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Central and peripheral coordination in movement sequences

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Summary. Motor coordination has been too poorly defined to be a useful construct in studying the control of movement. In general, motor coordination involves controlling both the timing and the kinematics of movement. Yet the motor behaviors typically used for the study of coordination have required controlling only the timing or the spatial aspects of a movement. To understand better the basis of motor behavior, this study examined movement sequences, a class of movement in which both the timing and the kinematics must be controlled. In one experiment we studied a reaching and grasping movement sequence to characterize the central coordination of movement sequences. In another experiment we studied a throwing movement sequence to characterize the peripheral (kinesthetic) coordination of movement sequences. An heuristic model is presented to explain how central and peripheral mechanisms of coordination might interact to produce accurate movement.

Introduction

Our repertoire of motor behavior is diverse, ranging from simple force production at a single joint to the active movement of nearly every joint of the body, as in gymnastics. Some movements are relatively discrete, as in pointing at a target, while others are cyclical, as in locomotion. The nervous system controls different kinematic variables, such as distance, direction, speed, and time, in different movements. Some movements are controlled exclusively by central processes (e. g., very brief movements), while others are influenced by sensory input. Thus, it might be the diversity in our motor repertoire that has made the development of a strong unifying concept of motor coordination so elusive.

One class of movements that might unify our notions of motor coordination is the movement sequence, as exemplified in Figure 1. This figure illustrates the movements of two joints, each joint rotation controlled by a different muscle, in which the motions of the joints overlap in time without being synchronous. Thus, the entire movement sequence can be divided into a period of nonoverlapping movement (i. e., only joint rotation 1) and a period of overlapping movement. A heavy vertical bar identifies the onsets of the two joint rotations after the activation of the agonist muscles crossing these two joints. This definition of movement sequences excludes multiple joint movements in which all the joints start and stop moving at the same time. It also excludes cyclical movements in which movement within each cycle is completed before the next begins (e. g., finger tapping). This is not to say that there are not elements of motor coordination in synchronous or cyclical movements, nor does this definition exclude discrete cycles of cyclical movements, as in locomotion where each step includes sequential rotations of the hip, knee, and ankle.

The essence of motor coordination within movement sequences lies in the temporal relationship between different joint rotations and in the specification of this timing by the spatial relationship between joints. Returning to the generalized movement sequence in Figure 1, processes that coordinate movement sequences would dictate the time at which the second joint begins actively to rotate, on the basis of the angle of the first joint to rotate in the sequence. Thus, the success or accuracy of the overall movement would require the second movement to be initiated when the first joint reached a particular angle.

This concept of motor coordination can be further clarified by its application to naturally occurring movement sequences, such as locomotion, speech, reaching and grasping, typing, and playing a musical instrument. The throwing movement sequence exemplifies this concept. In throwing, the vertical position on the target struck by the object being thrown depends on two parameters: the launch velocity and the launch angle. The launch velocity is determined by the motion of the arm (e. g., joint rotation 1 in

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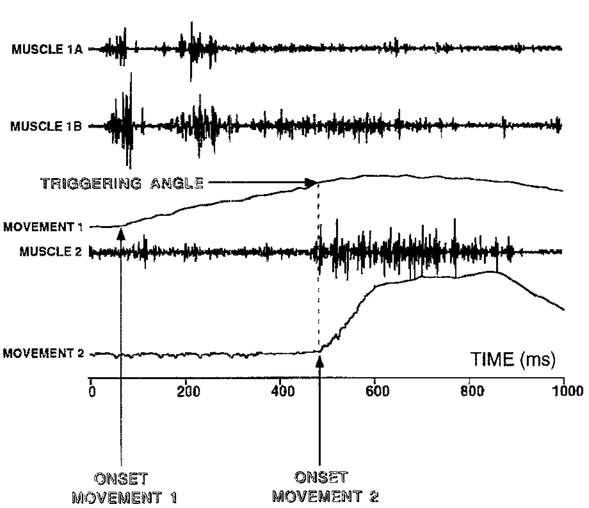

Fig. 1. Schematic example of a movement sequence involving two joints in which one joint does not begin to rotate until the other joint has reached a particular angle

Figure 1), and the launch angle is determined by where in the throwing arc the hand releases the object (e.g., joint rotation 2 in Figure 1). The coordination of this movement lies in the timing of the hand movement based on the kinematics of the arm movement. Similarly, in a reaching-and-grasping movement, the coordination lies in the timing of the hand opening, when the hand is oriented with respect to the object to be grasped, and when the hand is closed.

Results from two experiments are described, one examining a reaching-and-grasping movement sequence, and the other examining a throwing-movement sequence. The primary distinction between these two experiments is that the first examined how central mechanisms coordinate movement sequences and the second examined how peripheral mechanisms coordinate them. From these two experiments an heuristic model for motor coordination is developed, in which central and peripheral influences are merged. Preliminary reports of these experiments have been previously presented in abstract form (Cordo, 1990b; Cordo, Carlton, & Carlton, 1991; Bevan et al. 1991; Cordo & Schieppati, 1991).

Methods

The two different experiments were conducted on normal human subjects aged 18–50. Because each experiment was conducted on different movements in different laboratories, the methodology for each is described separately.

Reaching-and-grasping movement sequence. This experiment was performed on 8 subjects. Each subject sat at a table with the right arm resting on the table surface, palm down, with the tips of the thumb and index finger touching. A length of 1-inch steel rod, bent into an L-shaped handle, projected from an aluminum block 40 cm in front of the subject. This handle was inserted into three sockets in the aluminum block, which were vertically aligned at 15, 24, and 33 cm above the table surface. The last segment of the handle, which the subject grasped, could be oriented either horizontally or vertically by rotation of the handle within its socket.

The motor task for the subject was to reach and grasp the handle, taking 500 ms from the time the hand began to move to the time of contact with the handle. The timing was constrained by the subject being presented with a sequence of four tones, 500 ms apart, through headphones. The subject was instructed to initiate the reach on the third tone and to contact the handle on the fourth tone.

In different blocks of trials, the handle was positioned at one of the three heights, oriented either horizontally or vertically. When the handle was oriented horizontally, the subject received one of two possible instructions: “Do not rotate the hand” or “Supinate the hand 180° on the way to the target.” When the handle was oriented vertically, the subject was instructed: “Supinate the hand 90° on the way to the target.” Thus, there were a total of nine different conditions combining three heights of reach and three hand orientations. Ten repetitions of each condition were performed in contiguous blocks for a total of 90 trials.

Electromyographic (EMG) activity was recorded from six muscles in the right arm and shoulder. Intramuscular wire electrodes were inserted into the flexor digitorum superficialis in the index or middle finger compartment, the extensor digitorum communis in the index or middle finger compartment, and the supinator brevis. Surface electrodes were used to record from the biceps brachii, anterior deltoid, and upper trapezius. The EMG activity was bandpass filtered (40–500 Hz) and amplified to obtain a signal which did not exceed ±5 volts. An accelerometer mounted on the dorsal side of the wrist indicated hand movement and handle contact. The accelerometer signal and the EMG signals from the six muscles were digitized with a sampling rate of 1,000 samples per second.

The accelerometer data were used to identify the onset time and the duration of each movement. All subjects were able to constrain movement times to within ±20 ms of the required duration; therefore, in the analysis of data, all movements were assumed to be of equal duration. The EMG data were averaged by the alignment of trials with respect to movement onset.

The EMG data for each muscle and for each subject were rectified and then averaged either with respect to reaching height or with respect to hand orientation. In the averages for reaching height, each of the three averages contained the 30 trials for movements with a particular height, regardless of the hand orientation. Conversely, in the averages for hand orientation, each of three averages contained the 30 trials for movements with a particular hand orientation, regardless of the height.

Throwing-movement sequence. This series of experiments was performed on a total of 20 subjects. Each subject sat at a table and placed their right arm in several supports and braces to constrain motion of the arm to the elbow joint. An opaque screen covered the elbow, denying the subject direct visual contact with the right arm and hand. The right wrist was held firmly in a U-shaped cuff in 90° supination (i.e., thumb up). Under the surface of the table, this cuff was attached to one end of a lever that pivoted around the same axis as the elbow joint. An hydraulic cylinder rotated the lever from the other end. This cylinder and an electronically controlled servovalve was used to rotate the elbow passively, with constant velocity rotations, in the extension direction. The velocity of elbow rotation was randomly varied from trial to trial, making the arrival time of the elbow at the target angle unpredictable to the subject.

The motor task performed by the subject was to open the right hand abruptly when the elbow passed through a prespecified angle, termed the “target angle”. This movement sequence superficially resembles Frisbee throwing, although the subject did not have to rotate the elbow actively. An electrogoniometer, attached to the right thumb and index finger, produced a timing pulse when the hand started to open.

A video display facing the subject provided knowledge of results at the onset of the hand opening, indicating to the subject the elbow angle at which the hand actually opened. Other than this after-the-fact knowledge of results, the subject received no visual information about the position of the elbow or the speed of rotation.

Without visual feedback about the position or movement of the elbow, nor the ability to predict the arrival time of the elbow at the target angle, the only way that the subject could accurately open the hand at the target angle was to use kinesthetic information related to the elbow movement to trigger the hand movement. The term *kinesthetic* is used here to mean any sensory input from cutaneous, joint, or muscle receptors related to the position or velocity of elbow rotation. Prior to data collection, each subject received enough practice at the slowest elbow velocity to locate the target angle, which usually amounted to 5–10 trials.

Four experiments were carried out, and some subjects participated in more than one experiment. In two of these experiments, the starting angle of the elbow was always 120° (full extension = 180°), and the target angle was always 145°. Thus, the distance to the target was always 25°. During each trial, the elbow always rotated to 157°, well beyond the target angle. The only difference between these two experiments was the range of elbow velocities, i. e., movement times over the fixed distance to the target angle. In one of these experiment (SLOW), the range of movement times was 300–1,500 ms, in 200-ms increments (i. e., seven different velocities between 18° and 83°/s). In the other of these two experiments (FAST), the range of movement times to the target angle was 110–560 ms in 75-ms increments. Both SLOW and FAST had a total of 70 trials, 10 with each movement time to the target. Furthermore, in FAST, the simple reaction time was measured 10 times for each subject, when the subjects were asked to open the hand as quickly as possible after they felt the elbow begins to move; the fastest velocity (240°/s) was used to determine reaction times.

In the last two of these experiments, the starting angle was no longer constant. At the end of each trial, the elbow returned in random order to 111°, 114°, 117°, 120°, 123°, 126°, or 129°, that is, to ±3°, 6°, or 9° on either side of 120°. The same range of movement times (i. e., velocities) was used as in SLOW. Each experimental session included 10 trials at each velocity and each starting angle, for a total of 490 trials. If it was desired, subjects were given a rest period at the midpoint of the session. In one of these last two experiments, the instruction was the same as in the first two experiments (SLOW and FAST): to open the hand when the elbow passed through the absolute target angle of 145° (TARG). In the other, the instruction was to open the hand after the elbow had rotated a distance of 25°, regardless of the starting angle (DIST). Thus, in TARG, the subject opened the hand when the elbow reached a specified angle, independent of the distance rotated, and in DIST, the subject opened the hand after the elbow rotated a specified distance, independent of the absolute elbow angle.

The time and the elbow angle at which the subject opened the hand were measured for each trial from elbow- and hand-displacement records. These measurements were averaged for each subject for like conditions.

Results

Reaching and grasping – central control of movement sequences

When subjects reached and grasped the handle, the activation patterns of the six muscles were related to the height of the reach and the orientation of the hand. While all six patterns were related to target height or hand orientation, the upper trapezius, the supinator, and the finger flexor exemplify these relationships most clearly. The EMG activity of these three muscles from one typical subject is shown in Figure 2, averaged with respect to the target height on the left and with respect to hand orientation on the right. Zero time represents the onset of hand movement as detected by the accelerometer. Handle contact occurred approximately 500 ms later. Vertical dotted lines are drawn at 170-ms intervals from the onset of EMG activity. Differences in the averaged activation patterns would indicate the involvement of a muscle in controlling the kinematic variable (i. e., height or orientation) upon which the average was based.

The control of reaching height is analyzed in the averages on the left. For each muscle, the thin solid line represents the average for movements to the lowest handle position, the dotted line to the middle position, and the heavy solid line to the highest position. Of these three muscles, the upper trapezius was the only one in which activation patterns were significantly influenced by height. The trapezius was activated about 100 ms before movement began. During the first 170 ms of activation, the averages are indistinguishable. During the second 170-ms interval, the averages diverged and then converged at the beginning of the third 170-ms interval. During the second 170-ms interval, activity was greatest for reaches to the highest handle position and smallest for reaches to the lowest handle position. At the beginning of the fourth 170 ms, the finger flexors were activated to reduce the hand aperture as the hand approached the handle.

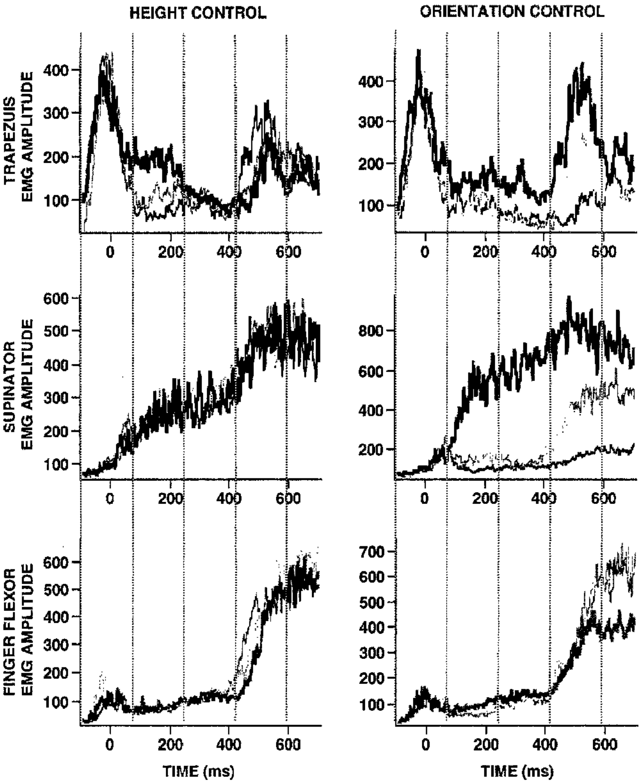

Fig. 2. Control of height and hand orientation in a reaching and grasping movement sequence

The control of hand orientation is presented on the right side of Figure 2. For each muscle, the thin solid line represents the average for reaching and grasping movements with 0° supination, the dotted line with 90° supination, and the heavy, solid line with 180° supination. The supinator is the muscle most clearly influenced by hand orientation. For 0° supination, activity remained at a low level throughout the reaching movement. For 180° supination, activity abruptly diverged at the beginning of the second 170-ms interval, at the same time that the trapezius activity diverged (i. e., left side, Fig. 2). For 90° supination, supinator activity abruptly diverged at the beginning of the fourth 170-ms interval, the same time as the finger flexor muscles were activated. The activation pattern of the trapezius muscle was significantly influenced by hand orientation as well as by reaching height.

From the time that the trapezius muscle became active until the handle was contacted, changes in muscle activity

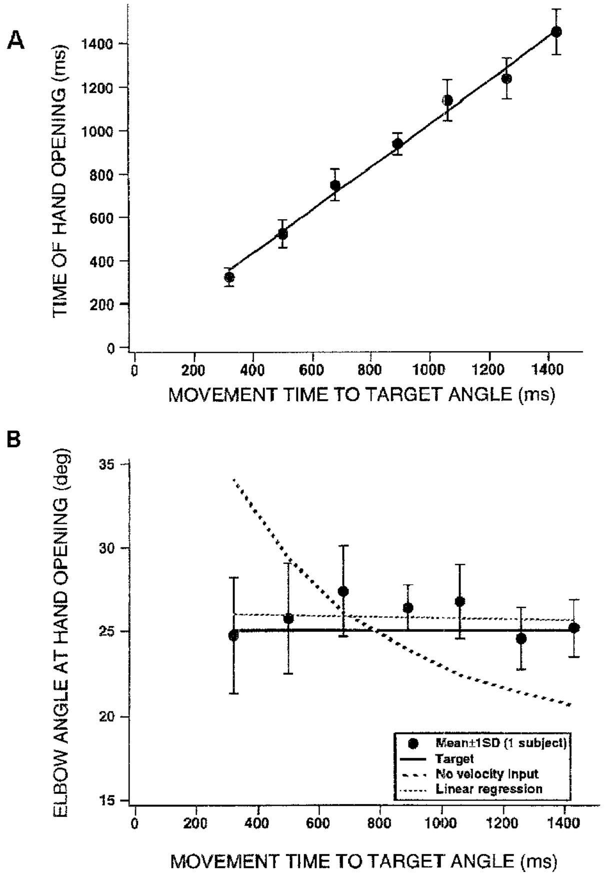

Fig. 3 A, B. Evidence for kinesthetic control of throwing-movement sequence and the use of velocity information

occurred at periodic intervals of 170 ms in duration. During one or more of these intervals, the amplitude of muscle activity was modulated to control reaching height: a form of spatial coordination. Alternatively, the intervals were used to trigger a change in muscle activity at different times during the reach to orient the hand: a form of temporal coordination. Thus, both spatial and temporal coordination are controlled, and in this reaching and grasping movement appear to be time-locked in 170-ms intervals, i. e., at 6.5 Hz. We presume that the 6.5-Hz timing signal for this movement was generated by neural structures within the central nervous system of each subject.

Throwing: peripheral control of movement sequences

The performance of the subjects in the throwing motor task indicated that kinesthetic information related to elbow position and elbow velocity was used to coordinate this movement sequence. Figure 3 shows the results from a typical subject in the SLOW experiment. In this experiment, the starting and target angles were always in the same position (120° and 145°, respectively), and therefore, the same distance apart (i. e., 25°). Seven different velocities of elbow rotation were presented in random order. In Figure 3 A, the time that the hand opened is compared to the time that the elbow reached the target angle. For the subject to have performed perfectly, this relationship should have a slope of 1.0 and it should pass through the origin. The linear regression fit to the data points had a slope of $m = 0.985$ and a Y intercept of $b = 41.9$ ms, $p \leq .05$.

In Figure 3 B, these data are replotted as the elbow angle at which the hand was opened (rather than the time it was opened) versus the movement time of the elbow to the target angle. (Figure 3 B is a natural outcome of Figure 3 A, owing to the use of constant velocity elbow rotations.) The data points are averages of 10 trials (± SD) for one subject, and the slope of the linear regression (straight dashed line) is $m = 0.001$, $p > .05$. The declining exponential (dashed curve) represents a prediction for performance if kinesthetic information about elbow velocity was not available. The basis of this prediction is explained below. The data, however, do not conform to this prediction; rather, they fit a prediction for performance if kinesthetic information about both elbow position and elbow velocity was available (solid horizontal line at the target angle, i. e., perfect performance).

The reason that kinesthetic information about the velocity of elbow rotation is essential for accurate performance is that it takes a finite length of time for the nervous system to act on peripheral input and initiate a movement based on this input. This delay is presumably due to conduction delays, neural processing time, and muscle contraction. This delay was estimated by measurement of the simple kinesthetic reaction time when the subject opened the hand as quickly as possible in response to a sudden elbow rotation. The mean reaction time was about 140 ms.

For the subjects to open the hand when the elbow was actually at the target angle, they would have had to identify a point on the way to the target angle, such that the remaining distance to the target would be covered during the last 140 ms. Because the velocity changed unpredictably from trial to trial, this distance would have had to be adjusted appropriately for different elbow velocities. Thus, to avoid the overshoots and undershoots predicted by the dashed line in Figure 3 B, the subject would have had first to detect the velocity of elbow rotation and then set a triggering angle at an appropriate distance in front of the actual target angle. Such an operation would involve a computation in which the loop delay would be multiplied by the elbow velocity to calculate the distance the elbow would rotate, at that velocity, in the last 140 ms. This is the distance in front of the target angle at which the triggering angle would have to be set for accurate performance. Clearly, this subject was able to perform this computation.

The FAST experiment provides an estimate of the time required to perform this computation. In FAST, the movement times of the elbow to the target angle were as brief as 120 ms. Figure 4 compares the time that the hand opened with the time the elbow reached the target angle in a typical subject. The data points are means of 10 trials (± 1 SD) for one subject. For the six slowest movement times, the slope of this relationship was $m = 1.08$ with a Y intercept of $b = -8.13$ ms, again close to perfect performance. However, this relationship asymptotes at a hand-opening time of 195 ms for this subject, indicating that the subject was unable to process kinesthetic information about velocity and move in response to this information in less than 195 ms. (The average asymptote occurred at 200 ms.) In

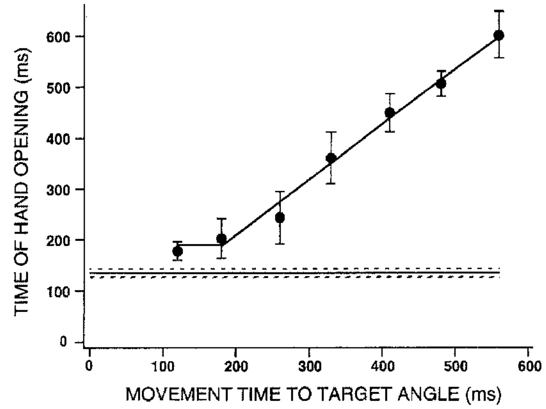

Fig. 4. Estimate of processing time for velocity information to calculate the triggering angle

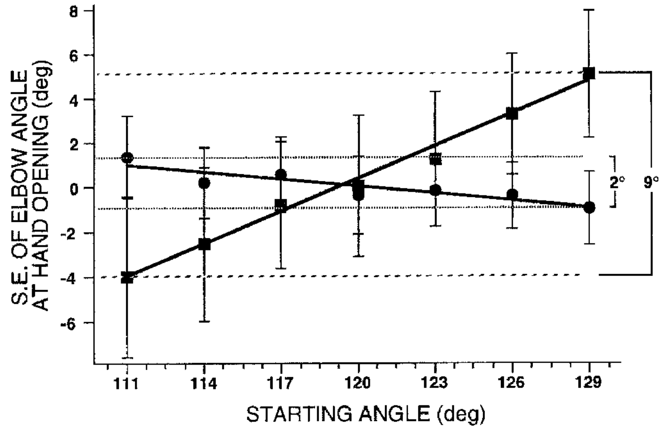

Fig. 5. Influence of unpredictable starting angle on performance in throwing-movement sequence

contrast, this subject's simple reaction time was 148 ± 8 ms. Thus, the requirement of hand-opening in the target added an additional 50–60 ms to the minimal time within which the subject could open the hand.

Up to this point, the data indicate that the nervous system extracts kinesthetic information about the velocity of elbow rotation to calculate a triggering angle in front of the target angle. In the actual performance of this task, the next required step would be to know when the elbow reached this triggering angle; this would require additional kinesthetic information about the position of the elbow. The TARG and DIST experiments were designed to determine whether information about the position of the elbow is encoded as the absolute angle in joint space or the angular distance rotated.

In the TARG experiment, the subject had to locate the target angle as an absolute joint angle, because the angular distance to the target changed unpredictably. In the DIST experiment, the subject had to locate the target angle as an angular distance, because the absolute target angle changed unpredictably.

In Figure 5, the data from the TARG (squares) and DIST (circles) experiments are compared by the constant error of the elbow angle at which the hand opened being plotted against the starting angle. Each data point is the mean of 70 trials (± 1 SD) for one subject, and is collapsed across elbow velocity. In the TARG experiment, the variation in the starting angle produced a systematic 9° variation in the elbow angle at which the hand opened, roughly half of the range of the starting angles (i.e., 111°–129°). Trials in which the starting position was less than 25° from the target angle resulted in overshoots, and trials in which the starting position was more than 25° from the target angle resulted in undershoots. In the DIST experiment, however, the 18° range of the starting angles produced a variation of only 2° in mean hand-opening angle. Thus, subjects performed about 4–5 times more accurately when they were required to use kinesthetic information related to the distance moved than when they had to use information about absolute joint angle.

Discussion

The class of movements termed *movement sequences* was used to investigate the spatial and the temporal relationships of motor coordination from the perspectives of both muscle activity and kinematics. The two experiments described in this paper were designed to identify the characteristics of the neural control signals that coordinate movement.

Central control of movement sequences

In the reaching and grasping movement sequence described above, one of the most striking results was that EMG activity was modulated at discrete times occurring periodically during the movement. For example, in reaching and grasping movements with a movement time of 500 ms, the periods occurred every 170 ms, suggesting the action of a central oscillator with a frequency of 6.5 Hz.

Previous studies of periodic behavior based on coupled oscillators or common central drive have focused predominantly on cyclical movements such as finger tapping (e.g., Kelso et al., 1979; Kelso & Schöner 1988; see also Summers, 1993, and Heuer, 1993, in this volume). While these previous experiments have provided a better understanding of entrainment behavior in cyclical movements, they have failed to generalize their results from cyclical movements to discrete movements. One of the more important results of the reaching and grasping study presented in this paper is that it demonstrates oscillatory properties of muscle activity and joint rotations in discrete movements.

A second important result of the reaching and grasping study is that the results could explain past observations on timing in movement sequences (e.g., Terzuolo & Viviani, 1980; Shapiro et al., 1981; Tuller et al., 1982; Fischman, 1984; Carter & Shapiro, 1984) leading to the Proportional Duration Hypothesis. This hypothesis was formulated to explain the observation that, in many movement sequences, the intervals between the components of the movement sequence shrink and expand in proportion to the overall duration of the movement sequence. According to this hypothesis, the timing of the intervals is preplanned as part of a motor program that incorporates both the sequence of movements to be made and the relative timing of these movements. On the basis of the results presented

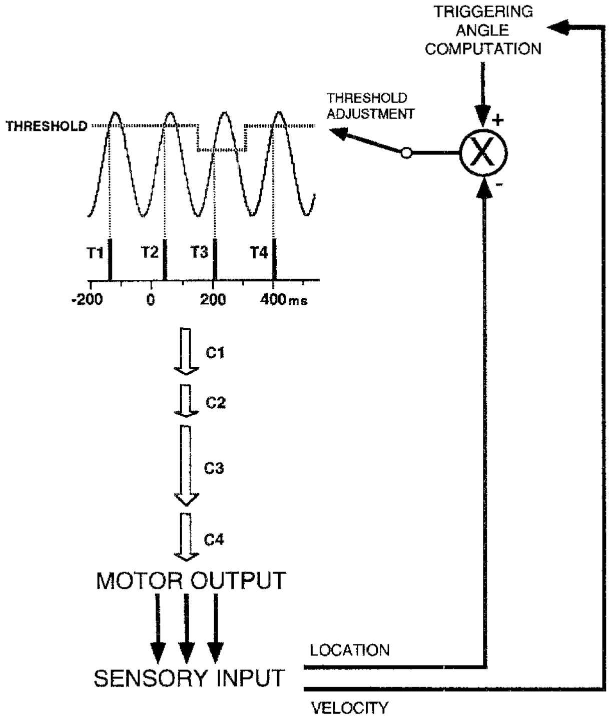

Fig. 6. Model of the interaction between central and peripheral mechanisms that coordinate movement sequences

in this paper, and as is discussed below (see Figure 6), the relative timing of individual movements in a movement sequence could be provided by a neural oscillator or other form of automatic timing mechanism. The proportional relationship between the duration of each segment, within a movement sequence, could automatically result from a change in frequency of such an oscillator.

A final result of the reaching-and-grasping study worth noting is the distinction of two different mechanisms for controlling the amplitude of a kinematic variable, by modulation of the amplitude of muscle activity over a fixed period of time (i.e., the control of reaching height) and by modulation of the timing of muscle activity (i.e., the control of hand orientation). The modulation of the amplitude of muscle activity is what is usually described in studies of movement. However, the modulation of the timing of muscle activity has not been described well. In effect, what the subject was doing in this experiment was to begin rotating the hand later when less rotation was needed.

Peripheral control of movement sequences

Passive elbow rotations were employed in the present experiments to enable us to identify what kinematic information the nervous system extracts from kinesthetic input. This question is important not only from an information processing perspective, but also for hypothesizing which specific sensory receptors provide this critical information. We have also examined active elbow rotations against a spring load and have obtained similar results (Cordo, 1990a).

Our data indicate that velocity information was used to coordinate this movement sequence. If velocity information was used, muscle-spindle 1a afferents probably contributed to this information, for 1a afferents are the only peripheral receptors that are known to encode accurately movement velocity (Matthews, 1963). However, the role for velocity input in controlling this movement is not to correct velocity errors, as in a typical servocontroller; rather, it is to provide a reference value for a movement triggering mechanism.

In the experiment that examined a throwing movement sequence, we also demonstrated that kinesthetic information can be encoded either as an absolute angle in joint space or as a distance moved. Our data clearly show that information about distance moved is much more accurate than that of absolute angle. This result contrasts with earlier reports that suggest that position is more accurate than distance (e.g., Kelso, 1977; Kelso et al., 1980), leading to the speculation that distance is only indirectly represented by the nervous system (e.g., Carlton & Newell, 1985). The disparity in accuracy between these two types of kinematic information (i.e., 2° vs. 9°) indicate that, in the SLOW and FAST experiments, the nervous system used distance information to determine that the elbow had reached the triggering angle.

Like the reaching and grasping study, this study also points to the importance of timing in the coordination of movement. In the throwing movement sequence, kinesthetic information about joint kinematics (i.e., distance and velocity) was used to control the timing of a subsequent joint rotation (Figure 3A). This form of sensory control differs from traditional ideas of sensorimotor servocontrollers (e.g., Hammond, 1960; Houk, 1979). The sensory triggering mechanism described here is a form of digital control, in which sensory information causes a joint to change from the state of not moving to one of moving (Cordo, 1990a). Kinesthetic triggering of movements is not an entirely new way of thinking about the sensory control of movement; it was originally described by Sherrington as part of the "chain reflex hypothesis" (Sherrington, 1906).

Integration of central and peripheral mechanisms

The mechanisms that coordinate the two movement sequences examined in this study might superficially seem to have little to do with each other. An important common feature, however, is the timing of muscle activity and the timing of movement onset. In the reaching-and-grasping movement sequence, timing might be provided by a central oscillator, whereas in the throwing-movement sequence, timing is provided by peripheral sensory input. However, central and peripheral mechanisms do not operate in isolation. Figure 6 illustrates one possible means by which these two mechanisms could interact.

According to the model depicted in Figure 6, an oscillator of central origin provides the basic periodicity for controlling muscle activity, as is suggested by the data in Figure 2. To trigger the successive components of a movement sequence (i.e., C1, C2, C3, C4), the oscillator signal passes through a threshold detector, producing a trigger signal at a particular phase of each cycle (i.e., T1, T2, T3, T4). The motor output produces reafferent kinesthetic input, and external mechanical disturbances produce exafferent kinesthetic input related to the position and the velocity of joint rotation. Velocity input is used to calculate a triggering angle against which the position of the joint is compared. If necessary, kinesthetic input from one component of the movement sequence is used to adjust the timing of the next. For the first two periods depicted in Figure 6, the phasing is near the positive peak. In the reaching-and-grasping movement sequence depicted in Figure 2, the threshold would have been set at a constant level throughout the movement, thereby resulting in all of the periods being equal in duration (i.e., 170 ms).

On the basis of the model presented in Figure 6, the interval between trigger signals would not necessarily have to be constant. In fact, frequent exceptions occur to the proportional-duration phenomenon in normal movement, as was pointed out by Gentner (1987). According to the model presented here, these variations in interval could be produced by peripheral input. These variations in interval could therefore have functional purposes: to adjust for unexpected changes in movement velocity, to compensate for internal and external disturbances, or even to assist in motor learning.

Kinesthetic input related to the velocity and distance of movement (Figure 6, bottom) could be compared to adjust, if necessary, the threshold of one of the trigger signals to advance or delay the initiation of a component of the movement sequence (Figure 6, top right). The comparison of distance and velocity information to produce a trigger signal is analogous to the comparison performed by a common electronic circuit, a digital comparator. In a digital comparator, two analog inputs are compared, and the output logic (i.e., 0 or 5 V) is determined by which of the two input signals is greater. The trigger signals in Figure 6 would successively trigger a sequence of muscle activations to produce a movement sequence such as the reaching-and-grasping movement. This model could account for the proportional-duration hypothesis if the frequency of the oscillator signal were to change as a function of the overall movement time.

In conclusion, we have used a particular class of motor behavior – movement sequences – in order to understand motor coordination. A useful concept of motor coordination must include both the temporal and the spatial aspects of movement. Motor behaviors in which the joints all move synchronously are not ideally suited for addressing the issue of motor coordination because these movements require spatial coordination, but little temporal coordination. For the opposite reason, cyclical, nonoverlapping movements (e.g., finger tapping) are not ideally suited: they require temporal coordination, but little spatial coordination. In contrast, movement sequences require both spatial and temporal coordination, and this class of movement could be helpful in developing a strong unifying concept of motor coordination.

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