On the Coordination of Two-Handed Movements

J. A. Scott Kelso
Haskins Laboratories, New Haven, Connecticut
University of Connecticut

Dan L. Southard and David Goodman Motor Behavior Laboratory, University of Iowa

In a set of three experiments, we show that after an auditory "go" signal, subjects simultaneously initiate and terminate two-handed movements to targets of widely disparate difficulty. This is the case when the movements required are (a) lateral and away from the midline of the body (Experiment 1), (b) toward the midline of the body (Experiment 2), and (c) in the forward direction away from the body midline (Experiment 3). Kinematic data obtained from high-speed cinematography (200 frames/sec) point to a tight coordinative coupling between the two hands. Although the hands move at entirely different speeds to different points in space, times to peak velocity and acceleration are almost perfectly synchronous. We believe that the brain produces simultaneity of action as the optimal solution for the two-handed task by organizing functional groupings of muscles (coordinative structures) that are constrained to act as a single unit.

Recent theoretical development in motor behavior has mainly focused on whether movements are under closed-loop feedback, or open-loop programmed control (Adams, 1971, 1977; Schmidt, 1975). Much of the data has been generated from linear-positioning tasks involving a single limb. In contrast, little is known about the principles governing interlimb coordination, even though much of human movement involves the coordinated participation of both hands and hence the concerted operation of the cerebral hemispheres (Luria, 1973). Part of the reason for this state of affairs may be that coordina-

tion does not lend itself easily to measurement. Rather, we seem content to rely on anecdotal evidence for insights into such problems.¹

A crucial problem for the development of a viable theory of movement coordination concerns the significant units with which the nervous system works. Candidates for this status have ranged from signals to individual motoneurons to synergies (collectives) of muscles. The latter may be viewed as synonymous with coordinative structures (Easton, 1972), defined as functional groupings of muscles that are constrained to act as a single unit (Turvey, 1977). The rigorous investigation of muscle collectives has been minimal in spite of powerful logical arguments that they must be the significant units of control (e.g., Bernstein, 1967; Turvey, 1977).

In the present article we present data that illustrate the muscle linkage conception in a

We thank Mike Linton and Pat Briley for technical assistance, Carol Putnam for cinematographical analysis, and Phil Striegel for running subjects in Experiment 1.

Requests for reprints should be sent to J. A. Scott Kelso, Haskins Laboratories, 270 Crown Street, New Haven, Connecticut 06510.

This research was supported by Biomedical Research Support Grant FR-07035 from the General Research Support Branch, the National Institutes of Health and by U.S. Public Health Service Grant 1 R01 AM20231-01 (National Institute of Arthritis, Metabolism, and Digestive Diseases).

¹ A favorite example is the difficulty an individual often encounters when attempting to rub the stomach and pat the head at the same time.

voluntary, acquired skill involving the participation of both hands. We believe this demonstration to be significant, since previous evidence for such muscle collectives comes from potentially prewired activities like walking (Boylls, 1975; Grillner, 1975; Shik & Orlovsky, 1976) and breathing (Gurfinkel', Kots, Pal'tsev, & Fel'dman, 1971). We also introduce a behavioral paradigm, which, combined with high-speed cinematographical movement analysis, may have broad potential for understanding the processes underlying the control of movement.

Our question was a simple one: Suppose that an individual is asked to produce movements of the upper limbs to targets each of which varies in amplitude and precision requirements. How will he or she respond? A relationship between movement duration, movement amplitude, and target demands, formulated by Fitts (1954), allows us to examine this question experimentally. The equation relating the foregoing parameters is known as Fitts's law, in which movement time = $a + b \log_2 (2A/W)$, where a and bare constants, \overline{A} is the amplitude of the movement, and W is the width of the target. The key aspect of this formulation is that movement time depends on the ratio of movement amplitude to movement precision. Thus, the movement time for a 4-cm movement to a .5-cm target width (8:1 ratio) is practically identical to an 8-cm movement to a 1-cm target.

Consider a one-handed movement condition in which the target size is large and the amplitude is short (an easy condition) and a condition in which the target size is small and the movement amplitude is long (a difficult condition). Movement time in the easy condition will obviously be shorter. But what happens when these conditions are combined for both hands? Does the hand producing a short movement to an easy target arrive much earlier than in the more difficult condition, or are the movements initiated and terminated simultaneously?

A pilot experiment was conducted to examine this question. Ten subjects performed one-handed and two-handed movements (in-

volving extension of the wrist-forearm linkage) of equal and varying difficulty as quickly and as accurately as possible following an auditory stimulus. A major finding was that movement times for the easy task under combined conditions (i.e., easy for one limb and difficult for the other) were nearly doubled compared with single-limb counterparts and conditions in which both hands performed the easy task. Therefore, the hand moving to the easy target under combined conditions appeared to wait for the hand traveling to the difficult target so that they could strike together.2 This finding indicates that in spite of differences in target demands and movement length between each hand, response duration appears to be held constant. Duration, then, could be interpreted as a major parameter in the program for two-handed movements. One of the drawbacks of the pilot experiment was that subjects were instructed, at the onset of an auditory signal, to leave the home keys simultaneously. Indeed, trials in which reaction time differences between the hands were greater than 15 msec were excluded. Although this criterion was exceeded on a very small proportion of trials, we felt that the emphasis on simultaneous reaction time may have biased subjects to also terminate the movements simultaneously. The procedure used in Experiment 1, therefore, was simply to instruct the subjects to strike the designated targets as quickly and as accurately as possible, without any reference to reaction time simultaneity. We felt that removal of this potential bias would provide a cleaner picture of how limbs perform under combined conditions.

Experiment 1

Method

Subjects. The subjects were 12 right-handed volunteers, ranging in age between 18 and 25

² In fact, we were later to find out by using highspeed cinematographical techniques that the hand performing the easy task did not "wait" for its more difficult counterpart, but rather moved at an entirely different velocity (see Figure 4).

years. The results obtained from 1 subject were excluded from the data analysis because limited peripheral vision prevented his performing the task in certain movement conditions without an exceptional number of errors. Although the subjects were not paid individually for their participation, a \$5 bonus was awarded to the most accurate subject with the best overall response times (i.e., reaction times and movement times combined).

Apparatus. The apparatus consisted of a Plexiglas base (76 cm long, 16 cm wide, and .8 cm thick) mounted on a standard table (76-cm high) such that the long edge of the base was parallel to the front edge of the table. Two normally closed momentary contact switches (Cherry keyboard switch, Model M62-0900), centered 4.5 cm apart, served as the home keys. The base was constructed so that two hinged masonite targets could be positioned along the longitudinal centerline of the base, anywhere from 2 cm to 32 cm from the home keys. Two target widths were used: The easy target was 7.2 cm wide, and the difficult target was 3.6 cm wide. These were located at either a short distance (6 cm) or a long distance (24 cm) from the home keys. A single target was used in one-handed conditions and two targets were used in the twohanded condition, allowing for all combinations of target width and target distance to be used. A redlight-emitting diode served as the warning light and the sound from a Minisonalert provided the stimulus to move. These were mounted on a 50 cm × 15 cm board centered 10 cm behind the apparatus and directly in front of the subject. The onsets of warning light and stimulus tone were controlled by a Digital Equipment Corporation PDP8/A computer that also collected reaction times, movement times, and total response times.

Task. The subject's task was to move his or her index fingers from the home keys to the targets as fast and as accurately as possible after receiving the auditory stimulus from the Minisonalert. 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. All movements from the home keys to the targets were lateral.

Procedure. Eight experimental conditions were used, which varied depending on (a) whether a one-handed or two-handed movement was required, (b) whether the target was easy or difficult and, (c) whether the movement was of short or long amplitude. The nature of the task was explained to subjects, and instructions emphasized both speed and accuracy in striking the target(s). When the experimenter was certain that the subject understood the instructions, all eight conditions were performed by the subject. Each condition consisted of 25 trials with a 5-sec intertrial interval and a

1-sec to 3-sec variable foreperiod between the warning light and the stimulus to move. Only the last 20 trials of each condition were used in the data analysis; the first 5 trials served as familiarization. When each trial block was completed, the subject was given a 3-min break, during which the experimenter rearranged the targets in preparation for the next movement condition. All movements to targets were monitored by the experimenter. If the subject missed the target or hit the target with anything other than the index finger, that trial was excluded from the data analysis. Also excluded were reaction times greater than 600 msec or less than 90 msec and movement times greater than 600 msec and less than 30 msec.

Design. A within-subject design was used with all 11 subjects performing in all experimental conditions, whose order was randomized. From the 20 trials in each condition, mean reaction time, movement time, and total response time were computed for each hand. There were four one-handed and four two-handed conditions, making a total of 12 separate means for each subject and for each dependent variable. Preplanned contrasts using Dunn's procedure (Kirk, 1968, p. 79) were carried out on the means of interest.

Results and Discussion

The mean reaction times, movement times, and total response times are shown for each condition in Figure 1. Given the current debate regarding the use of simple versus choice reaction time as a reflection of the time it takes to select and prepare (or "program") upcoming motor responses (e.g., Klapp, 1977; Sternberg, Monsell, Knoll, & Wright, 1978), we prefer not to interpret our results within that theoretical framework. Our chief concern was whether subjects initiated and terminated movements simultaneously, especially under conditions in which the task demands were different for each hand.

No significant hand differences in reaction time were found (p > .05). More interestingly, subjects appeared to initiate hand movements in paired conditions virtually simultaneously. This is apparent in Figure 1, where it is shown that the largest difference between left-hand and right-hand reaction times was 8 msec (9 and 10). Thus, subjects left the home keys together even in the absence of instructions to do so. The average within-subject correlation between left and right hands in paired conditions was

Total Response Time	Movement Time	Reaction Time		Lett Target	Home Keys		ght rget	Reaction Time	Movement Time	Total Response Time
					• •		1[]	. 218	159	377
371	151	220	[] 2		• •					•
267	62	205		4	• •					
					• •	□ 3		218	78	296
306	49	219		•□	. • •	□ 5		224	85	309
403	166	237	[]•		. • • •		7[]	240	169	409
393	155	238	[]10		• •	□•		246	133	379
363	140	243		12	• •-		11[]	240	158	398

Figure 1. Mean reaction time, movement time, and total response times (in msec) for single and two-handed movements directed away from the midline of the body. (For actual dimensions of the targets and their distance from the home keys, refer to the text.)

also extremely high (range, .95-.97), further supporting the simultaneity of initiation.

As can be seen in Figure 1, one-handed movement times for the easy task (3 and 4) were much faster than their difficult counterparts (1 and 2), as Fitts's law predicts (p < .05). This effect is also evident when examining two-handed movements (5 and 6 vs. 7 and 8, p < .05). Movement times for one-handed and two-handed movements of the same difficulty were not significantly different (p > .05). However, when the task demands were varied for each hand, movement times for the easy task (9 and 12) were significantly higher than movement times for paired easy conditions (5 and 6, p < .01). Clearly, the difficult task determined movement time in two-handed conditions.

The movement time data in Figure 1 also indicate that two-handed movements of equal difficulty were executed simultaneously (5 vs. 6 and 7 vs. 8). Furthermore, paired movements of varying difficulty were also executed virtually simultaneously. Movement times to the easy target (9 and 12) were only slightly faster than movement times to the difficult target (10 and 11). In fact, when total response times are considered, this difference (19 msec) was further reduced (p > .05). Thus, coordinating the movements of both hands eliminated 84% of the difference in total response time found in the individual conditions.

The overall error rate across the eight experimental conditions was 8%. These

rates ranged, as expected, from a small error rate in one-handed conditions (6%) to higher errors in two-handed difficult conditions (13%). The majority of these errors was due to the subject missing the target or failing to strike the target with the designated finger.

The results of Experiment 1 essentially replicated those of the pilot experiment. The reaction time data strongly suggest that subjects initiated two-handed movements at the same time. Furthermore, paired movements to targets of equal or unequal difficulty were terminated simultaneously, as is evident in their corresponding movement times and total response times. Even though the task demands were different under combined conditions, the hands appeared to perform in a unitary manner. One drawback to this conclusion is that the outcome of Experiment 1 may have arisen as a result of the targets being placed in the subject's peripheral vision. Thus, subjects may simply have attended to or monitored movement to the difficult target, leaving the contralateral hand to perform a subsidiary role.8 In Experiment 2 we wanted to check whether this was a necessary and sufficient condition for the apparent time dependence between the hands. The way we chose to confront this issue was

³ This potentially confounding problem was raised by John Morton, to whom we are grateful, at a preliminary presentation of the data to the Medical Research Council, Applied Psychology Unit, Cambridge, England.

Total Response Time	Movement Time	Reaction Time	Home Keys T	argets	Home Keys	Reaction Time	Movement Time	Total Response Time
				01	⊕	231	218	449
445	221	224	⊕ 2 []					
				□3	•	228	140	368
369	140	229	⊕4□	l				
385	150	235	⊕6□	□ 5←	•	243	145	388
448	216	232	⊕8 []	. 07	ө	237	220	457
451	213	238	⊕ 10[]	9 <i></i> -	· 😝 .	253	192	445
427	183	244	⊕12□	Q11~	·	238	209	447

Figure 2. Mean reaction time, movement time, and total response times (in msec) for single and two-handed movements directed towards the midline of the body.

to have both movements terminate in focal vision. To accomplish this, we simply interchanged targets with home keys so that the former were placed directly in front of the subject.

Experiment 2

Method

Subjects. Subjects were 12 student volunteers who had not participated in Experiment 1 or in the pilot study. Data obtained from 1 subject were lost due to equipment malfunction.

Apparatus. The apparatus was similar in design to that used in Experiment 1, the only difference being that the position of the home keys and targets was interchanged. Thus, the targets were now directly in front of the subject, and the home keys could be adjusted to different distances from the targets. The task consequently involved flexion primarily of the elbow joint toward the midline of the body. Target dimensions and movement amplitudes were the same as in the previous experiment.

Procedure and design. The procedures for Experiment 2 were identical to that of Experiment 1, except that subjects received only 20 trials per condition. The first 5 trials served as familiarization and were not included in the analysis. Preplanned comparisons were carried out on relevant mean reaction times, movement times, and total response times.

Results and Discussion

The mean reaction times, movement times, and total response times are shown for each condition in Figure 2. As in Experiment 1, no significant hand differences in reaction time were found (p > .05). The largest difference between the hands was 15 msec (9 and 10), which was not significant. That subjects' hands were leaving the home keys

together is further supported by the high within-subject correlation between the left and right hands (range, .74-.98).

The data again indicated the expected relationship between one-handed movements for the easy task (3 and 4) and the onehanded movements for the difficult task (1 and 2), with the easy task clearly resulting in faster movement times (p < .01). This effect was also evident in two-handed movements (5 and 6 vs. 7 and 8, p < .01). Once again, the two-handed movements of equal difficulty (5 vs. 6 and 7 vs. 8) were executed simultaneously. As in Experiment 1, the difficult task appeared to determine the movement time in two-handed conditions. The slight movement time advantage of the easy task (9 and 12) over the difficult task (10 and 11) in combined conditions was reduced when total response time was considered (p > .05). Again, 83% of the difference in total response time in one-handed conditions was eliminated when the hands were combined. The overall error rate across the eight experimental conditions was 1.8%.

The results of Experiments 1 and 2 revealed identical effects in that simultaneity of initiation and termination occurred in all combined movement conditions. It should be noted that in both experiments the task involved symmetrical muscle groups resulting in movements in opposite directions. To further examine the generality of the simultaneity effect, we used a task that also involved symmetrical muscle groups but that required movements in the same direction. Consider the case in which the subject must produce two-handed movements of varying

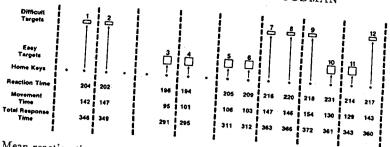


Figure 3. Mean reaction time, movement time, and total response times (in msec) for single and two-handed movements in the forward direction.

difficulty in the forward direction. An opportunity is afforded the subject to terminate the easy task before the difficult one. Thus, if both hands are initiated together and proceed forward at the same rate, the subject could feasibly strike the near target first, and the simultaneity effect would break down

Experiment 3

Method

Subjects. Subjects were 12 student volunteers who did not participate in either of the previous

Apparatus. The basic model of the apparatus was the same as in Experiments 1 and 2. However, the equipment was altered so that movements could be made forward in the sagittal plane, rather than laterally. This was accomplished by having two identical pieces of Plexiglas (106 cm long, 7 cm wide, and .8 cm thick), each with a single home key and moveable and interchangeable targets. Target widths and distances from the home keys were the same as in Experiments 1 and 2. The two pieces of apparatus were positioned parallel to each other, extending forward from the seated subject. The warning display and auditory stimulus setup was identical to the previous two experiments. The onsets of warning light and stimulus tone were controlled by a PDP 8/A computer, which also collected reaction times, movement times, and total response times.

Procedure and design. The procedures and design for Experiment 3 were identical to those of Experiment 2, with all subjects performing in all eight experimental conditions in a randomized

Results and Discussion

The mean reaction times, movement times, and total response times are shown for each condition in Figure 3. The subjects initiated

movements together, as indicated by the null effect of right hand versus left hand in the paired conditions and the high within-subject correlation (range, .82-.98).

The easy versus difficult task manipulation was effective, as is indicated by the longer movement times to the far target, both in the one-handed condition (3 and 4 vs. 1 and 2, p < .01) and in paired conditions of the same difficulty (5 and 6 vs. 7 and 8, p <.01). The difficult task once again exerted a major influence on the movement time in combined conditions, as is evident in the increase in movement time of the easy hand when the contralateral hand performed the more difficult task. The major finding of simultaneity once again appeared, with the slight movement time advantage of the easy task (10 and 11) over the difficult task (9 and 12) being further reduced when one considers total response time (M difference, 14 msec, p > .05).

The overall error rate across the eight experimental conditions was 1.0%.

General Discussion

There is a remarkable consistency in the pattern of results across the three experiments. First, notice that movement times for the so-called difficult task in one-handed conditions were greater than for the easy task. Second, the easy-difficult difference carried over to two-handed movements when the task was the same for each hand. But most interesting is the finding that the large and highly significant differences in movement time present in the individual conditions were virtually lost when the hands were combined. Examination of total re-

sponse time across the three experiments reveals that there is a small but consistent difference for paired movements, ranging from 13.0 to 14.5 msec (representing an approximately 80% reduction of the difference found in one-handed conditions). This set of findings cannot be attributed to a peripheral vision problem (see Experiment 2) nor to the fact that in Experiments 1 and 2 the hands always moved in opposite directions. When subjects were afforded the opportunity to break down the apparent time dependence between the hands in Experiment 3, they did not take it. In all three experiments, then, subjects initiated and terminated symmetrical movements of their hands to different points in space virtually simultaneously.

A key issue for this article concerns whether the limbs are controlled as separate units in the easy-difficult case or, conversely, whether they are constrained to act as a single unit. More specifically, do the central commands prescribe the details of the intended movements for each hand or, alternatively, are central commands referred to functional groupings of muscles that operate fairly autonomously to produce simultaneity of action? It seems tempting, for example, to interpret the present data in terms of a central program specifying different commands for each limb. The parameter that remains constant in this case-movement durationmight be viewed as setting the limits for the commands generated. This is not an unreasonable position, for there is ample evidence from the reaction time-movement time studies that duration is a major variable influencing the programming process (Kerr, 1978 for a review). Furthermore, recent neurophysiological data suggest that the duration parameter is centrally preprogrammed (Brooks, 1974; Kozlovskaya, Atkin, Horvath, Thomas, & Brooks, 1974). When, unbeknownst to monkeys producing rapid alternating elbow movements, the location of mechanical stops was altered, they nevertheless maintained movement duration constant. Thus, rather than oscillating between the stops as quickly as possible, they exerted force against the newly placed stops,

keeping the originally learned rhythmic pattern stable.

But a rather different mode of control may be suggested by Bernstein's (1967) original work and by subsequent research on activities such as locomotion (see Boylls, 1975; Grillner, 1975; and Shik & Orlovsky, 1976, for reviews) and respiration (Gurfinkel' et al., 1971). Movements are viewed as centrally programmed, not in terms of individual muscle contractions, but rather according to muscle linkages. A linkage is defined as a group of muscles whose activities covary as a result of shared efferent or afferent signals (Boylls, 1975). For example, extensive studies on locomotion in animals reveal that movements are organized in terms of basic flexor and extensor linkages -spinal locomotor automatisms (Shik & Orlovsky, 1976)-involving both proximal and distal joints.

This basic mode of motor organization is revealed in an experiment-somewhat analogous to the present studies-performed by Kulagin and Shik (1970) on mesencephalic cats running on a treadmill at two different speeds. In this situation, the movements of the two sides of the body are different, just as they are in normal activities such as turning or circling. Although the speeds of symmetrical limbs were obviously different and took the form of strict alternation, the duration of the step cycle remained constant. This was achieved by lengthening the stance phase and shortening the swing phase on the slower belt with a concomitant shortening of the stance phase and a lengthening of the swing phase on the faster belt.4 It appears that a low-level mechanism is involved in this interaction between the two sides of the body, for an identical result occurs in the spinal animal (Grillner, 1975).

The picture of interlimb coordination that emerges from studies of this type is that the task of central signals is not to prescribe the details of the intended movement but rather

⁴ The stance or support phase is the interval in the step cycle during which the foot is in contact with the ground. The swing or transfer phase refers to the period of limb retrieval for the next step.

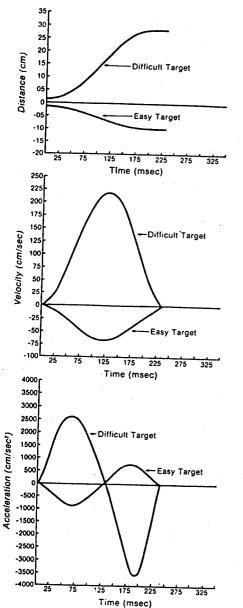


Figure 4. The pattern of displacement, velocity and acceleration over time for two-handed movements of unequal difficulty obtained from single frame kinematic analysis (frame rate = 200 frames/sec). (Note the almost perfect synchrony between the peaks in the velocity-time and acceleration-time curves. Over a series of six trials, the mean time difference in peak velocities was 9 msec, whereas the mean time difference between peak accelerations was 14 msec for positive acceleration and 4 msec for negative acceleration. Given variation from trial to trial, these differences may be viewed as trivial. Also, there was no systematic pattern as to which limb reached peak velocity first.)

to organize functional groupings of muscles -coordinative structures (Easton, 1972; Turvey, 1977)—in a relatively autonomous fashion. Viewed in light of the present experiments, this style of control argues that the brain sets the level of activity in lowlevel automatisms based on the spatial demands of the task, but leaves them to generate the pattern of interlimb coordination seen in simultaneous movements. Indeed, we have data suggesting that in a task in which the spatial demands vary on each side, the limbs are constrained to function as a single unit. High-speed cinematographic analysis (200 frames/sec) reveals that the limb moving to the easy target does not hover over the target or "wait" for its difficult counterpart, but moves at an entirely different speed. More important, and as Figure 4 reveals, the limbs under easy-difficult target conditions reach peak velocity and peak acceleration at practically the same time during the movements. Thus, although the limbs move at different speeds, their velocity and acceleration patterns are nearly perfectly synchronized. This suggests a strong interaction between the limbs and is not conducive to an independent programming view. The apparently fixed and reproducible interaction between the limbs seen in the present experiments to produce simultaneity of action may be viewed as the discovery of a coordinative structure or muscle linkage, a goal that has motivated much of the Russian work on motor control (e.g., Gurfinkel' et al., 1971). The notion that motor coordination involves a reduction of the degrees of freedom of the motor apparatus, first advanced by Bernstein (1967), and lately extended by Turvey (1977), requires the existence of low-level coordinative structures that govern the interaction between limbs. Such collectives are not necessarily prefabricated, as Easton (1972) has argued in the case of reflexes. Rather, they are functional and can be marshalled temporarily and expressly for the purpose of accomplishing a particular behavioral goal.

This perspective on coordination raises numerous theoretical issues. Boylls (1975), for example, has discussed how the deployment of coordinative structures is parameter-

ized. The structural prescription is defined as a set of qualitative ratios of activities in the linked muscles, independent of absolute activity levels. The metrical prescription of a coordinative structure specifies the absolute level of activity in linked muscles. The latter may be viewed as a scalar quantity that multiplies the activities of all muscles in the linkage. Boylls argued, with respect to the anterior lobe of the cerebellum, that structural prescriptions are tuned by adjusting the relative amounts of activity distributed among descending tracts from the cerebellum, whereas metrical prescriptions are governed by the absolute activity levels in those tracts. This view receives strong support from Orlovskii's (1972) data showing that cerebellar stimulation during cat locomotion affects only the magnitude of muscle contraction, leaving unchanged both the period duration and the timings of periods relative to the cat cycle. This indeed may be the principle characteristic of a coordinative structure. Namely, when a group of muscles is constrained to act as a unit, some temporal relationship is preserved invariantly over changes in the magnitude of activity (Turvey, Shaw, & Mace, 1978).

Our data on two-handed movements fit theoretical perspective rather well. When the movement kinematics are examined, it is obvious that the magnitude of forces produced for each hand is different. (See Figure 4.) Thus, the equilibrium points for each hand may be preset and the neural output may be specified accordingly in terms of the magnitude of forces required (Bizzi, Polit & Morasso, 1976; Kelso, 1977). However, the underlying temporal structure remains invariant between the hands so that they preserve a synchronous relationship to each other. Hence, the metrical prescription (specified by the spatial parameters) is modulated for each hand, yet the structural prescription (the relative timing between the hands) remains invariant.

In conclusion, Experiments 1, 2, and 3 represent an initial attack on a problem that has been largely ignored by motor behavior researchers, namely interlimb coordination. Consequently, aside from some recent theorizing of a preliminary nature (Fowler &

Turvey, 1978; Turvey, 1977) formal theoretical development has been sadly lacking. We feel that our behavioral paradigm, especially when combined with movement analysis techniques, has broad potential for examining coordination issues. Our data suggest that when the motor system is faced with controlling multiple degrees of freedom, as in the two-handed task, it solves the problem optimally by constraining the limb musculature to act as a single unit. If this is so, then variables designed to influence one limb moving to a spatial target, such as slowing the limb down or requiring a change in the limb's angle of projection, should have concomitant modulatory effects on the other limb. Of course, we do not claim that the performer cannot break down these constraints with practice. Many motor tasks require the hands to perform in a relatively independent rather than tightly coupled manner. In the broader perspective, therefore, highly skilled performance might be viewed as a release from the type of temporal invariance exhibited in these experiments.

References

Adams, J. A. A closed-loop theory of motor learning. *Journal of Motor Behavior*, 1971, 3(2), 111-149.

Adams, J. A. Feedback theory of how joint receptors regulate the timing and positioning of a limb. *Psychological Review*, 1977, 84, 504-523.

Bernstein, N. The coordination and regulation of movements. Oxford, England: Pergamon Press, 1967.

Bizzi, E., Polit, A., & Morasso, P. Mechanisms underlying achievement of final head position. Journal of Neurophysiology, 1976, 39, 435-444.

Boylls, C. C. A theory of cerebellar function with applications to locomotion. II. The relation of anterior lobe climbing fiber function to locomotor behavior in the cast. COINS Technical Report, 1975, 76(1). Department of Computer and Information Science, University of Massachusetts.

Brooks, V. B. Some examples of programmed limb movements. Brain Research, 1974, 71, 299-308.

Easton, T. On the normal use of reflexes. American Scientist, 1972, 60, 591-599.

Fitts, P. M. The information complexity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 1954, 47, 381-391.

Fowler, C. A., & Turvey, M. T. Skill acquisition: An event approach with special reference to searching for the optimum of a function of several

- variables. In G. E. Stelmach (Ed.), Information processing in motor control and learning. New York: Academic Press, 1978, 1-40.
- Grillner, S. Locomotion in vertebrates: Central mechanisms and reflex interaction. *Physiological Reviews*, 1975, 55, 247-304.
- Gurfinkel', V. S., Kots, Y. M., Pal'tsev, Y. I., & Fel'dman, A. G. The compensation of respiratory disturbances of the erect posture of man as an example of the organization of interarticular interaction. In I. M. Gelfand (Ed.), Models of the structural-functional organization of certain biological systems. Cambridge, Mass.: MIT Press, 1971.
- Kelso, J. A. S. Motor control mechanisms underlying human movement reproduction. Journal of Experimental Psychology: Human Perception and Performance, 1977, 3, 529-543.
- Kerr, B. Evaluating task factors that influence selection and preparation for voluntary movements. In G. E. Stelmach (Ed.), Information processing in motor control and learning. New York: Academic Press, 1978, 55-69.
- Kirk, R. E. Experimental design: Procedures for the behavioral sciences. Belmont, Calif.: Brooks-Cole, 1968.
- Klapp, S. T. Reaction time analysis of programmed control. In R. Hutton (Ed.), Exercise and sports sciences reviews. Santa Barbara, Calif.: Journal Publishing Affiliates, 1977.
- Kozlovskaya, I. B., Atkin, A., Horvath, F. E., Thomas, J. S., & Brooks, V. B. Preprogrammed

- and feedback guided movements of monkeys. Behavioral Biology, 1974, 12, 243-248.
- Kulagin, A. S., & Shik, M. L. Interaction of symmetrical limbs during controlled locomotion. Bio-physics, 1970, 15, 171-178.
- Luria, A. R. The working brain. New York: Basic Books, 1973.
- Orlovskii, G. N. The effect of different ascending systems on flexor and extensor activity during locomotion. *Brain Research*, 1972, 40, 359-371.
- Schmidt, R. A. A schema theory of discrete motor skill learning. *Psychological Review*, 1975, 82, 225-260.
- Shik, M. L., & Orlovsky, G. N. Neurophysiology of locomotor automatism. *Physiological Reviews*, 1976, 56, 465-501.
- Sternberg, S., Monsell, S., Knoll, R. L., & Wright, C. E. 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: Academic Press, 1978.
- Turvey, M. T. Preliminaries to a theory of action with reference to vision. In R. Shaw & J. Bransford (Eds.), *Perceiving, acting, and knowing*. Hillsdale, N.J.: Erlbaum, 1977.
- Turvey, M. T., Shaw, R. E., and Mace, W. Issues in the theory of action. In J. Requin (Ed.), Attention and performance VII. Hillsdale, N.J.: Erlbaum, 1978.

Received March 15, 1978