these changes may index the major ways that invariance can be observed: some variables must change but others must remain the same if the internal structure of the action is to be preserved. This strategy has proved successful in uncovering co-ordinative structure styles of organisation in many different types of activities (Boylls, 1975; Fowler, 1977; Kelso, 1981; Kelso and Tuller, in press; Kugler, Kelso and Turvey, 1980). The most well-known examples come from studies of locomotion. For example, when a cat's speed of locomotion increases, the duration of the "step cycle" decreases (cf. Grillner, 1975; Shik and Orlovskii, 1976). Changes in the speed of locomotion are known to be accomplished by distributing more force into the support or stance phase of the cycle. That is, there is an increase in the activity of extensor muscles in an individual limb when it is in contact with the ground. Significantly, an increase in propulsive force during the stance phase does not disrupt the *relative timing* among linked extensor muscles, even though their absolute magnitudes and durations change considerably

(Engberg and Lundberg, 1969; see also Madeiros, 1978 and Shapiro, Zernicke, Gregor and Diestal, 1981, for human evidence).

Constancy of timing relationships across scalar changes in rate has been reported for other activities of a cyclical kind such as mastication and respiration (see Grillner, 1977, for review). However, the stability of temporal relationships over metrical change has also been shown to characterise less obviously cyclical activities including postural control (Nashner, 1977), voluntary arm movements (Lestienne, 1979) and handwriting (Viviani and Terzuolo, 1980). Similarly, Freund and Budingen (1978) demonstrate that the rise time of voluntary contraction in rapid, discrete movements is constant no matter how strong the contraction is or how far the limb has to move. According to Freund and Budingen (1978), "the independence of the time of contraction of skeletal muscles from the final force level or angle of movement is regarded as a necessary condition for the synchrony of synergistic action" (p. 2).

From the overall results of the experiments reported here there is good reason to believe that the motor system solves the problem posed in the present task by constraining the limbs to function as a single, synergistic unit within which component elements vary in a related manner. The behavioural data in Experiments I and III indicate that the large and highly significant differences in movement time found between easy and hard conditions are reduced considerably when the hands are combined. The small but consistent tendency for the easy limb to strike its target first was further reduced when total response time was the dependent measure.

Although their experimental conditions were rather different from ours (10 and 30 cm movements with a weighted stylus to a 1 mm target), Marteniuk and MacKenzie's (1980) results are similar to the present findings as well as our earlier studies. Their data also reveal a significant slowing of the easy hand and a speeding up of the difficult one under mixed conditions compared to two-hand controls. Although they make much of the statistical fact that the easy hand reaches its target earlier, the average difference between the two limbs was only 20 ms, which is in sharp contrast to the difference between the two hand control conditions (mean difference = 68 ms, see Marteniuk and MacKenzie, Table 2).<sup>3</sup> In addition, Marteniuk and MacKenzie (1980) report a "dramatic overshoot" in terms of spatial error for the easy hand under mixed conditions compared to its control, further suggesting a strong coupling between the limbs both spatially and temporally.

The picture of interlimb co-ordination becomes clearer in the present work when the space time trajectories and consequent kinematic characteristics are examined. A number of features of the kinematic data emerge that are worthy of note and which implicate certain underlying processes. In Experiment I it is obvious that the net forces produced in the horizontal direction are different in magnitude for each limb under conditions of varying spatial demand, as revealed by peak accelerations. Moreover, there is considerable inter-trial variability in these values. Even though the metrics change, however, times to peak velocity and acceleration are quite stable; the temporal

<sup>3</sup> As a relevant aside, none of our subjects (and we have tested over 70) in the original Kelso *et al.* (1979) studies and in the present Experiments I and III perceived that the movements were non-simultaneous under combined conditions as revealed through post-experiment interviews. The same has been the case in Marteniuk's work (Reference Note 1), suggesting further that the small differences between the limbs, though occasionally statistically different, are not meaningfully different.

structure remains remarkably invariant (cf. Figures 4 and 5). When an obstacle is placed in the way of one limb (Experiment II) there is still a strong tendency for the limbs to preserve their relative timing, although it is clear that this is not absolutely mandatory for some subjects. It seems apparent, nevertheless, that the scaling requirements on one limb influence the other; what we cannot provide at present is a principled reason for why the effects are greater for some subjects than others. One idea, which we are exploring, is that there may be a critical scaling value on obstacle height to which subjects are perceptually sensitive, that influences whether the limbs are treated as a symmetrical unit or not. The analogy here comes from recent work on locomotion, in which it can be shown that at certain critical values of velocity (related to minimum energy criteria) horses shift from one locomotory pattern to another, e.g. walking to trotting (Hoyt and Taylor, 1981). In our experiments, there may be a critical value of obstacle height in relation to the limb dimensions of the performer, that specifies which co-ordinative structures are to be marshalled.

Although we have not paid much attention to the initiation time data (since it was not the main concern here), it is interesting that there is a general elevation in initiation time in the obstacle experiment, particularly when two limbs are involved. Recent work in this area (see Keele, 1981 for review) suggests that the time to prepare a movement (as reflected in initiation time) is a function of the upcoming movement's complexity (cf. Henry and Rogers, 1960; Sternberg, Monsell, Knoll and Wright, 1978). Moreover, Keele (1981, pp. 1410-1411) suggests that preparatory time increases when two elements are timed differently. To the extent that this occurs in the present Experiment II, there is support for Keele's (1981) analysis; certainly the effects on initiation time are much smaller when the limbs share common timing (cf. Kelso *et al.*, 1979a,b).

The strong tendency for the temporal structure of two-handed movements to be preserved in the face of scalar variation in kinematic values provides support for the Bernstein view that it is not individual muscles that are controlled, but rather muscle linkages that govern the interaction between limbs in a relatively autonomous way. As we have emphasised elsewhere, these are neither fixed motor programs nor prefabricated reflexes; they are modulable and functional units of action directed toward accomplishing particular goals.

In a remarkable but not widely known treatise on cerebellar function, Boylls (1975) argues that the structural aspects of movement—as indexed by qualitative ratios and relative timing among linked muscles and kinematic events—are specified in terms of the relative amounts of activity distributed among descending tracts from the anterior cerebellar lobe. Absolute activities in these tracts specify values on metrical parameters. Obviously we cannot measure neural activity in our paradigm, but we do have some data that is consistent with Boylls' theory. In an identical study to Experiment I, Tuller and Kelso (Reference Note 2) examined interlimb coordination in split-brain patients. Although the movements were slower overall than in normal subjects, the relative timing between the limbs in the easy-difficult conditions was again near synchronous (mean movement time difference = 13 ms). These data suggest that the details of timing may not be prescribed at higher cortical levels, but rather arise from the functioning of autonomous structures, perhaps at the level of cerebellum and below. Interestingly, Orlovskii's (1972) research has shown that



cerebellar stimulation during cat locomotion affects only the magnitude of muscle contraction, leaving the timing among muscles unchanged relative to the step cycle (cf. Shik and Orlovskii, 1976, for review).

The discovery of co-ordinative structures (or muscle linkages) and their rigorous analysis continues to be the goal of much of the Russian work on motor control (e.g. Gelfand, Gurfinkel, Tsetlin and Shik, 1971) and seems crucial if we are to understand how the many degrees of freedom of the motor system are regulated. Investigations have begun of the space-time characteristics of single limb movements to targets (e.g. Abend, Bizzi and Morasso, in press; Soechting and Lacquaniti, 1981) and the present work is an extension to the localisation behaviour of both limbs. It seems reasonable to propose that in our task the equilibrium positions of both limbs can be defined independently as a function of the spatial demands of the task (Kelso *et al.*, 1979a,b; Marteniuk and MacKenzie, 1980). Recent work on single-limb movements suggests that final position can be specified in terms of a balance (or equilibrium point) between the length-tension ratios of agonist and antagonist muscles (e.g. Bizzi, Dev, Morasso and Polit, 1978; Cooke, 1980; Fel'dman, 1966, 1980; Kelso, 1977; Kelso and Holt, 1980; Lestienne *et al.*, 1981). In localising limbs, the muscle-joint ensemble behaves dynamically like a nonlinear oscillatory system with specifiable parameters of equilibrium length and stiffness (cf. Bizzi *et al.*, 1978; Kelso, 1977; Fel'dman, 1966; Kelso, Holt, Kugler and Turvey, 1980). The fact that in our task the magnitude of force produced by each limb is different, adds support to the notion that stiffness and equilibrium length are potentially modulable parameters of two-handed movements.

We strongly suspect, however, that the relatively invariant timing relations between the limbs arise from parameter specification of the muscle-joint linkage system rather than because of special timing mechanisms. In identifying the behaviour of muscle collectives with autonomous nonlinear oscillators, observables such as time and trajectory are not explicitly represented. Instead, they are a consequence of the system's dynamic parameterisation (e.g. equilibrium lengths, stiffnesses).

In our final remarks let us consider how the oscillator-theoretical framework might accommodate the present data on the co-operative behaviour of two limbs producing movements of different amplitude. Two main claims would seem to require evaluation. The first, strong claim (one that we have not actually made) says that the behaviour of the two limbs is *perfectly* synchronised. The second claim (one based on empirical fact) says that there are small, but systematic departures from synchrony that are often not statistically significant. That is, there is a tendency in our data for the limb moving to the near target to arrive slightly earlier than the limb moving to the more distant target. These small departures from perfect synchrony may be amplified when high accuracy demands are placed on subjects (e.g. Marteniuk and MacKenzie, 1980) or if the movements are of widely different amplitudes. However, both claims of perfect synchrony between the limbs and of near-synchrony between the limbs may be accounted for in a principled way by the same type of model.

Consider the perfect synchrony claim first. Let us assume that each limb can be treated as a single-dimensional system and that the stiffness parameterisation is the same for each limb. The equilibrium points, however, must be differentially specified to conform with task requirements. In this case, if both limbs behaved as linear systems they would necessarily produce identical movement times. In linear mass-spring

systems, for example, amplitude and frequency are independent. Thus, assuming constant stiffness over the range of motion, small and large movements must have the same period; the movements will be perfectly isochronous.

Deviations from isochrony can be explained if one makes the additional assumption of stiffness non-linearity. That is, that the average stiffness is not absolutely constant throughout the motion. In "soft", non-linear springs, for example (e.g. Jordan and Smith, 1977), stiffness actually decreases with increasing distance from the equilibrium point. Extrapolating to the present case, movements of large amplitude will be slightly slower than those of short amplitude, because they have smaller average stiffnesses over the range of motion. Moreover, the greater the amplitude difference between the two limbs the greater should be deviations from isochrony. Thus, if the limbs are viewed as behaving like linear oscillatory systems, perfect isochrony is predicted. Consistent deviations from isochrony, however, can be accommodated by the assumption that the limbs in this case behave as "soft" non-linear oscillators in which stiffness is defined differentially for short and long movements.

In conclusion, the present data reveal a dissociation between force scaling and timing that is indexical of muscle-joint ensembles when they are temporarily constrained to function as a single unit. Such units appear to share the same abstract functional organisation as autonomous non-linear oscillatory systems.

This research was supported by NINCDS Grant NS-13617, BRS Grant RR-05596 and Contract No. N00014-83-c-0083 from the U.S. Office of Naval Research. We thank Betty Tuller for very helpful comments on an earlier version, Stephen Monsell and two anonymous reviewers for their thought-provoking reviews and Elliot Saltzman for many helpful discussions on the mysteries of movement and the nature of oscillators. We also thank the many individuals (too numerous to name) who have talked with us about these data at various colloquia in which they have been presented.

### Reference Notes

1. MARTENIUK, R. G. Personal communication, October 1980.
2. TULLER, B. and KELSO, J. A. S. Interlimb coordination in split-brain patients. Manuscript in preparation.

### References

- ABEND, W., BIZZI, E. and MORASSO, P. (in press). Human arm trajectory formation. *Brain*, in press.
- BERNSTEIN, N. A. (1967). *The Coordination and Regulation of Movements*. London: Pergamon Press.
- BIZZI, E., DEV, P., MORASSO, P. and POLIT, A. (1978). Effects of load disturbance during centrally initiated movements. *Journal of Neurophysiology*, **41**, 542-56.
- BOYLLS, C. C. (1975). A theory of cerebellar function with applications to locomotion. II. The relation of anterior lobe climbing fiber function to locomotor behavior in the cat. *COINS Technical Report 76-1*, Department of Computer and Information Science, University of Massachusetts.
- COOKE, J. D. (1980). The organization of simple, skilled movements. In G. E. STELMACH and J. REQUIN (Eds), *Tutorials in Motor Behavior*. Amsterdam: North Holland.
- DELCOMYN, F. (1980). Neural basis of rhythmic behavior in animals. *Science*, **210**, 492-8.
- ENGBERG, I. and LUNDBERG, A. (1969). An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiologica Scandina*, **75**, 614-30.

- FEL'DMAN, A. G. (1966). Functional tuning of the nervous system with control of movement or maintenance of a steady posture. III. Mechanographic analysis of execution by man of the simplest motor tasks. *Biophysics*, **11**, 766-75.
- FEL'DMAN, A. G. (1980). Superposition of motor programs—II. Rapid forearm flexion in man. *Neuroscience*, **5**, 91-5.
- FITTS, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, **47**, 381-91.
- FOWLER, C. (1977). *Timing Control in Speech Production*. Bloomington, Ind.: Indiana University Linguistics Club.
- FRIEND, H. J. and BUDINGEN, H. J. (1978). The relationship between speed and amplitude of the fastest voluntary contractions of human arm muscles. *Experimental Brain Research*, **31**, 1-12.
- GELFAND, I. M., GURFINKEL, V. S., TSETLIN, M. L. and SHIK, M. L. (1971). Some problems in the analysis of movements. In I. M. GELFAND *et al.* (Eds), *Models of the Structural-functional Organization of Certain Biological Systems*. Cambridge, Mass.: MIT Press.
- GREENE, P. H. (1971). Introduction. In I. M. GELFAND, V. S. GURFINKEL, S. V. FOMIN and M. L. TSETLIN (Eds), *Model of the Structural-functional Organization of Certain Biological Systems*. Cambridge, Mass.: MIT Press.
- GREENE, P. H. (1972). Problems of organization of motor systems. In R. ROSEN and F. SNELL (Eds), *Progress in Theoretical Biology*. New York and London: Academic Press.
- GRILLNER, S. (1975). Locomotion in vertebrates. *Physiological Reviews*, **55**, 247-304.
- GRILLNER, S. (1977). On the neural control of movement—A comparison of different basic rhythmic generators. In G. S. STENT (Ed.), *Function and Formation of Neural Systems* (Life Sciences Research Report, Vol. 6). Berlin: Dahlem.
- HENRY, F. M. and ROGERS, D. E. (1960). Increased response complexity for complicated movements and a memory drum theory of neuromotor reaction. *Research Quarterly*, **31**, 448-58.
- HOYT, D. F. and TAYLOR, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature*, **292**, 239-40.
- JORDAN, D. W. and SMITH, P. (1977). *Nonlinear Ordinary Differential Equations*. Oxford: Clarendon Press.
- KEELE, S. W. (1981). Behavioral analysis of movement. In V. B. BROOKS (Ed.), *Handbook of Physiology: Section 1: The Nervous System. Volume II. Motor Control, part 2*. Baltimore, Md.: American Physiological Society.
- KELSO, J. A. S. (1977). Motor control mechanisms underlying human movement reproduction. *Journal of Experimental Psychology*, **3**, 529-43.
- KELSO, J. A. S. (1981). Contrasting perspectives on order and regulation in movement. In J. LONG and A. BADDELEY (Eds), *Attention and Performance IX*. Hillsdale, N.J.: Erlbaum.
- KELSO, J. A. S. and HOLT, K. G. (1980). Exploring a vibratory systems analysis of human movement production. *Journal of Neurophysiology*, **43**, 1183-96.
- KELSO, J. A. S., HOLT, K. G., KUGLER, P. N. and TURVEY, M. T. (1980). On the concept of coordinative structures as dissipative structures: II. Empirical lines of convergence. In G. E. STELMACH (Ed.), *Tutorials in Motor Behavior*. New York: North-Holland Publishing Co.
- KELSO, J. A. S., HOLT, K. G., RUBIN, P. and KUGLER, P. N. (1981). Patterns of human interlimb coordination emerge from the properties of nonlinear limit cycle oscillatory processes: Theory and data. *Journal of Motor Behavior*, **13**, 226-61.
- KELSO, J. A. S., SOUTHARD, D. L. and GOODMAN, D. (1979a). On the nature of human interlimb coordination. *Science*, **203**, 1029-31 (a).
- KELSO, J. A. S., SOUTHARD, D. L. and GOODMAN, D. (1979b). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, **5**, 229-38 (b).
- KELSO, J. A. S. and TULLER, B. (in press). A dynamical basis for action systems. In M. S. GAZZANIGA (Ed.), *Handbook of Cognitive Neuroscience*. New York: Plenum.

- KIRK, R. E. (1968). *Experimental Design: Procedures for the Behavioral Sciences*. Belmont, Calif.: Wadsworth Publishing Co.
- KLIMA, E. S. and BELLUGI, U. (1979). *The Signs of Language*. Cambridge, Mass.: Harvard University Press.
- KUGLER, P. N., KELSO, J. A. S. and TURVEY, M. T. (1980). On the concept of coordinative structures as dissipative structures: I. Theoretical lines of convergence. In G. E. STELMACH and J. REQUIN (Eds), *Tutorials in Motor Behavior*. New York: North-Holland Publishing Co., pp. 1-47.
- LESTIENNE, F. (1979). Effects of inertial load and velocity on the braking process of voluntary limb movements. *Experimental Brain Research*, **35**, 407-18.
- LESTIENNE, F., POLIT, A. and BIZZI, E. (1981). Functional organization of the motor process underlying the transition from movement to posture. *Brain Research*, **230**, 121-31.
- MADEIROS, J. (1978). Investigation of neuronal mechanisms underlying human locomotion: An EMG analysis. Unpublished doctoral dissertation, University of Iowa.
- MAREY, E. (1894). *Le mouvement*. Paris: G. Masson.
- MARTENIUK, R. G. and MACKENZIE, C. L. (1980). A preliminary theory of two-handed movement control. In G. E. STELMACH and J. REQUIN (Eds), *Tutorials in Motor Behavior*. Amsterdam: North-Holland.
- NASHNER, L. M. (1977). Fixed patterns of rapid postural responses among leg muscles during stance. *Experimental Brain Research*, **30**, 13-24.
- NEWELL, K. M. (1980). The speed-accuracy paradox in movement control: Error of time and space. In G. E. STELMACH and J. REQUIN (Eds), *Tutorials in Motor Behavior*. Amsterdam: North-Holland.
- ORLOVSKII, G. N. (1972). The effect of different descending systems on flexion and extension activity during locomotion. *Brain Research*, **60**, 359-71.
- PAVLIDIS, T. (1973). *Biological Oscillators: Their Mathematical Analysis*. New York and London: Academic Press.
- PETERS, M. (1981). Handedness: Coordination of within- and between-hand alternating movements. *American Journal of Psychology*, **94**, 633-43.
- POLIT, A. and BIZZI, E. (1978). Processes controlling arm movements in monkeys. *Science*, **201**, 1235-7.
- SALTZMAN, E. (1979). Levels of sensorimotor representation. *Journal of Mathematical Psychology*, **20**, 91-163.
- SCHMIDT, R. A., ZELAZNIK, H. N., HAWKINS, B., FRANK, J. S. and QUINN, J. T. Jr. (1979). Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychological Review*, **86**, 415-51.
- SHAPIRO, D. C., ZERNICKE, R. F., GREGOR, R. J. and DIESTAL, J. D. (1981). Evidence for generalized motor programs using gait-pattern analysis. *Journal of Motor Behavior*, **13**, 33-47.
- SHIK, M. L. and ORLOVSKII, G. N. (1976). Neurophysiology of locomotor automatism. *Physiological Reviews*, **56**, 465-501.
- SOECHTING, J. E. and LACQUANITI, F. (1981). Invariant characteristics of a pointing movement in man. *Journal of Neuroscience*, **1**, 710-20.
- STEIN, P. S. G. (1977). Application of the mathematics of coupled oscillator systems to the analysis of the neural control of locomotion. *Federation Proceedings*, **36**, 2056-9.
- STERNBERG, S., MONSELL, S., KNOLL, R. L. and WRIGHT, C. E. (1978). The latency and duration of rapid movement sequences: Comparisons of speech and typewriting. In G. E. STELMACH (Ed.), *Information Processing in Motor Control and Learning*. New York and London: Academic Press.
- TURVEY, M. T. (1977). Preliminaries to a theory of action with reference to vision. In R. SHAW and J. BRANSFORD (Eds), *Perceiving, Acting and Knowing: Toward an Ecological Psychology*. Hillsdale, N.J.: Erlbaum.
- TURVEY, M. T., SHAW, R. E. and MACE, W. (1978). Issues in the theory of action: Degrees of freedom, coordinative structures and coalitions. In J. REQUIN (Ed.), *Attention and Performance VII*. Hillsdale, N.J.: Lawrence Erlbaum.

- VIVIANI, P. and TERZUOLO, C. (1980). Space-time invariance in learned motor skills. In G. E. STELMACH and J. REQUIN (Eds), *Tutorials in Motor Behavior*. Amsterdam: North-Holland.
- WILSON, D. M. (1966). Insect walking. *Annual Review of Entomology*, **11**.
- WINFREE, A. T. (1980). *The Geometry of Biological Time*. New York: Springer-Verlag.
- WOODS, B. T. and TEUBER, H.-L. (1978). Mirror movements after childhood hemiparesis. *Neurology*, **28**, 1152-8.
- YAMANISHI, J., KAWATO, M. and SUZUKI, R. (1980). Two coupled oscillators as a model for coordinated finger tapping of both hands. *Biological Cybernetics*, **37**, 212-225.

*Revised manuscript received 10 October 1982*