A second possibility is that a break occurred in both chromosomes involved in the inversion loop, and their rejoining produced an interstitial deletion (Fig. 2B). The possibility of a single dose of radiation or some other similar phenomenon breaking both chromosomes would be enhanced by the homologous pairing occurring in the inversion loop. In this instance the inversion would be important in the production of this deletion, but the inversion would occur by a process separate and different from crossing-over.

A third possibility is that the inversion loop brought two parts of the same chromosome close together and that a single damaging agent, such as radiation, caused two breaks which then united to form an interstitial deletion with loss of the acentric fragment (Fig. 2C). Novitsky (*5*) described an experimental system in which radiation caused restitution of the normal sequence from a paracentric inversion in *Drosophila*. This process could be similar to that observed in the present family, although the inversion here seems larger than the deleted segment; however, the resolution of the current cytogenetic techniques may be misleading and the inverted segment may be the same length as the deletion. Finally, the present findings contrast with those of Novitsky in that we found a deletion rather than restitution of the normal chromosome. But the same phenomenon could account for these observations and it may have been a matter of chance that Novitsky did not observe the deleted products; alternatively, the deletions in *Drosophila* might have been lethal and hence not observed in the progeny. At present we do not know which of these three possibilities applies to our patient, although the second two are favored over the first because they explain the formation of an interstitial deletion which the cytogenetic findings suggest is present.

Only a few paracentric inversions of human chromosomes have been described, but this situation may change with the recent improvements in chromosome banding techniques. To date, no recombinants have been observed in the offspring of the carriers of paracentric inversion carriers, but when such observations are made, it may be possible to determine whether our observation represents a common event in humans or that our explanation is incorrect. However, for the moment we are reluctant to believe that the chromosome changes in the patient and her mother are unrelated.

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## On the Nature of Human Interlimb Coordination

Abstract. *Movement time varies as a function of amplitude and requirements for precision, according to Fitts' law, but when subjects perform two-handed movements to targets of widely disparate difficulty they do so simultaneously. The hand moving to an "easy" target moves more slowly to accommodate its "difficult" counterpart, yet both hands reach peak velocity and acceleration synchronously. This result suggests that the brain produces simultaneity of action not by controlling each limb independently, but by organizing functional groupings of muscles that are constrained to act as a single unit.*

Much of human movement involves the coordinative use of both hands, yet, in spite of a resurgence of interest by psychologists and neurophysiologists into problems of motor control (*1, 2*) little is known about the principles governing interlimb coordination. Perhaps the most important problem facing the development of a theory of coordination is the determination of the significant units with which the nervous system works. One commonly held view is that central command signals specify the states of individual muscles. An alternative is that control decisions are referred to functional groupings of muscles—coordinative structures or linkages (*3*)—that are constrained to act as a single unit (*4*).

The rigorous investigation of muscle collectives has not taken place despite powerful logical arguments that they must be the significant units of control (*5*). Experimentation in motor behavior over the last decade has focused to a considerable degree on issues concerning control by closed-loop feedback or by open-loop programming (*6*). We now report data on a task involving both hands that strongly favors an interpretation based on muscle linkages. We believe this demonstration to be significant since previous evidence for muscle collectives comes from potentially prewired activities such as locomotion (*7*) and respiration (*8*).

How will a person respond when asked to produce movements of the upper limbs to targets each of which varies in amplitude and precision requirements? A relationship between movement duration, movement amplitude, and target demands formulated by Fitts (*9*) allows us to examine this question experimentally:

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

where $MT$ is movement time, $a$ and $b$ are constants, $A$ is the amplitude of the movement, and $W$ is the width of the target. The units of this formula are referred to as "bits" which also serve as units for the index of difficulty of the movement. This fundamental relationship, known as Fitts' law, has been empirically demonstrated in single-limbed movements under a wide variety of environmental conditions including, for example, microscopic (*10*) and underwater (*11*) tasks. The key aspect of the formulation is that movement time depends on the ratio of movement amplitude to movement precision. Thus the movement time for a 3-cm movement to a 0.25-cm target width (a 12:1 ratio) is practically identical to that for a 12-cm movement to a 1-cm target width (*9*).

Consider a one-handed movement condition in which the target size is large and the amplitude is small (termed easy), relative to a condition in which the target size is small and the movement amplitude is large (termed difficult). Movement time in the first case will obviously be shorter in duration. But when these conditions are combined for both hands, does the hand producing a short movement to an easy target arrive much earlier than the more difficult condition, as Fitts' law might predict? We have found that subjects respond virtually simultaneously to targets of various difficulty when asked to respond as quickly and as accurately as possible after an auditory stimulus. In addition to the experiment

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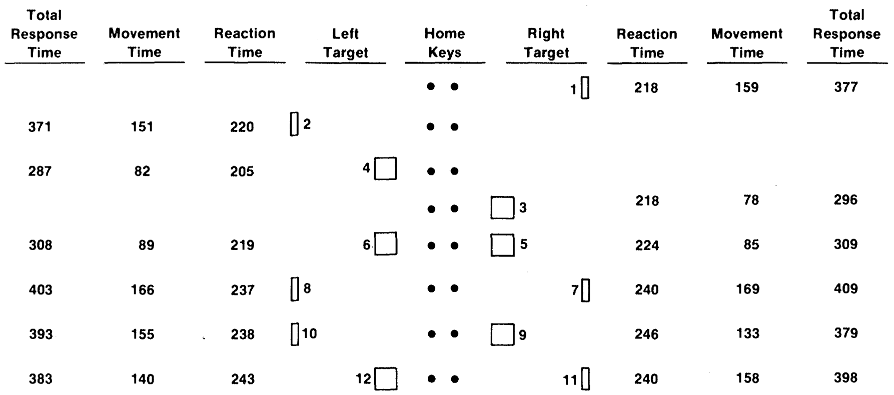

| Total Response Time | Movement Time | Reaction Time | Left Target | Home Keys | Right Target | Reaction Time | Movement Time | Total Response Time |
|---|---|---|---|---|---|---|---|---|
| | | | | • • | 1 ▯ | 218 | 159 | 377 |
| 371 | 151 | 220 | ▯ 2 | • • | | | | |
| 287 | 82 | 205 | 4 □ | • • | | | | |
| | | | | • • | □ 3 | 218 | 78 | 296 |
| 308 | 89 | 219 | 6 □ | • • | □ 5 | 224 | 85 | 309 |
| 403 | 166 | 237 | ▯ 8 | • • | 7 ▯ | 240 | 169 | 409 |
| 393 | 155 | 238 | ▯ 10 | • • | □ 9 | 246 | 133 | 379 |
| 383 | 140 | 243 | 12 □ | • • | 11 ▯ | 240 | 158 | 398 |

Fig. 1. Mean reaction time, movement time, and total response times for single- and two-handed movements varying in amplitude and precision requirements.

reported here, we have confirmed this finding in four different experiments (total $N = 52$) (*12*). We have also performed a high-speed cinematographic analysis of the two-handed task in order to study the movement control used by the subject.

In our initial experiment, 12 undergraduate volunteers were studied under eight randomly ordered experimental conditions varying on three task dimensions: (i) single-handed or two-handed movement, (ii) wide (7.2 cm) or narrow (3.6 cm) target, and (iii) short (6 cm) or long (24 cm) target distance from the home keys. The subject's task was to move the index fingers from the home keys to prefabricated masonite targets as fast and as accurately as possible. The movements were lateral and involved extension in the frontal plane of the finger-wrist-forearm linkage. A red light-emitting diode served as the warning light for the start of a trial, and the sound from a mini sonalert placed directly in front of the subject was the signal to move. For single-hand conditions, the subject depressed the left (or right) home key with the left (or 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 struck the respective targets following the auditory stimulus.

Each of the eight conditions consisted of 25 trials with a 5-second intertrial interval and a 1 to 3 second variable foreperiod between the warning light and the signal to move. Only the last 20 trials of each condition were analyzed; the first five trials served as familiarization for subjects. 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. From the 20 trials in each condition, a mean reaction time (RT), movement time (MT), and total response time (RT + MT) were computed for each hand. Planned contrasts according to Dunn's procedure (*13*) were carried out on the means of interest (Fig. 1). For reaction time the difference was significant ($P < .01$) between one- and two-handed conditions both for the difficult task (mean of 1 and 2 versus mean of 7, 8, 10, and 11) and the easy task (mean of 3 and 4 versus mean of 5, 6, 9, and 12). The significant difference between one- and two-handed movements for the easy task, however, appears to be due to the elevated reaction time in the two-handed condition in which easy and difficult movements are combined (mean of 9 and 12). This is evident in the significant difference in reaction time ($P < .01$) between two-handed movements of equal difficulty (5 and 6) and two-handed movements of varying difficulty (9 and 12). Reaction time in this case may be viewed as reflecting the time it takes to select and prepare or program the upcoming motor response. The motor program in this case may be viewed in terms of commands that are structured before the movement sequence begins (*14*). Given control of perceptual factors, the more complex the upcoming response, the longer it should take to prepare the appropriate program. Under this hypothesis [for which there is now abundant evidence in speech (*15*) and motor production tasks (*16*)] then in our study, two movements appear to require more time to program than one when one or both of the two movements is difficult. In contrast, programming time for two movements is virtually the same as for one movement when the task is easy. Overall, the difficult task seems to determine programming complexity when two-handed movements are required.

Subjects initiate hand movements in paired conditions virtually simultaneously, even though not specifically instructed to do so (Fig. 1). The largest difference (8 msec) between left- and right-hand reaction times in two-handed conditions (9 and 10) is not significant ($P > .05$). The average within-subject correlation between left and right hands in paired conditions was also high (range, .95 to .97), further supporting the simultaneity of initiation.

In another experiment in which six subjects were instructed to strike one target just before the other, movement initiation times were no longer simultaneous. On 80 percent of the trials, subjects first initiated movement to the target designated to be struck first. Reaction times to initiate the first of two alternating movements increased about 50 msec relative to the reaction times for two-handed movements shown in Fig. 1. Given our previous assumptions regarding reaction time, changing the temporal structure of the upcoming movements—that is, asking subjects to strike one target first as well as to minimize the time between target 1 and target 2—seems to have increased motor programming requirements. A factor that appears to determine programming complexity is the timing structure of the upcoming movements.

Although these reaction time effects are interesting in light of current attempts to understand the nature of motor programming in humans, our chief concern was the movement time effects. Single-handed movement times for the easy task are much faster than their difficult counterparts (Fig. 1). Movement times for single- and two-handed movements of the same difficulty are not significantly different ($P > .05$). When an easy task is paired with a difficult one, however, movement times for the easy task (9 and 12) are significantly elevated over paired easy conditions (5 and 6) ($P < .01$). The difficult task thus determines movement time in two-handed conditions.

The movement time data (Fig. 1) also indicate that two-handed movements of equal difficulty are executed together (5 versus 6 and 7 versus 8). Furthermore, paired movements of different difficulty are also executed virtually simultaneously. Movement times to the easy target (9 and 12) are only slightly faster than movement times to the difficult target (10 and 11). When total response times are considered this difference (19 msec) is eliminated ($P > .05$).

Fitts' law, generated for single-limbed movements, does not accommodate our data on two-handed movements. If it did, movement times to the easy target would be considerably less than those to the difficult one. Yet we found simultaneity when the spatial demands of the task were disparate for each hand. The key issue concerns whether the limbs are controlled as separate units in the easy-difficult condition or, conversely, whether they are constrained to act as a single unit. More specifically, do central commands prescribe the details of the intended movements for each hand, or are central signals referred to functional groupings of muscles that operate fairly autonomously to produce simultaneity of action? It is tempting to explain our data in terms of the central program hypothesis. The parameter remaining constant in this case—movement duration—might be viewed as "setting the limits" for the commands generated. But we have reason to suspect this interpretation in favor of the hypothesis, originally put forward by Bernstein (*5*) and lately extended by Turvey (*2*), that movements are 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 (*7*). For example, extensive studies on locomotion reveal that movements are organized in terms of basic flexor and extensor linkages—spinal locomotor automatisms (*17*)—involving both proximal and distal joints.

Viewed in light of our experiments, this style of control argues that the brain sets the level of activity in low level automatisms based on the spatial demands of the task, but leaves them to generate the pattern of interlimb coordination seen in simultaneous movements. Kinematic data obtained from high-speed cinematographic analysis (200 frames per second) support this hypothesis and illustrate the tight interactive coupling between the limbs. Although the hands, under easy-difficult target conditions, move at different speeds, their velocity and acceleration patterns are almost perfectly synchronous (Fig. 2). This apparently fixed and reproducible interaction between the limbs leading to simultaneity of action may be viewed as evidence for a muscle linkage or coordinative structure (*3, 4*). Much Russian research on motor control has sought such a structure (*18*). Such collectives are not necessarily prefabricated, as Easton (*3*) has argued in the case of reflexes. Rather, they are functional and may be marshalled temporarily and expressly to accomplish a particular behavioral goal.

On the basis of Boylls' analysis of cat locomotion (*7*), Turvey *et al.* (*4*) proposed that the chief characteristic of a coordinative structure is that the temporal relationship between muscles involved in a particular skill is preserved invariantly over changes in the magnitude of muscle activity. Our data fit this theoretical perspective well. An examination of the movement kinematics reveals that the force produced by each hand is different (Fig. 2). Thus, the equilibrium points for each hand may be preset and the neural output specified accordingly in terms of the magnitude of forces required (*19*). The underlying temporal structure, however, remains invariant between the hands such that they maintain a synchronous relationship to each other. The study of the underlying neural mechanisms of simultaneous movements lies with the neurosciences, as does the elucidation of the mode of control.

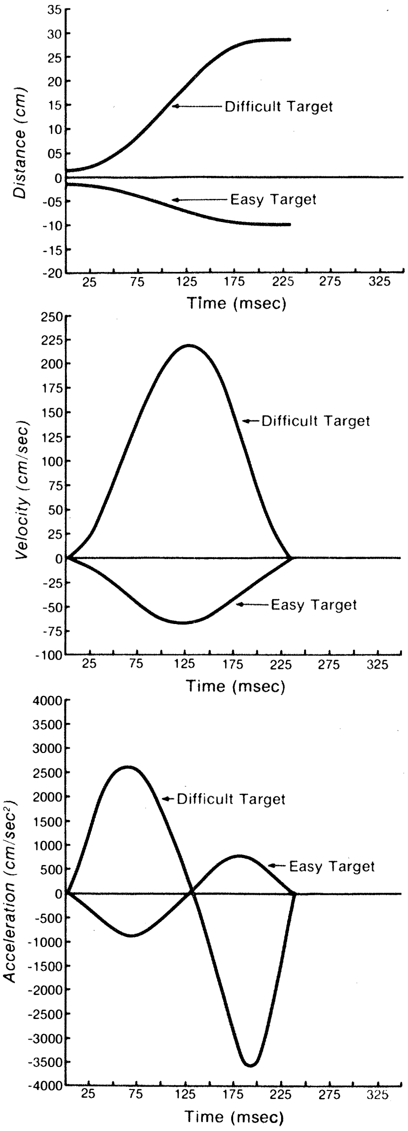

Fig. 2. The pattern of displacement, velocity, and acceleration over time for two-handed movements of unequal difficulty obtained from single frame kinematic analysis (frame rate, 200 frames per second). Note the almost perfect synchrony between the peaks in the velocity-time and acceleration-time curves. 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. There was no systematic pattern as to which limb reached peak velocity first.

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